DATE DUE	BORROWER'S NAME

C.F.C.
with love from
MLC.

Aspects of Form

ASPECTS OF FORM

A Symposium on Form in Nature and Art
edited by Lancelot Law Whyte

Lund Humphries, *Publishers*

First edition 1951
Second edition 1968

Original edition issued in 1951 in collaboration with the Institute of Contemporary Arts on the occasion of their Exhibition "Growth and Form" held at 17–18 Dover Street, London W 1

Published by Lund Humphries, 12 Bedford Square, London WC1

Typography by John Denison-Hunt M.S.I.A.

Made and printed in Great Britain by Percy Lund, Humphries & Co. Ltd

Contents

Contributors

†DR. S. P. F. HUMPHREYS-OWEN

†C. C. L. GREGORY

PROFESSOR C. H. WADDINGTON, F.R.S.:
Professor of Animal Genetics, Edinburgh.

†PROFESSOR F. G. GREGORY, F.R.S.

DR. J. NEEDHAM, F.R.S.:
Master of Gonville and Caius College, Cambridge.

PROFESSOR A. DALCQ:
Professor of Human Anatomy and Embryology in the University of Brussels.

DR. H. B. COTT:
Strickland Lecturer in Zoology, Cambridge.

PROFESSOR K. Z. LORENZ:
Director, Max-Planck Institut für Verhaltensphysiologie, Seewiesen.

DR. W. GREY WALTER:
Director, Physiological Department, Burden Neurological Institute, Bristol.

DR. R. ARNHEIM:
Art Critic and Psychologist, Sarah Lawrence College, New York.

PROFESSOR E. H. GOMBRICH:
Director, Warburg Institute, London.

Editorial Preface to the 1968 edition

by Lancelot Law Whyte

During the seventeen years that have passed since the original (1951) edition of this book, the scene has greatly changed. But the publishers and I have decided not to attempt to have these essays brought up to date. Three contributors have died and so many new facts have been discovered that the others would not be able to summarize the achievements in their fields in short papers. However, the book still provides a valuable foundation for those interested in form (in this context 'form' includes 'structure') and it has no competitor. It is therefore being treated as a classic, and the text re-issued without modification.

But it has been strengthened by two additions: this *Editorial Preface* on the scientific advances made during this period, and a *Supplement to the Bibliography*, providing a sample (35) of the hundreds of relevant books that have appeared recently. So this volume not only shows what the editor and eleven contributors were thinking in 1951, but enables readers to obtain a picture of the situation today, if the hints contained in this Preface are supplemented by a selection of these recent books. (A more detailed discussion than is given in this Preface will be found in my *Atomism, Structure and Form. A Report on the Natural Philosophy of Form*, in the Kepes (1965) work cited in the Bibliography.) If a similar survey were attempted today the following subjects would have to be treated in addition: molecular biology, cytology, evolutionary aspects of organic form, and mathematical methods of analyzing structures and forms.

The main changes on the scientific side can be summarized very simply: greatly increased interest in spatial form, many new and important facts, and only relatively minor advances in theory. Indeed the contrast between the rapidly advancing identifications of natural structures and the relatively stationary theory could not be more striking. For many scientists the primary emphasis appears to have switched from the *discovery of new fundamental laws* to the *progressive identification of natural structures*. The search for structures is on, the jigsaw puzzle of natural patterns is here and there already solved, and the pace is growing hot. We have, it seems, passed into a new phase of the scientific endeavour, particularly in biophysics, where many paths are convergent and the prizes great. For the acrostic is finite and every valid identification may make the rest easier.

In one respect this shift of emphasis is welcome. For the role of abstract theory, comprehensible only to high specialists, is growing less, and that of natural forms, set in three-dimensional space immediate to the visual sense and thus easily intelligible, is increasing. This immediacy of natural forms does something to restore to exact science its proper role as an instrument of human, and not merely specialist, understanding.

For convenience I shall treat various aspects of the new situation separately, though their interactions are crucial.

Interest. During the last twenty years, interest in what may be called the *morphological point of view*, i.e. in spatial form, has deepened and broadened. There is today not only a more explicit and vigorous concentration on discrete structure in many empirical realms, but this general method of approach has been taken up keenly by groups outside the natural sciences. I can mention only one or two of the more striking examples known to me. What I call a *new school of form* has developed on many campuses in the U.S.A., mainly in the Architecture, Design, and Art Departments, but also elsewhere since this attitude transcends academic divisions and serves to unify knowledge and teaching. I have the impression – from a series of visits to the U.S.A. lecturing on problems of form – that a rather novel attitude, on the way to becoming a new branch of scholarship, is developing: the unified study of all kinds of natural and man-made structures.

I have long expected to see academic recognition of this new discipline and it is now becoming explicit in the teaching of design in a wide sense. Not only are some of these campuses organizing classes in *Fundamental Design* based on the consideration of mathematical, physical, and organic forms, but in Israel an Architectural Department (Technion at Haifa) is teaching *General Morphology* with an integrated Syllabus covering the basic principles of mathematical, crystallographic, organic, and some man-made forms. There are here difficulties to be overcome, such as the lack of teachers and text-books adequately covering this field. But if the present trend continues other universities may soon be using General Morphology not only as an appropriate element of basic training in the natural sciences, but as a way of displaying the unity of many unduly separated academic disciplines. '*This is a world of form and structure and can only be properly understood as such*' is the *leitmotif* of this new unifying discipline.

Another example of this increased interest is the demand for literature on form. Two examples: this book has been on sale in the U.S.A. as a paperback since 1961, and a six volume series, edited by G. Kepes, was issued in New York in 1965 under the title *Vision and Value*, the first volume, already referred to, being on *Structure in Art and Science* (see Supplement to Bibliography). It is also a sign of the times that the Massachussets Institute of Technology Humanities Department during the winter 1967-8 held a three months' Seminar on *Structure* in all fields of scholarship.

Every fresh emphasis in basic attitudes meets resistance. Much of the academic world in the U.S.A. divides itself into two groups with sharply contrasted points of view. There is the enthusiastic, forward-looking, Gestalt- and organismic-minded school of form, some of whose members can already see its value in their own realm. Many of these display an evangelical euphoria: they believe they are the carriers of a new vision of nature, life, and scholarship (I need not say that I am with them). But there is also a more traditional group, still carrying the insignia of authority, who react against the new 'morphism' and coldly stress an apparently unquestionable fact: *Only the long-proven atomic-analytical-quantitative-statistical method has yet achieved the continuing advances* *which uniquely characterize mathematical science.* Against that tremendous historical success the achievements of the morphological approach *seem* like brilliant but isolated acts of identification, lacking the marks of authentic progressive scientific advance. Even the mathematical theory of crystal symmetry and structure (*c.*1890) looks in retrospect like a single achievement of mathematical genius, so complete as to leave the way open only to minor advances.

So it seems – to the prejudiced mind. For, as every younger exact scientist knows, the Quantum Mechanics of 1923/30 is *not* merely atomic-analytical, it is *also* explicitly concerned with *spatial* symmetry properties, i.e. with morphology. Quantum Mechanics is a mixed theory, combining both methods and therefore in certain respects too complex and paradoxical to satisfy permanently the highest judgment, like Einstein's. This is certainly an aspect of form within the scope of this book, but it is highly technical. In my view, based on a study of the physical theories of this century, *Quantum Mechanics is a halfway house between classical atomism, and* – (can it be anything else than?) – *an authentic morphological physics, a morphology of measurements made in space.* It may well be that the anomalies of current particle theory and the baffling subtleties of the differentiative growth of a fertilized seed into a functional adult both require the same kind of calculus! For both are complex, both combine cyclic-stationary and one-way-relaxation processes, and both are now baffling scientists whose basic training has been, perhaps, over-analytical or over-static.

This problem can be viewed in a more direct manner at a point where this survey of recently discovered aspects of form touches a major intellectual drama: *Will the urgently needed theory of protein structure and function be atomistic in the traditional sense, or morphological in some new manner?* Is the atomic approach, so successful until now, appropriate to such tremendously complex and yet highly ordered systems as functional protein? To put it bluntly: *Can standard chemistry* (say, that based on the Quantum Mechanics of 1930) *cover all aspects of life?* A few scientists, perhaps still affected by the excitement generated by the Crick-Watson identification of the DNA helices (see below), say 'Of course!' Others say 'Wait and see!' Both schools expect some answer within a decade or two. For, I repeat, the pace is hot on the empirical side, to which we must now turn.

Molecular Biology. In the entire history of science there has been nothing similar to the dramatic advances in the new realm of molecular biology which occurred between 1945 and 1965, and are still continuing. We can now see in retrospect what a few pioneers anticipated and helped to bring about: the fusion of mathematics, physics, and biology into a new integral science of biophysics, in which molecular biology, or the study of the changing arrangements of chemical atoms during organic processes, holds a central place. At no earlier time would such a convergence of techniques have been possible. What scientists had learnt in the challenges of the Second World War was here applied to the challenge presented by organisms: all available techniques, and new ones designed for the purpose, were applied to a convergent planned attack on organic ultra-structure. This paid off brilliantly in an entirely fresh vision of the structure of the basic life processes at work in all organisms.

The science of molecular biology came into existence with a rush around 1950. Of the new insights gained the most fundamental and significant was the identification by Crick and Watson in 1953 of the spatial pattern (a double helix) of the main structural determinants of heredity (probably common to all cellular organisms) in the DNA chains in the chromosomes. This was a novel aspect of form with a vengeance: an entirely new discovery of a geometrical structure determining the stability and continuity of life! It is not surprising that some scientists claimed that the 'secret of life' had been uncovered, and that it was now clear that life was merely *ordinary chemistry*, though to an observer on the side-lines it appears that a new explicitly *morphological chemistry* may be required.

Structural Cytology. These widely advertised molecular advances form part of a wider investigation of the organic structures at all levels in the cell: from the small molecular units to the polymers, giant molecules, enzymes, enzyme-complexes, organelles, and single cells. Today the cytologist exercising his intellectual imagination has begun to see right into the extraordinary integrated hierarchy of working structures which exists in every cell and probably undergoes coordinated pulsations at every level in course of function. He does not yet understand it, but in the work of the last twenty years he has learnt that during the life cycle of the organism a process of replication occurs at many levels. He has to visualize the cell as at once highly complex and highly coordinated. The processes of the cell have, as it were, two aspects: that of precise molecular geometry and that of process coordination. The molecular patterns are there beyond doubt, but so also is the integration of their processes. Thus the entire hierarchical pattern of the cell must, it seems, undergo unified pulsations in the course of its several functions. This is more than standard chemistry. A new global, hierarchical, and morphological 'chemistry' is at work.

Here a fascinating aspect of organic structure has come within sight. With every major step of increasing magnification a deeper level of structure with its own characteristic patterns of organization becomes visible. Moreover as the ultimate molecular and atomic levels are approached these patterns become more exactly geometrical, i.e., more accurately ordered as linear, helical, or cylindrical structures, or plane membranes, etc. We are thus faced with a challenging paradox: how can this approach to geometrical precision at the basic levels be combined with the plasticity, capacity to pulsate in course of function, and global coordination which must (one assumes) be possessed by all functional organic structures? There is no doubt that at the deepest levels organic structures combine rather strict forms of geometrical ordering with variety, mobility, cyclic changes, and the tendency to maintain, and when necessary restore, organic coordination. Such questions touching the relation of structure and process have ceased to be philosophical. They are now on the advancing frontier of the new biophysics.

Other Advances. Here I can do no more than list a few of the recent discoveries in other fields: crystallography (new types of crystalline order); solid state (deepened understanding of the types of structure corresponding to the different properties of various materials); liquids (combination of disorder with local order, islands of order); very high order properties (lasers, etc.); cosmology (clusters of galaxies); the mechanism of muscle (towards identification of the structure which converts chemical into mechanical energy); steps towards the synthesis of parts of living cells (e.g. natural DNA made to replicate in a man-made environment); brain function (steps towards understanding of the hierarchical grouping of nerve cells by which visual information is processed, step by step, into categories more closely related to thought processes). These are some examples of the experimental and observational achievements of twenty years.

I will conclude by mentioning a few general aspects of the present situation which may be of interest to the non-specialist.

Hierarchy. Ever since the thinkers of ancient Greece a philosophical tradition has interpreted various aspects of experience in terms of a hierarchy, or sequence of higher and lower levels. There are signs that *structural hierarchies*, in which a whole at one level is divisible into parts at the next lower level, are now of scientific importance. This universe displays, *prima facie* at least, two great structural hierarchies, which are partly distinct: an inorganic and an organic. The first extends from galaxies down to atoms and ultimate particles (if such exist), and the second from communities and single organisms down through many levels of organic structure to the chemical atoms of which organisms are composed. This suggests that a hierarchy of energies may be necessary.

Since 1951 several sciences have reached the stage where this hierarchical organization of natural systems has become of importance for quantitative theory. For example, in 1958 J. D. Bernal showed that the structure of certain protein molecules must be considered as containing four levels, from 'primary structure' (the ordering of the chemical groups along the main thread of the polymer), up through secondary and tertiary levels to 'quaternary' structure (the global form of the molecule as a whole). Another example: during the last few years astronomers have observed clusters of galaxies, themselves possibly arranged in 'super-clusters'. Thus hierarchical ordering may be a general characteristic of the universe, in some degree affecting all structures, large and small. Indeed hierarchical organization may be one of the most important aspects of spatial form. One is led to ask: In what manner, if at all, are the degrees of freedom of parts restricted by the existence of the whole? There is, as yet, no general answer to this important question.

The 'cosmological principle', that in certain respects this universe looks the same wherever you are, may be fundamentally wrong; it may make a lot of difference whether you happen to be inside a cluster of galaxies, a single galaxy, or a solar system, or in the relatively empty spaces between. Indeed it may be that aspects of the fundamental laws so far discovered are not basic, but are due to the neglect, till now, of the hierarchical ordering of things, and of the status of the various systems in the pervasive hierarchies of nature. If so, the next advances in some realms of science may be achieved by taking the hierarchical aspects adequately into account. This very general aspect of form may have been too long neglected. If so this book is timely in now stressing hierarchy, but should contain, not a page or two, but a chapter on it.

Morphic Processes. Since around 1870 the branch of physics concerned with natural tendencies – i.e. processes going one way towards some characteristic terminus – has been somewhat unbalanced in its emphasis. Much attention has been paid to the tendency towards dynamical disorder (heat processes, entropy), and much less to the extensive and important class of contrary processes leading towards spatial order. Curiously enough this class has not yet a clear scientific name of its own, though it must be responsible for the existence of organisms and of organisms with minds. In my view Schrödinger insulted this pre-eminent class of processes by giving them a negative and, in certain technical respects, misleading name: *negative entropy* (now structural neg-entropy).

To do something to correct this unbalance, to emphasize the positive aspect of these formative processes, and to make clear how extensive and rich with consequences they are, I have given them a scientific name: *morphic**. This is defined to mean 'displaying a movement toward greater three-dimensional spatial order, symmetry, or form'.

As these morphic processes are directly responsible both for the existence of forms, and of brain-minds themselves generating forms and responsive to forms, I list a few examples:

*Essay in Jones (1968). See Bibliography.

The formation in the realms of

physics: of atoms, molecules, crystals, polymers, and all ordered states, including solar systems and structured galaxies.

the transition to organisms: of heterogeneous polymers, membranes, catalysts, and pulsating molecular hierarchies.

biology: of organelles, cells, tissues, organs, and organisms, i.e., of all the characteristic structures of the organic realm.

cerebral physiology: of the brain modifications or processes underlying all mental processes such as memory, classification, choice, and will.

The morphic building of hierarchies. All these morphic processes generate new ordered units, i.e. arrange parts to form new wholes. Thus morphic processes build up the hierarchies of structure, while entropy processes tend to disperse ordered units and to break down hierarchies. This is an intriguing vista of two great tendencies in the universe and their contrary effects on the hierarchies of structure. Exact science has only recently begun to study this in a systematic manner. Yet the idea is old. Fifty years ago N. Hartmann (Philosophische Grundfragen der Biologie, 1912) discussed the successive levels of formative processes in organisms, thus combining in a speculative manner two ideas which would a half-century later become topical: morphic processes and functional hierarchies!

I end this Preface with a salute across the Atlantic to one of the most imaginative students of form alive today: R. Buckminster Fuller. As a gifted inventor of new engineering structures, a teacher and interpreter of modern design methods in many fields, and a devotee of spherical and tetrahedral forms, Buckminster Fuller has deeply influenced more than one generation of the new school of form in the U.S.A. and elsewhere. It is fitting that some years after he had described and used certain geometrical patterns in his 'geodesic' structures, similar forms were found in virus! This is not so surprising as it might seem. The possible variations of simple three-dimensional patterns are restricted, and it is therefore natural that explorations of form should converge. Buckminster's hitting the mark was not just a happy chance, but an expression of the convergence on form which marks the second half of this century.

Note added in proof. It is a sign of the attention now being paid to form and structure that since the above Preface was written there have come to my attention several further items which should be mentioned.

The publication of James D. Watson's *The Double Helix* enables the non-technical reader to share the personal and intellectual excitement of this fertile discovery and to observe an unusual variant of the scientific spirit of our time achieving the solution of one piece of the great jigsaw puzzle of natural structures.* I recommend this book to readers interested in the progressive identification of such structures, so that they may better understand similar discoveries in the future. One of these should be on the character of the coordinated structure of giant protein molecules which enables them to carry out their manifold functions and contains another aspect of the complex 'secret of life'. Many aspects of form cooperate in organisms. The 1953 DNA identification concerns one of these, and the structural determinants of heredity, in the chromosomes or in the cytoplasm, only achieve their total biological task within the still obscure global co-ordination of the fertilized egg-cell and developing organism.

Another mark of the present time is the recent foundation of the *International Society for Stereology* (Gk. στερεος, solid) by Dr. E. R. Weibel of Berne and Dr H. Elias of Chicago, Editor of *Stereology*. This Society seeks to promote the inter-disciplinary study of three-dimensional structures and forms in all realms, and its formation may prove a landmark in the *unified* study of natural structures.

Less directly relevant, but perhaps also of interest to readers, is the formation (1961) of the *Society for Morphological Research*, based at the California Institute of Technology, the purpose of which is to develop Dr F. Zwicky's 'method of morphological analysis' by applying it to physical and social problems. This method is presented in several of Dr Zwicky's writings since 1957. It is proposed as a comprehensive procedure for analyzing, and

* An objective historical account giving credit to the workers who made this culminating discovery possible is given in the review in the *Times Literary Supplement* (May 23, 1968), and a more detailed survey in an article by L. D. Hamilton in *Nature* (May 18, 1968).

perhaps facilitating, the solution of 'morphological' problems, in the general sense of those concerned with any kind of structure, not only spatial, but also logical, mathematical, or social. This is a wider field than that of *Aspects of Form* and the *Society for Stereology.*

It would be a great thing if the younger generation could be made aware what a thrilling time this is to be alive, when the human intellect is at last coming seriously to grips with the great problem of structure in external nature and in ourselves, including the relationships between the structures of the different realms.

L.L.W.
27 May, 1968

Preface to the 1951 edition *by Herbert Read*

THE INCREASING SIGNIFICANCE given to *form* or *pattern* in various branches of science has suggested the possibility of a certain parallelism, if not identity, in the structures of natural phenomena and of authentic works of art. That the work of art has a formal structure of a rhythmical, even of a precisely geometrical kind, has for centuries been recognised by all but a few nihilists (the Dadaists, for example). That some at any rate of these structures or proportions—notably the Golden Section—have correspondences in nature has also been recognised for many years. The assumption, except on the part of a few mystics, was that nature, in these rare instances, was paying an unconscious tribute to art; or that the artist was unconsciously imitating nature. But now the revelation that perception itself is essentially a pattern-selecting and pattern-making function (a Gestalt formation); that pattern is inherent in the physical structure or in the functioning of the nervous system; that matter itself analyses into coherent patterns or arrangements of molecules; and the gradual realisation that all these patterns are effective and ontologically significant by virtue of an organisation of their parts which can only be characterised as *aesthetic*—all this development has brought works of art and natural phenomena on to an identical plane of enquiry. Aesthetics is no longer an isolated science of beauty; science can no longer neglect aesthetic factors.

Aspects of Form discusses this rapprochement from several specialised points of view, and the editor, Mr. L. L. Whyte, brings the whole discussion within the focus of that unitary principle which is emerging as the explanation of all phenomena within the range of human perception and understanding. It is an exciting moment in the history of human thought, and the paths that lead forward are bright with intellectual promise.

Introduction *by Lancelot Law Whyte*

THIS VOLUME WAS CONCEIVED in January as a catalogue to the Exhibition on "Growth and Form" at the Institute of Contemporary Arts. But it at once grew out of recognition, and is delivered at six months as an independent symposium. Such rapid growth, even if at the expense of form, is perhaps evidence of a timely conception.

There is, I think, a special reason why busy scientists have responded to the initiative of the I.C.A. Form is very important and yet tantalisingly subtle. Exact science seems to know much, and yet it has so far only got to grips with the simplest forms such as crystals and bubbles. Complex forms still baffle it. All the powers of science do not let us see into the growing point of a plant, or the dominant centres of an embryo, or the grey matter of the brain, and understand exactly what is going on there when new forms develop. Our eyes look out on a complex world, but the brain unconsciously selects what interests us and makes it seem simple. Yet we do not know how the brain does this, and science has not yet discovered its own method of making complex forms appear simple.

This combined importance and elusiveness of form is perhaps the reason why contributors were so ready to help. There is something to gain from putting down one's ideas if they are not yet clear, and also from examining the ideas of colleagues in neighbouring fields. So this is less a work of popularisation, than an experiment in pooling ideas on a problem that is still being explored.

The artist knows well the pervasiveness and subtlety of form;

his interest in external forms and his pre-occupation with the formative processes of his imagination make him what he is. But the exact scientist is often shy of approaching the problem of form, and naturally so, for he has no scientific philosophy of form to guide him. Surprising as it is, this book seems to be the first attempt that has been made at a general survey of form in physics, biology, psychology, and art, though it will certainly not be the last. The nearest approach is perhaps the little symposium under *Forma* in the *Enciclopedia Italiana*, and the inadequacy of the present volume should stimulate the production of a more comprehensive Encyclopædia on Form in the future.

The eleven essays which follow are concerned with different aspects of *spatial form*, including both *external form* or visible shape, and *internal form* or structure, as well as *transformation*. The word "form" has many meanings, such as shape, configuration, structure, pattern, organisation, and system of relations. We are here interested in these properties only in so far as they are clearly set in space. Thus musical form, linguistic form, abstract mathematical form, and the forms of thought, of human personality, and of society, are excluded. (But Grey Walter's essay shows that science is not far from linking the forms of thought with the spatial patterns of the electrical rhythms of the brain !)

Common to the ideas of form, configuration, pattern, and structure, is the notion of an ordered complexity, a multiplicity which is governed by some unifying principle. Our theme is thus the *realisation of unity of spatial form in the complex processes of physics, biology, psychology, and art*. But "form" includes development and transformation. Indeed we can regard "matter" as that which persists, and "form" as that which changes, for no form is eternal. And form, like change itself, is in many fields still obscure.

Ever since Democritus sought understanding in *atoms*, and Plato and Aristotle in *forms*, there has been a vigorous competition between two sets of ideas: atomism—material analysis—quantitative precision, and form—unity—symmetry. These may really be complementary rather than antagonistic, but it is a remarkable fact that throughout this debate, that is during eighty human generations, no one has suggested how to combine them into one simple and comprehensive way of thinking; hence much of the disorder in thought. The influence of every great thinker and scientist has fallen on one side or the other: Democritus being followed by Newton, Rutherford, and all the atomists, and Aristotle by Aquinas, Goethe, and the morphologists in biology and other sciences.

The mutual challenge of these two schools, for instance in the old mechanism-vitalism quarrel, was healthy and stimulated progress, *until recently*. But there are signs that this antithesis must now be overcome, that if science is to advance it must discover how the ordering of parts gives form to the whole, in organisms for example. Certainly this symposium is no partisan manifesto. The aim is to present what is known about spatial form and structure, and to indicate what is not known. For an honest survey of any branch of science would leave half the pages blank to show the reader where nothing can be said.

But to save paper it must suffice to mention where some of the white sheets confessing ignorance should occur in this volume. A few at the very beginning, for the physicist does not understand the form of the nucleus of the atom, though it is the basis of the whole universe. Then a few more in astronomy, for we cannot say how the nebulæ came into existence, or whether the cosmos was ever "without form and void". A whole chapter would stay blank between physics and biology, to mark our ignorance of the form of protein in the organism, though its changes of structure underlie all organic processes, including my writing of this sentence. And so on right up to art, which, though for many the noblest of human activities, is still so obscure that Gombrich can provide, just for good measure in this volume, a new and intriguing interpretation, perhaps as useful as any yet.

Note that the psychologist of art and the art historian are included, but not the creative artist himself. There are dangers in the collaboration of scientist and artist, for superficial analogies between science and art are harmful to both. Yet the scientist's study of spatial forms and the artist's creation of them are both human activities, and we can find a common root if we look deep enough. The scientist's curiosity about natural forms ultimately leads him to consider how the mind selects and modifies forms in the processes of perception, and so to an examination of the sources of the aesthetic sense. And the artist who pauses to try to understand his own activities cannot remain content to regard them as "purely aesthetic". He must wonder why they seem to him so intensely important, and yet are so neglected and misunderstood by science, and by society. The divergence of the two attitudes can only be validly overcome in one way: by a broadened understanding of the importance of form in all realms, not only in the external world but also in the unconscious roots of all human activities. Indeed we may discover that there is nothing wholly formless in nature, that if there were it could never be known to man, and that every particular form has its own special significance within the universal order of which man is part.

These thoughts formed the background to the planning of this symposium. A general survey of form seemed timely. But there was no contemporary Aristotle, Leonardo, or Goethe, strengthened of course by twentieth century mathematical precision, to whom the I.C.A. could turn for a study of the problem. There could not exist such an all-round man in the absence of a scientific philosophy of form. So it had to be a symposium. Moreover "time, strength, cash, and patience" were all in short supply, to say nothing of paper. Something had to be accomplished quickly or caution might creep in and say: "The task is too difficult; the subject is not yet ripe; wait till science knows a little more". The reader must judge whether it was fortunate that the enthusiasm of the Editorial Committee and the Publishers overcame these doubts. Perhaps the topicality and interest of the theme, and the qualifications of the contributors, may compensate for the editorial blemishes of so rash an undertaking.

A glance at the articles may be helpful. Some assume more knowledge than others, but each can be read by itself.

To open the subject Humphreys-Owen examines the apparently simple but subtle question of the shapes of material objects. He suggests that as the physicist passes from larger objects towards the atom and its minute nucleus, the elementary idea of *visual shape* gives way first to *occupation of space*, and then to *abstract* *organisation*, so that ordinary spatial ideas may not apply in the smallest regions. Then C. C. L. Gregory describes how the astronomer views *static and changing forms*, discovers conic sections in the heavens, and uses the velocity of light to explore the cosmos.

We next take an abrupt step into biology, no one being ready to report on the structure of protein, which will one day smoothen the transition. Waddington discusses the character of *biological shapes*, contrasting both normal and pathological organic forms with similar aesthetic forms created by man. F. G. Gregory shows how plant form is governed by the interplay of internal and external influences, stressing the rôle of the *growing points* where all the shaping processes of the plant are concentrated. Needham emphasises the part played by minute *highly specific molecular units* (genes, enzymes, etc.) in creating organic form at all levels, through the cell parts, cells, and organs, to the gross shape of the organism.

Dalcq takes up the story of the *development of animal form and function* from the original fertilised egg, suggesting that the processes of embryological development in man seem to anticipate and prepare the subsequent development of the human mind. Here the "inventive" or formative character of living matter displays its most striking visible results. But some basic discovery is necessary to make morphogenesis fully intelligible.

Lest we should become too theoretical Cott takes us back into the open air, and describes the almost unbelievable versatility and adaptability of the evolutionary processes in modifying the *appearance* of animals so as to conceal or emphasise their physical shape in the interests of survival and reproduction. Here we see that it is often not the actual physical form which counts, but its appearance in a given setting to some species with an organ of vision, a point which remains with us through the subsequent articles. Still out of doors with animals in their natural habitat, Lorenz considers the rôles of two kinds of animal and human perception: *Gestalt* (the visual perception of single completed configurations, where the whole appears to dominate the parts), and *mosaic* (the perception of sharply defined parts), and gives a biological interpretation of intuition.

We now return to the laboratory, and under Grey Walter's guidance watch the changing *activity patterns in the brain* of a human subject as he looks and thinks, or relaxes and dreams, under the terminals of an electrical recording machine. These discoveries may prove to be as important as any of this century, for they open up an entirely new realm of knowledge with immeasurable possibilities. Here for the first time the processes of the brain and the activities of the mind, to use two descriptions of one thing, are subject to exact investigation and some degree of direct experimental control.

From these brain activity patterns it is a small step to the rôle of the visually-perceived configuration in determining aesthetic qualities. Arnheim shows how the *aesthetic significance* of a particular form depends not only on its actual shape and structure, but also on the formative processes of perception, the personal needs and tensions of the perceiver, and on his social and historical context.

Finally, to close our survey, Gombrich takes us for a ride on his hobby horse towards the conclusion that the root characteristic of aesthetic creation is not representation, image-forming, or abstraction, but simply the *making of a functional substitute*, an object which can serve in place an original (or desired) experience in respect of some function or need of the individual. Here again the significance of a form is seen to depend on the total organic situation within which it appears.

Every reader will discover for himself the ideas which strike him as most significant, but here is what impresses me about the volume as a whole: contemporary science appears to have recovered the ancient and mediæval sense of the importance of form, and yet it is almost completely ignorant of the basic laws of form. Every contributor recognises the challenge and yet none (with the partial exception of the physicist in relation to some simple systems) can cite a single *fundamental* principle concerning the development of the forms in his branch of science. Following the Pythagoreans, Plato, Aristotle, Aquinas, and Francis Bacon, exact science recognises that the form of a thing is its very essence, giving to this old idea a new, more precise, and comprehensive meaning. But it cannot yet give this ancient intuition reliable scientific expression in laws governing form and transformation. It is clear that there is a tendency towards form, not only in "external nature", as Aristotle knew, but also in the human organ of perception and thought. But science cannot yet formulate what eye and brain are doing all the time. It is as though the formative processes were too pervasive to be seen clearly.

Some understanding of this situation can be gained by considering the historical aspect, which has therefore been summarised in a Chronological Survey of the development of Western ideas of form and knowledge of natural forms. This survey is carried through into the twentieth century and shows that there has recently been a heightened awareness of the morphological character of the various sciences, as the study of *complex* forms of different kinds. But there is as yet no general method for treating the processes of complex systems. Atomism tries to reduce everything to actions (forces) between pairs of entities, but things are more complex than that. It may therefore be that the failure of science to come to grips with form is not due to any irrational subtlety about form, but merely to the fact that forms are, in general, more complex than the problems which science has already mastered. As it is, after three hundred years of exact science, we do not know whether the basic laws of nature are *atomic* or *morphological* in character, or of some other kind which arranges discrete parts to form single wholes and so provides a balanced picture of process.

A Selected Bibliography of books on form in various realms of thought has also been included, so that themes only briefly touched on in this volume can be pursued further. This is wider in scope, and covers mathematical form, form in human physique and temperament, and symbolic forms created by man, in addition to the main themes of the volume.

May I thank, on behalf of the I.C.A. and the Publishers, those many friends who have given generous help, but cannot be mentioned individually.

Physical Principles underlying Inorganic Form *by S. P. F. Humphreys-Owen*

THE WORD "FORM" in this article will refer to the shapes of material objects, the arrangement in space of groups of them, and the arrangement in space of their component parts. Our appreciation of form is partly sensory, but we can be helped by measurement and calculation to gain some confidence that what we perceive is not entirely unconnected with the outside world. The science of Physics is concerned with such measurements, and with the seeking of mathematical relationships between the numbers which are results of the measurements. Although one individual measurement, say of the diameter of a disc of paper, is just a number and provides no inkling of form, a number of them, together with measurements of angles between the diameters, can be combined and expressed as an equation. This equation, when plotted as a graph, reproduces well the form of the original disc. It can also be given to other human beings who have never seen a circle, but who have been trained in graph plotting, and when they plot the equation they obtain the sensation of a circle for the first time.

In such a way the science of Geometry would interpret form, by discovering that the essence of the form is a certain relationship between its dimensions in space. Geometry is an abstraction of all properties of matter other than that of "occupying space". Other sciences introduce, successively, other properties. Dynamics introduces change of position with time; Mechanics introduces the mass of material bodies and has discovered the mathematical relationships between mass and motion which give us our measurement of force and are expressed as Newton's laws of motion. Physics analyses rather deeper and attempts to express the results of Mechanics in terms of component parts, atoms, of bulk matter, together with experimentally discovered relationships connecting force with more fundamental properties, for example gravitational force connected with mass, and electrical force connected with electric charge.

The equations of Physics, derived from forces exerted on and between pieces of matter, are capable, when plotted on paper, of reproducing forms. This process consists of drawing a smooth line, or in three dimensions a smooth surface, through the points which represent individual measurements or inferences from measurements. The result is perceived by us as a form, and the fact that the equation from which the form is graphed is common to all observers makes it possible to claim that it is a representation of the form which does not suffer from personal idiosyncracies of sense perception. But in the analysis of matter performed by Physics we infer the existence of such things as atoms which are not directly perceived by our senses. We describe an observed form by imagining that these atoms are occupying definite positions in space under the influence of forces acting on them; yet we have no right to be completely certain of these positions, which are subject not only to uncertainty because of our experimental inaccuracies but also to certain other, fundamental, uncertainties which we shall mention later. What we do is to calculate *average* positions and smooth over individual uncertainties, and just because our senses are *also* of a relative grossness which cannot detect these uncertainties, this averaged description of form is successful in reproducing the sensation.

Up to this stage of the analysis, which is approximately the level at which we consider atoms as a whole occupying average positions, Physics and sensation run parallel. But when the analysis goes deeper, and events and relationships are inferred within the atom, we enter a world which can be called "beyond sense", and to which the vaguer word "organisation" is more applicable than the rather sensory word "form". In this world, the relationships are not given sensory interpretations, but are left expressed in terms of the actual measurements and calculations from which they are inferred. It seems that when we attempt to analyse form physically, we do not arrive at smaller and smaller replicas of the form we see; as the analysis proceeds the form gradually vanishes and is replaced by a system of happenings for which Physicists use the non-committal word "event". There is organisation amongst these events, which are not quite chaotic, but we have no right to picture this organisation in sensory images.

To interpret form we say that matter consists of atoms, or, more generally, of groups of atoms (molecules) which are mutually attracted by certain forces, but which are mutually repelled when they approach more closely than a certain spacing. Under the influence of these two opposing forces there is a distance apart for which molecules are in equilibrium with the forces balancing. This equilibrium spacing may or may not be the same in all directions. When it is very precise, that is, when the molecules are in stable positions relative to each other within only a small range of spacing, there will clearly be a tendency for the bulk matter to consist of an array of molecules arranged regularly in space, each separated by a fixed distance. This internal regularity contains the possibility, as we shall see, of producing external regularity such that the matter as a whole has an interesting shape.

But there is another factor which opposes this tendency to internal regularity: all molecules possess considerable motion which never dies down. When the matter is sufficiently dense, the molecules under the influence of this motion continually collide with each other and rebound. The result is that they are all travelling, vibrating, and rotating, in a chaotic and random manner. This is called heat motion and gives rise to the properties of temperature. It is the enemy of ordered arrangement because under its influence molecules tend to tear apart.

Matter possesses internal form to the extent to which this heat motion is tamed. The higher the temperature the more does this chaotic motion preponderate over ordered arrangement. At low enough temperatures the molecules are bound together and the heat motion is confined to vibration across small distances, the molecules being never very far from their equilibrium positions. This is the solid state and contains the maximum possibilities of form. When the temperature is higher, the bonds are partially broken and only small regions are roughly in regular arrangement (roughly, because they continually break down and reform). The order falls off beyond these regions, which are barely bound to each other. This is the liquid state, in which the matter is about as dense as a solid, but is much less ordered and contains random travelling as well as vibration. At a still higher temperature the bonds are completely broken and the molecules travel and collide with each other as individual entities with no semblance of regularity. This is the gas state, and is the most chaotic and unordered. In the gas the attractive force between molecules is quite incapable of overcoming the violent heat motion and the gas, unless contained in a vessel, does not hold together as a single piece of matter but disperses completely. In astronomy large masses of gas are encountered which are large enough to be held together by Gravity, but we shall not be concerned with them here.

Although the details of the happenings are not particularly simple, we can say that the transition from chaotic gas, through less chaotic liquid, to ordered solid is a matter of lowering the temperature, that is, of passing as much as possible of the heat motion out of the matter into neighbouring matter already at a lower temperature. We liquefy the gas, and then freeze the liquid.

The liquid, although internally still fairly chaotic, does hold together as a whole; it possesses a definite surface of demarcation. This liquid surface provides us with the first manifestation of the visible form inherent in the tendency of molecules to hold together. Molecules very near the surface are attracted by their neighbours, but there are more neighbours on the side away from the surface, towards the interior of the liquid, than there are on the side nearest the surface. The net effect is that there is an inwards attraction. Those molecules which happen not to be moving outwards at too great a speed are pulled inwards, and on the average the layer of molecules near the surface is slightly depopulated and the molecules in it are further apart. They are spaced at greater distances than the equilibrium and strive to reduce this spacing to the equilibrium value. The result is that the surface behaves as an elastic skin, tending to shrink. This effect produces the characteristic forms of liquid surfaces. It produces the typical smoothness of liquids and causes the shapes of small quantities such as dew-drops. The surface-shrinking tendency is to make the area of the surface as small as possible. The drop cannot be shrunk indefinitely because the repulsive force prevents further compression of the liquid, but the shape can be altered (the liquid being internally mobile) and small dew-drops are spheres, the shape with the smallest surface area for a given volume. When the quantity of liquid is larger, its weight distorts the sphere, and if it is resting on a solid surface it is pressed out sideways. At the extreme of very large quantities of liquid, the weight effect swamps the surface shrinking effect, and the surface becomes concentric with the Earth, as in the case of a placid lake.

But the form of the liquid surface is an example of the smoothing process of our senses. The surface appears smooth, but it is smooth only for a level of description which ignores the individual dance and vibration of the molecules and substitutes their average positions instead. Furthermore, because of the large residue of chaos in the liquid state, the average positions of the molecules bear little relation to their true equilibrium positions in the absence of heat motion. This first manifestation of form vanishes almost immediately in analysis. We cannot "trace" it beyond the bare fact of molecular attraction, and its manifestation is not connected with any detail of molecular arrangement, this detail having been degraded and destroyed by heat motion. Accordingly all liquids show much the same external form, there being no interesting varieties of form which we can trace to specific properties in the molecules. As analogy imagine a compact ball of midges dancing in the air. Seen with eyes out of focus, it is like a liquid drop, but seen with eyes more in focus (the first stage of physical analysis) it becomes a chaotic assemblage of individual midges. With eyes still more in focus (the next stage of analysis) the details of the midges can be seen, but these details have nothing to do with the shape of the ball, beyond the bare fact that somehow there is an attraction of one midge for another.

The next victory of form over chaos is the achievement of the solid state. Here the heat motion is limited to vibration about the equilibrium positions of the molecules and any form we observe can be traced rather further in the analysis, and ascribed to interesting spatial properties of these equilibrium positions. The ball of midges has become a swarm of bees each vibrating slightly, but clinging to each other in a manner intimately related to their individual structure. But the intimacy of the relationship between the form of solids and the properties of molecules and atoms is still limited. We have to smooth over the heat vibration, and also we smooth over the detailed events taking place within the atoms which give rise to the attractive and repulsive force and to their variation with direction. Indeed we can say now that the interpretation of visible form is firstly a smoothing of heat motion, in which we imagine the atoms and molecules having average patterns of equilibrium position relative to each other. Secondly, we smooth the events within the atoms sufficiently to account for the magnitude and direction of the mutual forces. When we have done these two things we have reached a limit beyond which our analysis is no longer expressible in sensory terms such as "form".

We have been hinting that the interesting forms produced by solids can be traced to some regular equilibrium pattern of the molecules. If this pattern is repeated indefinitely throughout the solid without dislocations we obtain the most striking external consequences of this pattern, as shown in the shapes of crystals, which are homogeneous solids with an internal pattern indefinitely repeated throughout. In practice we observe that not all solids are crystals. At one extreme we have the glass-like solids; with them there is apparently such latitude as to equilibrium position that the solid can freeze in any random arrangement of molecules which may have existed in the liquid state at the instant before freezing. Next we have solids which are crystalline to a degraded extent only. With them a pattern exists but it contains considerable scope for random variation. In this class crystallographers study such apparently unpromising materials as rubber. A third class is only of incidental interest; it contains solids consisting of

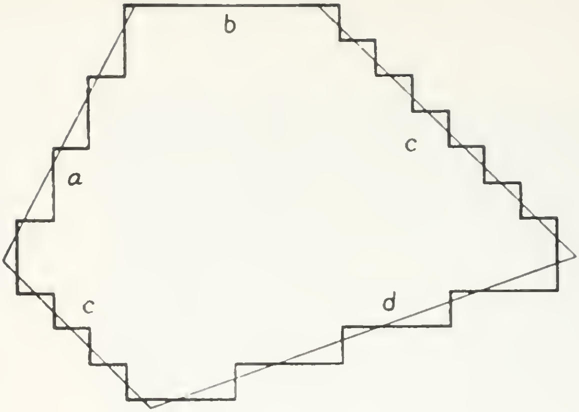


FIG. 1

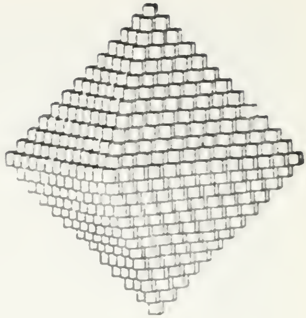


FIG. 2

grains, themselves crystalline, but which have been pressed together in a random manner.

The best manifestation of solid form is the ideal single crystal, in which one internal pattern is repeated perfectly throughout. Although this ideal is probably produced only within very small regions of actual crystals, we shall assume its existence for present purposes.

The outside shape of a crystal is a consequence of its inner arrangement, but it is the consequence of other factors as well. With a given inner arrangement quite a variety of striking outside shapes can be produced by altering the environment of the crystal while it grows. This incidental variety of shape is not at all well understood in its connection with the growing crystal's environment, but certain principles are clear. Let us take a typical simple inner arrangement in which molecules or groups of molecules are arranged row by row, column by column, such that each group can be represented diagrammatically as a point and that each point is at the corner of a cube. This arrangement exists in nature and is possessed by the "cubic" class of crystals. It is convenient for discussion because the inside of such a crystal can be regarded as made up of "unit cells" which are each little cubes, all of equal length of side. Then at any stage of the crystal's history we can visualise its outside surface as made up of the unattached faces, edges, and corners of these cubes. At first sight there is no reason why this cubic inner arrangement should lead to any particular outside shape; if we were to assume that new cubes could attach themselves with equal facility to any point on the growing crystal, the crystal would grow radially out from the invisible nucleus from which it started, and when big enough to be seen it would appear as a sphere. The surface of this sphere, on a molecular scale, would be a collection of steps and terraces of all possible slopes, and the shape would remain as a sphere as long as the addition of new cubes took place at a rate which was unaffected by the "kind of terrace". What we mean by kind of terrace is best seen by looking at Fig. 1. This is an entirely imaginary section through a cubic crystal which shows "faces", five of them, cut by this section, and that the angles they make with each other depend on the "kind of terrace" they possess. The faces *c* are of the same kind, the terrace being one up and one along. Face *b* is the smoothest possible on a molecular scale and if the crystal had this kind of face only, it would appear as a rectangular block. Face *a* is two down and one along, and face *d* is one down and three along. We can of course imagine faces which tilt in a third dimension as well, and Fig. 2 shows one such kind of face.

If the crystal looked like a sphere, or, in general, appeared curved, it would mean that its surface comprised very many different kinds of face, adjacent faces being only slightly different from each other. But real crystals do not look like this; they show only a few well-developed faces. The reason for this appearance is that the molecules which form the basic cubes do *not* settle with equal facility on to all points of the surface. The molecules in the surface of the crystal are not permanently bound there; there is a continual exchange due to heat motion. Some are being ejected and others are taking their place. A portion of the crystal surface grows when, on the average, more molecules enter it than leave it, and it grows faster if the molecules in it are more tightly bound, so that there is a less rate of loss due to heat ejection. Molecules are more tightly bound when they have many others as immediate neighbours in the surface, and this applies to positions such as the end of unfinished rows to a greater extent than positions, for example, such as sitting on the middle of face *b* in Fig. 1. This difference in the net rate of arrival of new molecules on to different positions on any arbitrary crystal surface formed by chance has two effects. First, the great majority of kinds of faces, which one can imagine by making cuts at any angle we please across a cube, do not preserve their identity when new molecules are added to them; they are transformed into relatively few kinds of face which persist on further growth. But the second effect is that this residue of faces which is left behind has also differences of rate of growth amongst its members. When these differences are very marked some of these faces disappear. In Fig. 3 the face *c* is growing so much faster than its neighbours of type *b* that it disappears.

Thus with a given internal arrangement the types of face which a real crystal shows are determined by the relative rates of growth of the types. This process explains why crystals are not usually curved but show a few plane faces; it explains part of the symmetry of crystals also; for there will often be terraces of molecules on opposite sides of the crystal which, from the point of view of arriving molecules, have identical strength of binding in their exposed positions. The types of face, and their relative area, which are shown by a real crystal depend greatly on the environment. For there are forces emanating from molecules (foreign ones as well) which are in the environment and very near the crystal, and these forces can alter the strength of binding in the various exposed positions and give rise to a different development of faces. In Fig. 4 circumstances might lead to the development of two types of face, the ordinary rectangular type *b*, and the face (that of Fig. 2) which cuts off corners. The figure shows successively the shapes produced with decreasing rate of growth

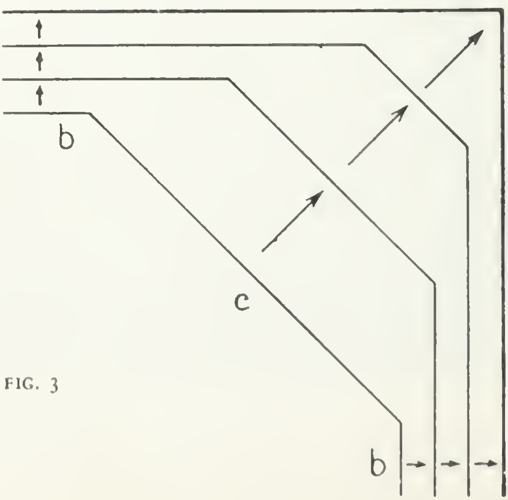


FIG. 3

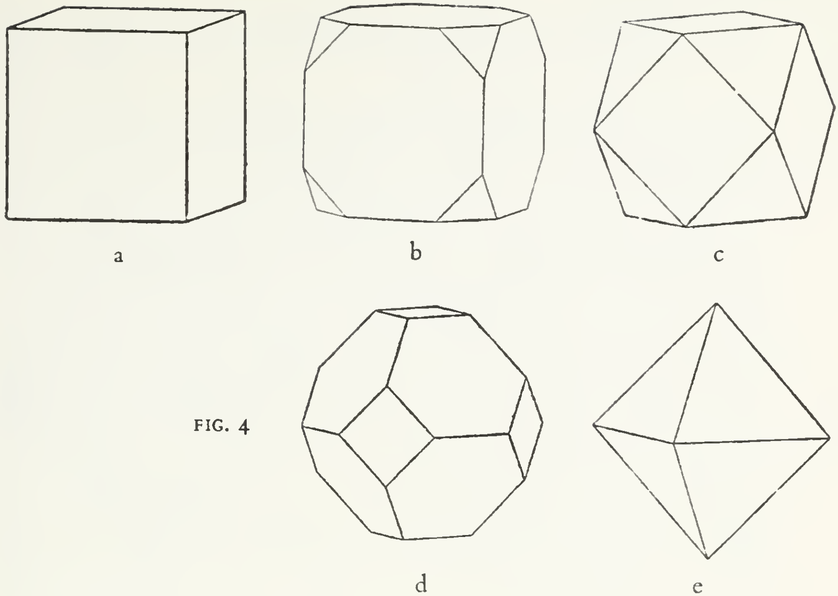


FIG. 4

of this face relative to *b*. At one extreme it grows fast enough to disappear, and the shape is a cube; at the other extreme it grows so slowly that it monopolises the shape, which then consists of its type only.

The types of face which can monopolise a shape are geometrically and aesthetically interesting. Seven of them are shown in Fig. 5. It must be admitted, however, that we are not in sight of controlling the growth of crystals so perfectly that any type of face, of any extent of development, can be produced at will.

One generalisation which has been suggested with regard to crystal shapes with a given internal arrangement and a given outside environment is that the crystal grows towards the shape in which total of the attractive forces emanating from its surface is least. This suggestion, worded in another way, has caused some difficulty in the theory of crystal growth; it is analogous to the principle which makes a small liquid drop spherical. In the latter case the force which shrinks the surface is compensated by the repulsive force which resists compression of the drop, and the net force is least when the surface area is a minimum. But

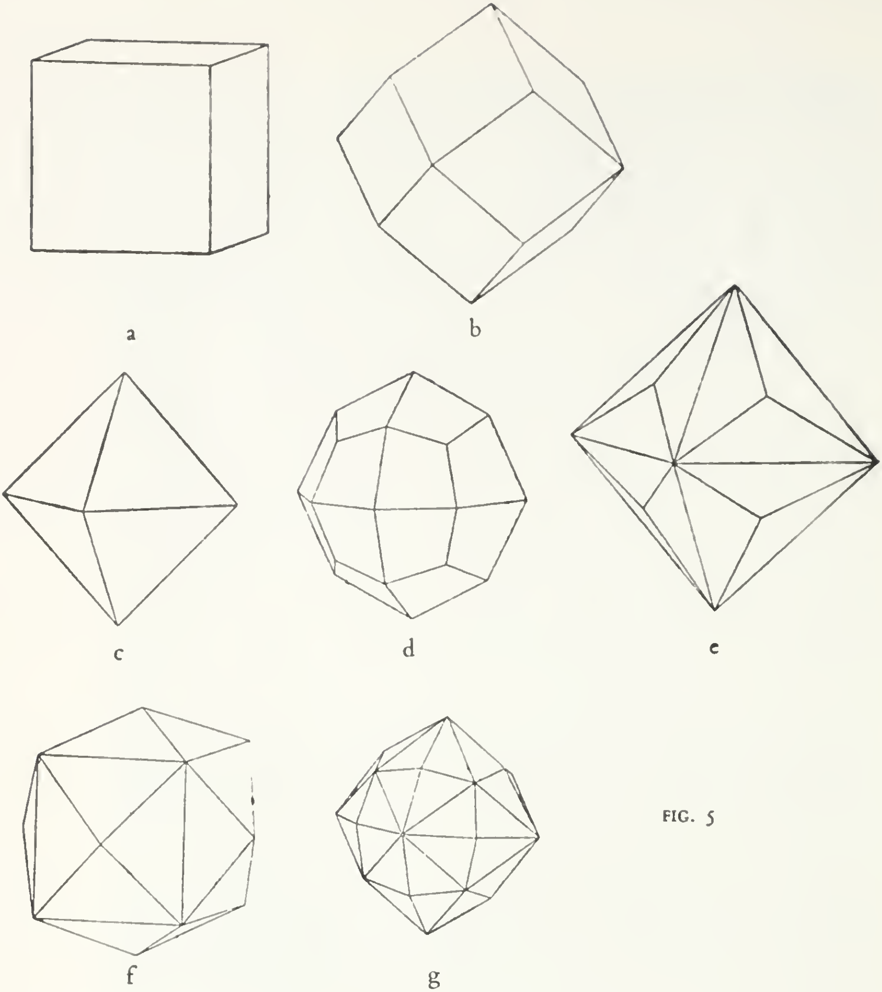


FIG. 5

the liquid can take up this shape of most stable equilibrium spontaneously because it is mobile inside. The solid crystal cannot; it can only grow towards the most stable shape. There seems to be no experimental evidence for a most stable shape of a crystal. Common salt (a cubic crystal) grows in pure solution as cubes or rectangular blocks indiscriminately. From the principle just mentioned we should expect all the sides to be equal, and all elongated rectangular blocks to go over to cubes. It may be that this theory is correct, but that the need for the crystal to *grow* towards its equilibrium shape makes the process so slow that we can never observe this happening in the periods of human observation.

The discussion we have given so far has illustrated the variety of shapes that can be produced with a given internal arrangement, under the influence of factors which alter the relative binding strengths of molecules settling in different positions on the surface. It may be far-fetched, but this rather suggests a beginning in inorganic nature to relate the shape to a balance with the environment, rather than to purely internal factors. The crystal form is essentially a product of the geometry of one unit repeating itself indefinitely throughout the solid, and when this is allowed to happen there is a definite limit to the complexity of the resulting form, the limit being set by the requirement of repeatability in space (without which we would not recognise the crystalline state). This method of achieving organisation thus has its limits both as regards aesthetic form, and as regards relationship with the environment.

The other great achievement of form in nature, the achievement of organic molecules and the evolution of Life, follows a different principle. In this the linkage between parts of the whole is much more "creative". New atoms are added, and new molecules evolved, all being linked so that each new development creates a radically new complex, with ever greater possibilities for interaction with the environment. The vast development of chemical binding which is Life creates an organism which is itself a stupendous dynamic chemical community. This is quite different in scope and character from the mere repetition of one molecule or group of molecules, however complicated each group may be, which is the crystal. Thus the dynamic inter-relationship of the protein molecule with other kinds of molecule produces Life, whereas the mere repetition of one protein molecule (though it may contain ten thousand atoms) produces but a crystal, and one of low symmetry at that. But the realm of form which is organic nature is discussed elsewhere.

When we said above that the crystal shape was partly traceable to incidental factors connected with relative rates of growth of different surfaces, and partly to the internal arrangement, we did not separate the two parts. The elucidation of the inner arrangement from the outer shape was historically prior to the great advance afforded by X-ray analysis (in which the way the crystal reflects X-rays passed through it gives information on the arrangement and spacing of the atoms). With a given inner arrangement, in spite of incidental variations of outside shape, the crystal form can be specified in terms of "elements of symmetry' which have been defined for the purpose. This restricted classification of crystal shapes in terms of symmetry has the advantage that it leaves out of account the variations not solely connected with the inner arrangement, and enables us to refer the shape to a corresponding symmetry of the unit cell. In our examples we have taken a unit cell with the symmetry elements of a cube. Other kinds of symmetry can exist, and they give rise to 32 "crystal classes". Furthermore the molecules or groups of molecules which the points of the unit cell represent each have symmetry elements of their own which play a part in the external symmetry. Taking into account these (which are called "space groups"), it has been shown by pure geometry that all the 32 crystal classes can be accounted for by a total of 230 space groups, and all these 230 have been found in natural crystals.

This analysis is based essentially on the requirement of repeatability in space, and it sets a limit to the variety of crystal symmetry. It is interesting to notice that the complete mathematical theory of crystal structure was published about 1890, before the advent of the modern atomic theory of crystal structure, and that it was made from pure geometrical considerations, without the need for physical postulates. But we must also notice that the crystal was "given" in the first place; it needs physical principles to account for the production of those plane faces which first aroused interest in the symmetry of the crystal. We also notice that the analysis is in terms of symmetry only, and does not lead to information on detailed positioning of the atoms; X-ray analysis had to be developed before this information could be deduced.

We have now completed a survey of the most striking spontaneous forms of nature (other than molecules and their organisation which leads to Life) which are sensorily perceived. We have found that these forms could be described by regarding the atoms merely as centres for forces exerted on each other, so that these centres tended to arrange themselves regularly in space. The description consisted of smoothing over the heat-motion and, by a piece of intellectual imagination, drawing a surface through the average positions of those centres on the boundary of bulk matter. Apart from the intellectual description, the act of seeing a form is an act of averaging, for the light reflected from each atom is not individually detected by the sensitive surface of the retina. What is detected is the merged emission from very many atoms, and this produces the smooth sensation of form. If, however, we concentrated on smaller and smaller parts of the matter with more and more powerful microscopes, in an attempt to perceive the small-scale form, and we reduced the heat motion as much as we could by cooling the matter, we should arrive at a stage in which the matter was smaller than the wave-length of the light we used. One cannot perceive form unless many individual parts of the matter each behave separately in reflecting light; this requires that the wave-length of the light be much smaller than the matter observed. We could then use light of smaller and smaller wave-length. Up to a certain point this would be successful; the most powerful microscopes known (the so-called Electron Microscopes) use wave-lengths which are smaller than the (relatively) large protein molecules which are viruses, and can show them as blurs, without shape. But beyond this point a fundamental difficulty is encountered because light of very small wave-length interacts with matter like a bullet; the light is reflected off in one direction and the matter in another. This violent disturbance of what we are trying to see renders it impossible to perceive, or infer, form and shape in the smallest physical entities. Whether we experiment with light or with other "missiles" all that we can say is that certain events occur when interaction takes place.

Only in a very limited sense can we even ascribe the property of "occupying space" to these smallest physical entities; our experiments can produce a certain number of interactions, and by analogy, and only by analogy, with large-scale collisions we can calculate a "cross-section" for the entities from the probability of a successful interaction. But this term has not the same meaning as the cross-section of a billiard ball. For one thing it refers both to the target and the missile. Indeed, in deep Physics we do not know of the existence of one entity by itself; all we observe is interaction between two entities, and the cross-section refers to them both.

The usual description of an atom as a collection of electrical entities (electrons) associated with a complex system (the nucleus) contains the inference that the electrons are "outside" the nucleus. Most would agree that this spatial statement is just permissible, but that any attempt to ascribe shape to the orbits of the electrons must fail. As for the nucleus itself, it is possibly illegitimate to give it any space-occupying property at all, other than in the experimental sense of "cross-section". In the deepest levels of the analysis form is the first to vanish, and later even the occupation of space loses meaning.

This article should not digress into atomic physics beyond its connection with our subject: form, so we will stop here. To the question whether a "deus ex machina" would perceive form in the fundamental entities of the physical world, the physicist would give answer that, in science, the question does not arise. If there is any validity in pure intuition divorced from observation and experiment, it is not for him to say.

Illustrations reproduced from *An Introduction to Crystallography* by permission of Messrs Longmans Green & Co. Ltd.

Shape and Distance considered by an Astronomer *by C. C. L. Gregory*

THE VARIETY OF FORM presented by the totality of natural objects, even if restricted to those which can be seen and handled upon the Earth's surface, would be so great that, without elaborate systematisation, it would be quite incomprehensible. The most generally accepted and widely applicable classificatory systems are those provided by the various branches of Natural Science.

Within science itself many such systems are in use; some are dependent upon the form of the object and some upon the means whereby the object is perceived.

If we understand by *form* something more than mere *shape*, if we mean by form all that can be known about the object with all the aids that science can provide, then it is to be expected that there will be systems of classification according to the various modes of apprehending the object. Thus, Mineralogy would naturally cover the form and composition of the various substances found upon the Earth's surface, including any meteoric matter that may have fallen from the sky, either in chunks or in the form of fine dust from vaporised meteorites or "shooting-stars". When the same material is moving at high speed in the tenuous atmosphere of some fifty or a hundred miles above the Earth's surface, where friction first causes it to glow, it comes within the province of Observational Astronomy and, if it be observed by Radar during daylight or when the sky is overcast, it would come within the most recent sub-division of Observational Astronomy, i.e. Radio Astronomy.

Thus natural objects may be classified in respect of their appearance, use, and other characteristics, and also with regard to the methods required for their investigation according to their size, distance from the observer, speed, etc. Even if we are concerned with shape only, unaided vision will not suffice if the object of our interest should happen to be, say, an atom, a star-cluster, or a train of sound-waves in air due to the movement of a violin-bow in contact with the strings of the instrument.

Science requires such very specialised tools, both physical and intellectual, for the examination and description of all that goes to characterise an object, that it is no wonder that special systems or separate sciences have come into existence, each dealing with some particular aspect common to a great variety of objects.

The multiple nature of science in all its varied activities has long been recognised and, in some cases, distinctive names are used. Unfortunately for the non-specialist there is always considerable overlap, and this is apt to prove both an initial difficulty to the learner, and also a possible source of error to the expert.

The general science of shapes is Geometry, originally concerned with measurements of lengths and angles on the ground and their relations—in fact, what we should now call surveying. As in the case of most other sciences, a division gradually came about, so that there are now two kinds of geometry. Geometry as a branch of theoretical mathematics (or pure geometry, as it is called) deals with ideal space. According to Bertrand Russell it is "an exercise in logic comparable to a game played with formal rules, and can no more be wrong than the game of dominoes." Geometry considered as applied mathematics can be right or wrong in describing measurable relations. In applied geometry, just as in applied physics, there are both *postulates* and *hypotheses*, and these are subject to modification or abandonment according to experimental findings. So long as science was concerned only with the object-world which was "to hand", so to say, and could know but little of the almost infinitely great world of astronomy, or the almost infinitely small in connection with the molecule, atom, and sub-atomic particle, so long as that was the case it mattered little whether "lengths", "angles", etc. were only "ideal", because it was just commonsense that they could be "approximated to" by the actual measurement of marks made on solid objects. But nowadays, when important distances are estimated in hundreds of millions of light-years or, on the other hand, in terms of "the radius of the electron", we must have a clear notion of precisely how it is proposed to measure these distances if we are going to substitute "ideal" lengths etc. for "measured" ones in our theoretical constructions, and then expect to use these for predicting further measures.

When we come to consider "growth" (or natural changes of any kind, for that matter) we must be just as careful to distinguish between "ideal" and "practical" time-measurement, as was the case for lengths and angles in connection with the very large or the very small. The span of human life is almost nothing compared with the time-interval which would be required to show significant changes in an average star, whereas quite important atomic changes may take place in the million millionth of a second. Although the astronomer knows a lot about actual clocks and time-determination, it seems probable that the final word has not yet been said about "ideal" clocks, and their relation to the time-system we use in practice.

Theoretical geometry is time-independent. It consists of relations, and of relations between relations. All these are logical implications of the axioms. The truth or falsity of the axioms of theoretical geometry is without meaning, the only requisite for them is self-consistency, i.e. that they are not mutually incompatible. Different systems of theoretical geometry have different axioms, but the whole of the geometry in each case follows from its axioms by logical implication. But the "interpretation", whether in time or in space, cannot yield information about time or space as experienced, though it may indicate how measures can be combined.

In applied geometry time is involved, but in what I shall call the first degree only, i.e. in the purely *qualitative* sense that to observe, to test, to measure, to advance, to retreat, to rotate a line about a point, a plane about a line etc., all take time, and change of some kind is involved. The important thing is, however, that the *amount of time taken* is of no consequence. Applied geometry and such branches of physics as Statics, Hydrostatics, parts of Pneumatics, Electrostatics, etc. are usually far easier than those sub-divisions in which the state of affairs is continually changing with the time, as is the case with Kinematics, Dynamics, and Electro-magnetism. It will readily be seen that we can test the various properties of lines, planes, surfaces, spaces, screws, levers, pulleys, electric charges, magnets, etc., by moving them into fresh positions in our own good time, and measuring the distances, angles, and forces at leisure. It will be obvious, also, that with rotating and revolving bodies, swinging pendulums, wave motion generally, and changing currents in electric circuits, the rate of motion is an additional quantity to be determined. If the rate of motion should prove to be constant, repeat itself over and over again (as for pendulums and wave-motions), or to follow some recognisable curve, then it may be represented graphically or mathematically, and the whole problem at once becomes quasi-static. This does not of course mean that the motion or the time-element are not real, or that they no longer exist; it only means that a form of representation has been invented, which is itself complete and without change, but nevertheless suffices for calculating all past and future states of an ideal system in motion, and the rate of motion at any desired epoch.

In its perfected form Newtonian Mechanics is such an "eternal system", and was at one time thought to be capable of predicting (in principle) the whole course of the material world. In positional astronomy Newtonian Mechanics still suffices for accurate descriptive purposes except in the case of the planet Mercury where there is a small discrepancy, first satisfactorily accounted for by Einstein. His Theory of Relativity first brought "four-dimensional geometry" to public notice, although a timeless representation of the forms of planetary orbits was already perfected by Hamilton within the Newtonian framework. Since all the separate bits of matter which together form the cosmos are in relative motion, the shapes of the various sub-systems change. This is true for the solar system, although in this case it has been calculated by Laplace that no large-scale changes are to be expected. If a photograph of the solar system could be obtained from a position right outside it, the Sun would appear as the great centrepiece, the various planets with their satellites, asteroids, comets, meteor-clouds, etc. appearing as little more than scattered points without much discernible pattern. But if we could imagine that a very very slow plate were used, so that it could be exposed continuously for, say, 100 years, then the paths of the planets and, in fact, the solar system as a whole, would have *shape*.

Thus shape in astronomy can appear in two ways. There are first the shapes of the various bodies themselves, the subject-matter of Applied Geometry. Then there are the "shapes-in-time" of the various systems of bodies which take account of their various motions; these would be shown on the imagined photograph by lines or trails. In still larger systems such as star-clusters and galaxies changes take place very slowly indeed. They have to be predicted by gravitational theory, the four-dimensional shapes so produced coming within the province of Dynamics, rather than Geometry.

Among those scientific writers especially noted for the gift of making hard things easy, were W. K. Clifford and Karl Pearson. For a clear account of the principles of Applied Geometry, as an introduction to considerations of form and process in nature, Clifford's "The Common Sense of the Exact Sciences" has probably never been surpassed, although the author died in the spring of 1879 at the early age of thirty-five. Clifford describes the experimental basis of his subject somewhat as follows:—

A "thing" takes up room. There is a boundary, called a surface, between the part of space occupied by the thing, and the rest of space outside it. If we take the example of a table in a room, we may suppose the space all round the table is filled with air; the surface of the table is then something just between the air and the wood, which separates them from one another. The surface of the table is not a very thin piece of wood, or of air: The surface is common to the wood and the air, but takes up no room whatever. If the surface of the table be of two colours, then the coloured areas are separated by a line. The line has no thickness whatever; it divides one colour from the other, and takes up no surface-room at all, any more than a surface takes up any space-room.

The surface of a thing is not an imaginary conception, but something we constantly observe; we can see it and feel it. Likewise a line on a surface which separates one part of the surface from another is also a matter of every-day experience. It is not an idea got at by supposing a string to become indefinitely thin. In just the same way, a point which divides a line into two portions must not be thought of as a very small particle.

Clifford suggests that the first observation we make about space is that a thing can be moved about from one place to another without altering its size or shape (as determined by measuring the distances between various parts of it). But this cannot be *tested* because, should alteration occur, any measuring-scale we could use might be subject to the same alteration, and so defeat our test. Nevertheless, as far as geometrical conditions alone are concerned, lengths which are equal to the same length are assumed to be equal to one another. This really amounts to assuming that two things which fit in one place (say, London), should also fit in another place (New York), although brought there by different paths. Clifford says: "Is it possible, however, that lengths do really change by mere moving about, without our knowing it? Whoever likes to meditate seriously upon this question will find that it is wholly devoid of meaning. But the time employed in arriving at that conclusion will not have been altogether thrown away."

Nowadays the most accurate determinations of length provided by rigid bodies are not made with *things* (rigid scales) but with the length of a "light-wave" of a precise colour (or frequency) under standard conditions. Since light is moving, time is involved to the *second degree*, and this prevents our consideration of using light for length-measurements under the heading of applied geometry.

Let us now consider some of the characteristics of the surfaces of things. It is obvious that the shape of a thing depends only on its bounding surface, and not at all upon the inside of it. Shape is a matter of angles—identity of shape depends on equality of angle.

The surfaces of the sphere, the ellipsoid, and the egg-like and orange-like spheroids are smooth all over. The last (the oblate spheroid) is the shape of a fast-rotating star or planet. It is most obvious in the cases of Jupiter and Saturn; both these planets rotate in a period of nearly ten hours. The Sun and Moon appear spherical, with rotation periods of 25 and 27 days respectively with reference to the direction of the distant galaxies.

The cylinder has two flat ends and a round surface between with circular edges. The cube has six flat sides with straight edges and four corners. Clearly an edge is a line and a corner is a point.

A plane surface is one which is the same shape all over and on both sides. The surface of a sphere is the same shape all over, but not on both sides. A plane surface can be manufactured by taking any *three* surfaces (three pieces of glass, say) and grinding them together in pairs until any two will fit one another all over. Plane mirrors for astronomical purposes can be made in this way which have less curvature than a free surface of liquid whose radius of curvature is equal to that of the Earth's surface, i.e. nearly 4,000 miles. If any *two* surfaces are ground together until they are of the same shape all over, they will be portions of the same sphere, the two surfaces showing opposite sides of the same spherical surface.

If a plane is divided by a straight line, the division has the same shape all along and on both sides. A circle is a line in a plane which has the same shape all along but not on both sides, and the curve which has the same shape all along, but does not lie in a plane, is known as a helix.

These definitions were first given by Leibniz, who also defined a straight line as the aggregate of those points of a body which are unmoved when it is turned about with two points fixed. If we suppose the two points to lie on the plane face of a body then, on rotation from one position to another, the straight line becomes the intersection of two planes.

We need not spend time discussing the properties of triangles and circles, since these are usually considered in great detail at school, but a word should be said about the conic sections, as these curves play an important part in nature, and especially in astronomy.

If we have a very tiny source of light above a plane surface, say, for example, the surface of a table, and we hold a circular disc in any position so that the whole of it is below the level of the light, then the shadow thrown on the table will be an oval curve called an *ellipse* (which is the shape of a planet's path round the Sun) except in two extreme cases, when it will be either a circle or a straight line. If the disc is held so that its highest point is on a level with the light, then the curve made by the shadow-edge on the table is a *parabola* (the curve a thrown stone would follow if there were no air); finally, if we hold the circular disc still higher up, so that a horizontal plane through the small light divides it into two equal parts, then the curve is an *hyperbola*. This is the curve which a comet would describe if ever it approached the Sun with sufficient speed for it to effect an escape from the solar system. (The paths of most of the comets are elongated ellipses). If we join points of the disc's circumference which are above the little light to it, and then continue these straight lines through the light until they reach the table, they will intersect the table in points which also lie on an hyperbola—for geometrical purposes this hyperbola forms with the outline of the shadow of the lower part of the disc *one complete hyperbola*, although in two separate parts.

As well as the conic sections, there are two spiral curves of special interest; the first is known as "the spiral of Archemedes", which is a plane curve such that, starting from any point on it, the radius increases (or decreases if you proceed in the other direction) proportionally to the angle it turns through. Another interesting spiral is the Equiangular or Logarithmic spiral invented by Descartes, which is carefully explained by Clifford. It is closely represented in nature, especially by the Galaxies or "Spiral Nebulæ."

A further word about measurement. We have already given some consideration to the measurement of length, which may be done with a uniformly divided and numbered scale, rod, or tape. Angles are said to be equal when they fit the same opening of the compasses. This, of course, is only a relative way of measuring angles, but there is also an absolute way, in terms of a natural unit. Length, time, and mass are said to be *dimensional* *quantities*, because in each case the particular quantity of length, time, or mass is a given number (which may be fractional) of some arbitrarily-chosen unit, such as a foot, a second, or a pound. Angles are often given in *degrees*, or in multiples or fractions of a *right-angle*. In such cases angle is a dimensional quantity; but a natural unit has been utilised for scientific purposes called a *radian*, which is about ·636 of a right-angle, or $57^\circ{\cdot}3$ nearly. Accurately the radian is the angle at the centre of a circle which is subtended by an arc whose length equals the radius. Thus, for a circle of unit radius, the length of the circumference, measured right round the circle, is about 44/7 units, or 2π units (where π, the ratio of circumference to *diameter* of all circles, is the number 3·14159.....). When the *radius* is one unit, the circumference is 2π units, or 2π radians; 360° is 2π radians, and one right-angle is $\frac{1}{2}\pi$ radians or, simply, $\frac{1}{2}\pi$.

Time cannot be measured directly, but only indirectly in terms of angles and angular speeds, the natural unit being radians per day, or radians per second. It is convenient, however, to measure the rate at which something rotates, or the rate at which a pendulum is swinging, in "cycles per second" or "vibrations per second". Here the unit angle is taken to be 360° or four right-angles, and the measure is termed *frequency*.

If you look in the "Radio Times" under "The Home Service", you will see "330 m. (908 kc/s"). This means that the wave-length used by this station for transmission is 330 metres long or, alternatively, that the frequency of the transmission is 908,000 cycles per second. In every second, therefore, a length equal to 908,000 × 330 metres leaves the transmitter, and this is called "the velocity of light". It comes to about 299,640 kilometres per second, or about 186,000 miles per second. Since velocity is without meaning unless it be velocity relative to something, it is clear that, if "velocity of light" is to have physical meaning, it must either mean *relative to the transmitter*, or else *relative to the surrounding medium* (if there is one).

To discuss the characteristics of wave-motion in detail would not be feasible within the limits of this article. A good account of wave-transmission and the relation between waves, simple harmonic motion, and uniform rotation is to be found in

C. G. Darwin's "New Conceptions of Matter", 1931. What we can actually *measure* are: (1) The frequency with which the successive waves are sent out, usually in terms of (a large sub-multiple of) the frequency with which the Earth rotates, i.e. *the inverse of a second.* (2) The length of the waves in terms of our standard of length. (We can, by reflection, obtain stationary waves, and actually measure the distances between successive nodes, but this is not a very accurate way of obtaining wave-length; the use of a "grating" is preferable). (3) The average speed in air of a train of waves (usually light-waves) over a measured distance on the Earth's surface. This can easily be corrected to what it would be in a vacuum, using the measured refractive index of air, and agrees well with values of the velocity of light found by other means.

Since all we know of the heavenly bodies is derived from their light and other radiations, it is important to consider the effect of the finite speed of light on celestial phenomena; consequently we have: (4) The apparent change of frequency of "celestial clocks" on account of the relative velocity of the Earth and the "clock" in the line of sight to the "clock". It is well known that this effect was first suspected by the Danish astronomer Olaus Römer in 1676, from examination of a series of careful observations of the eclipses of Jupiter's satellites, the frequency of the eclipses appearing slightly greater when the Earth and Jupiter are approching each other than when they are mutually receding. The relative velocity of the Earth and Jupiter is known from angular measurements only, when once the Sun's distance, or some planetary distance giving the scale of the solar system, is known. This relative velocity, when divided by the observed proportional frequency-change in the case of Jupiter's satellites, was found to be approximately constant and equal to about 192,000 miles per second, and so the first determination of the velocity of light was made. After the invention of the Spectroscope, similar frequency-changes were discovered which depended on the relative velocity of the earth and *any* of the heavenly bodies, but now it was frequency-changes in the light itself which were measured. They cause small displacements in the lines of the spectrum of a planet, star, galaxy, etc. and, since the undisplaced position of the line is known from laboratory determinations, the relative speed in the line of sight can be found. As is well known, very large recessional velocities have been found in this way for the distant galaxies, the greater their distance the greater being the speed at which they are receding. (These displacements of spectral lines are called Doppler shifts). (5) Owing to the finite speed of light, the heavenly bodies are not seen in precisely those directions in which they would appear were light instantaneous. Since we can only observe their *apparent* directions, the effect could never have been discovered were it not for the *variations* of the observer's speed caused by the Earth's rotation and orbital motion. These small periodic fluctuations in apparent direction were discovered by the third Astronomer Royal, Bradley, and are called *aberration*.

One further observation in connection with the velocity of light is that certain stars, called *Cepheid Variables*, are *pulsating stars*; as the star pulsates rhythmically changes occur in its brightness and its colour, also there is a "Doppler" effect showing, apparently, that the star's surface is alternately moving toward and away from us keeping time with the changes in brightness. If the velocity of the star's surface, so it is argued, were added to the velocity of light, then the light which was emitted when the surface was moving towards us would be travelling faster than the light which was emitted when the star's surface was moving away from us. If the movement of light in space were like the movement of moving objects, then the light which moved fastest would overtake the light which started earlier but was moving slower. If this were to happen, the pulsations would not always be seen to be in step with the changes of colour and brightness. As some of these stars on the confines of our own galaxy are of the order of 100,000 light-years distant, and those in other galaxies are still more distant, it certainly appears that the velocity of light in space must be independent of the velocity of the source.

But what is the velocity of light in space? If by this is meant velocity relative to some ether, then it should be easy, it might be thought, to devise an experiment that would measure the velocity of the earth relative to this ether of space but, as everyone knows, this is now believed to be impossible. Thus we are led to suppose that the velocity of light cannot be given physical meaning in the ordinary sense of velocity i.e. that light increases its distance from a persisting mark at a constant rate, and that this very considerable rate is constant from its start in the surface of a material body until its termination in the surface of another (or the same if reflection be used). Perhaps the fact that the velocity of light is considered to remain constant no matter what finite velocity is added to it or is subtracted from it is less surprising than the supposition that it starts from rest with its full velocity of 186,000 miles per second and then suddenly comes to a full stop in no time at all, or is even reversed by the slightest mirror hung on the slenderest of suspensions, with a scarcely perceptible impulse to the mirror.

It happens that the astronomer's primary scale of distance is independent of the speed of light, although astronomical distances are often expressed in "light-years". The starting point is the measurement of an arc on the Earth's surface in some unit of length, and this determines the Earth's radius in the same unit. (The Greeks measured the Earth's radius in this way in terms of the length of a marching step, or Stadium, the exact length of which, in modern units, is unknown). The first astronomical base-line is the equatorial radius of the Earth. This provides a base for the parallax (change in apparent position) of one of the minor planets, Eros for example, and this one measure, together with angular measurements, suffices to give the scale of the whole solar-system including, in particular, the Sun's distance. The Sun's distance is now used as the base-line for obtaining the parallaxes of the nearer stars. The Earth-to-Sun line is the base of a very long thin triangle having the star which is measured at its far tip. The angle there is called the angle of parallax, and can be found when the two base-angles have been measured and hence the distance is determined when the length of the base is known. The angle at the star, the parallax angle, is always less than one second of arc, even in the case of the nearest star. The sum of the three angles of this triangle together amount to two right-angles, or π *radians, if space is flat.* The star's parallax, then, is the difference between the sum of the base-angles, which is always greater than $179° 59' 59''$ and $180°$. On the accurate measurement of this small difference stellar distances depend.

Once we have obtained distances of sample stars in this way, we can use their proper motions (small angular displacements which are time-dependent to the second degree) to obtain the Sun's speed relative to the centre of mean position of the stars whose distances have been directly determined, together with those stars whose distances have been inferred with sufficient accuracy from luminosity comparison with sample stars. From a knowledge of the Sun's speed, so obtained, a still longer base-line becomes available, i.e. the distance between the two positions of the Sun (always, of course, with reference to the positions of observed stars) at two epochs separated by, say, 20 or 30 years. So estimates can be made of groups of still more distant stars, including some of the very brightest stars. There are many supplementary methods, for example the intrinsic brightness of these brightest stars, which can be recognised as tiny resolved images on recent photographs of extra-galactic nebulæ, provides a means of determining their distances. Repeating once more the process of deriving distances by comparing the apparent brightness (or size) of the recognised but far-distant with the apparent brightness (or size) of similar objects, whose distances we have already obtained, we derive estimates of distances of galaxies, and clusters of galaxes, right down to the limiting magnitude available with the largest telescopes. So these vast distances are measured in terms of the Earth's radius!

We have already moved a long way from the simple notions of shape and distance determination with which we started, and this journey was necessary because shapes and distances in astronomy usually refer to remote aggregates instead of the near objects of normal scrutiny. The surface of a star (if a globe of white-hot gas may be considered to have a surface) has an equilibrium configuration which, just like a bubble, will be an exact sphere so long as it is not subject to external forces, and small-scale phenomena are neglected. As we have already seen, the "shape" of aggregates moving in accord with Newton's Laws can only be got at by combining pictures taken over a time-interval.

The Universe is said to be composed of radiation and matter, both being forms of "energy", and energy is something which, like your bank balance, must be kept account of and may be either positive or negative. The chief distinction between what science designates radiation and matter respectively is that radiation always moves with the speed of light, while matter never does. Space is filled with radiation quite invisible to us, for example "cosmic radiation", a very penetrating sort of X-rays, is all the time passing through our bodies and into the ground. Were it to illuminate as does light, the whole heavens would appear brighter than the full moon!

The separate bodies which constitute the known cosmos range from tiny electrified particles repelled from the sun during exceptional solar activity and, completing the journey to the Earth in about two days, cause aurorae and magnetic storms—to giant stars with enough space inside them to contain the Earth's orbit.

We are not concerned here with the shapes of the detached atoms and molecules which populate space to the extent of about 10 or 20 to the cubic inch, and we do not know the size or shape of the particles which constitute the ring-system of Saturn, nor of those which make impenetrable to light the vast, shapeless cosmic clouds which prevent our seeing the (doubtless) bright, massive centre of our own galaxy, known both through its gravitational effects and more directly by its radio emission which penetrates the cosmic fog as easily as it does our more familiar London equivalent.

The shapes of those meteorites which survive descent through the Earth's atmosphere are, of course, known; a very fine collection is to be seen at the Science Museum, South Kensington. Irregularity of shape is a characteristic, so it seems, of the lesser asteroids, or minor planets, many of which circulate in the solar system, approximately between the orbits of Mars and Jupiter, in orbits of marked eccentricity, irregularly distributed both in orientation and in inclination to the average plane of planetary orbits. The larger asteroids and satellites of the planets, of a size comparable to our own Moon, appear spherical. This is to be expected because, for them, gravity, acting like the soap-film, is a force sufficiently strong to overcome the binding forces between molecules which normally tend to maintain any special shape which chance may give to a body. Thus gravity (and, in some cases, the centripetal force due to rotation) gives shape to the planets and stars, while the pressure of light, shaping the course of the smallest and lightest particles, in defiance of gravity, gives form to the tails of comets, and is a factor in supporting the vast pink calcium clouds which hover and stream above the Sun's surface in fantastic shapes—curtains, arches, mushrooms, and jets. (Figs. 1, a-d).

Whether gravity alone is sufficient to account for the shapes of the more regular galaxies, a number of which show spiral structure (Fig. 3), and some have a central bar like the Greek letter Φ is not at present known. Very strange shapes also are to be seen among the so-called planetary nebulæ—rapidly expanding gaseous globes, product of a "Nova" out-burst, but occasionally helical in appearance. (Fig. 2).

Are there any new shapes to be found, or distances to be determined? The answer is almost certainly: "Yes". The largest telescopes in the world are now engaged in investigating the largest and farthest known systems—clusters of galaxies, and on problems connected with the shape of space itself.

Illustrations: *explanatory notes*

FIG. 1 Sequence of four plates (a, b, c, d) showing changing form of eruptive prominence beyond the Sun's edge, photographed in hydrogen light at 16.03, 16.36, 17.03 and 17.23 hours on June 4th 1946 by Roberts at High Altitude Observatory, Colorado; reproduced by their courtesy.

Earlier photographs (May 30th to June 3rd) show this ribbon-like cloud dark against the Sun's disc and approaching the edge due to solar rotation. The apparent rate of ascent of the luminous gas is about 100 miles per second, but, possibly, what rises is only a region of excitation, and not 1,000 million tons of matter.

FIG. 2 *Planetary Nebula.* (N.G.C. 7293 Gregory, Helwan Observatory, Egypt). This large, faint, helical (corkscrew-like) object is probably the result of a Nova outburst many thousand years ago, called "Planetary" on account of the disc-like appearance of many that are smaller, and more recently formed. The radius is not known, but may be about 1,000 times that of the largest orbits of the solar system.

FIG. 3 *Spiral Nebula.* (M. 64. Ritchey, Lick Observatory, U.S.A.). This galaxy, more than a million light-years distant, consists, like our own, of thousands of millions of stars, and has the form of a double spiral more or less in a plane. The broad dark line near the centre is a common feature of galactic structure. It is due to a vast galactic cloud, opaque to light, but transparent to radio waves. Such a cloud in our own galaxy prevents our seeing its bright central condensation, situated in the constellation Sagittarius.

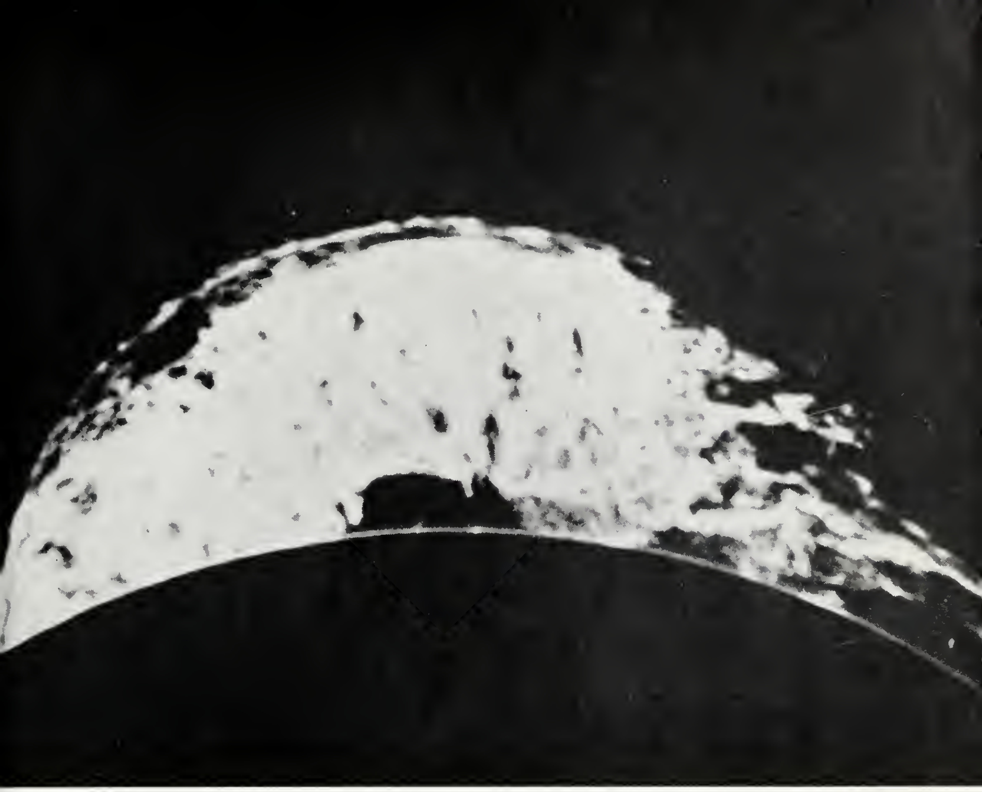


FIG. 1a

FIG. 1b

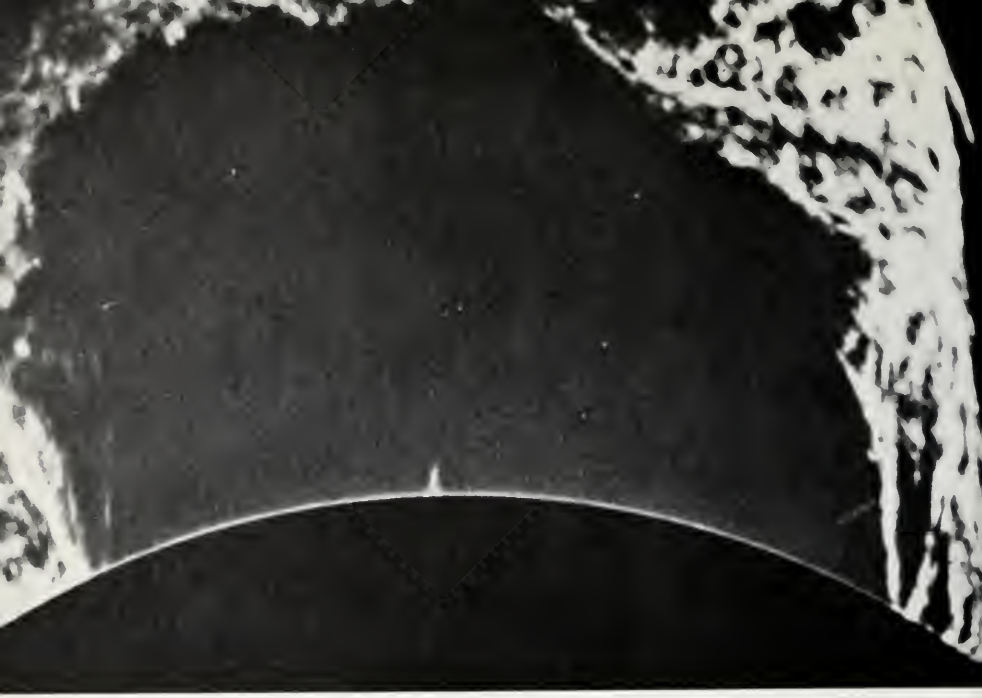
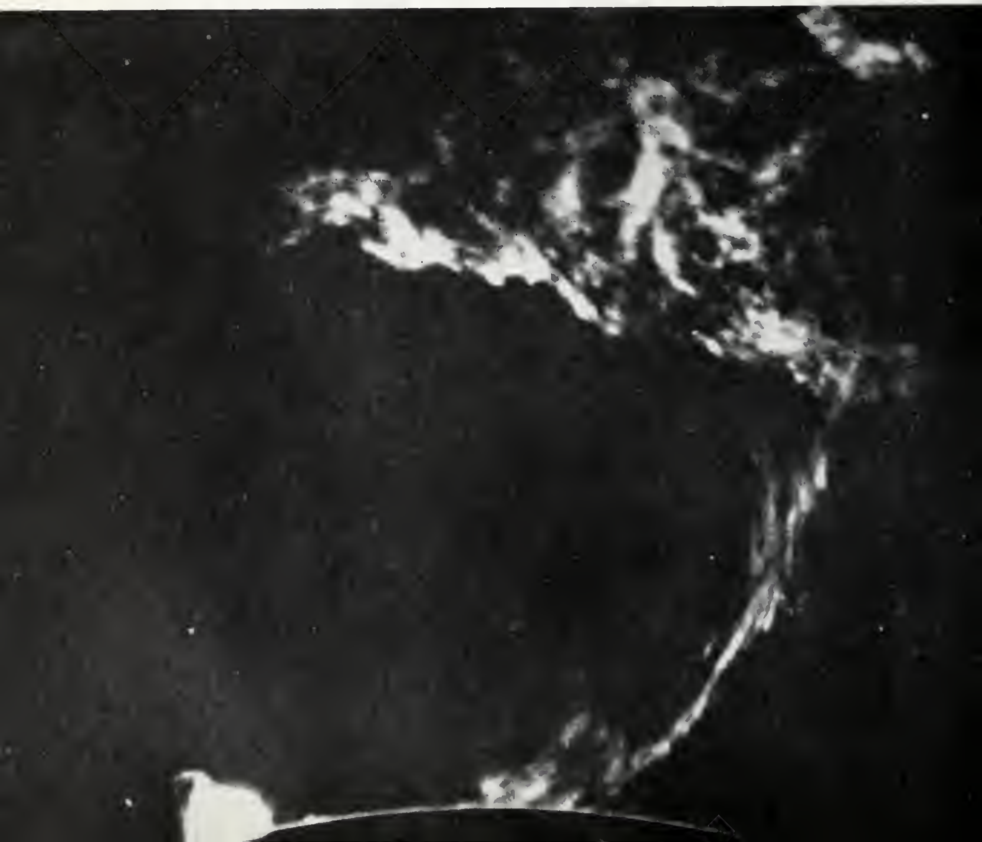


FIG. 1c
FIG. 1d



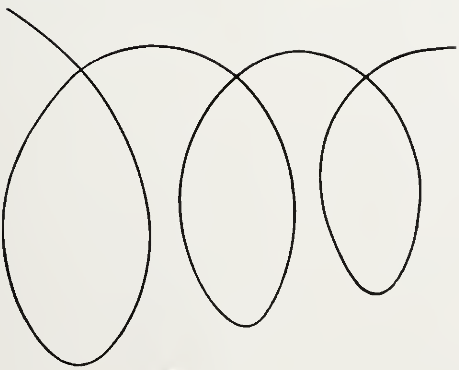


FIG. 2

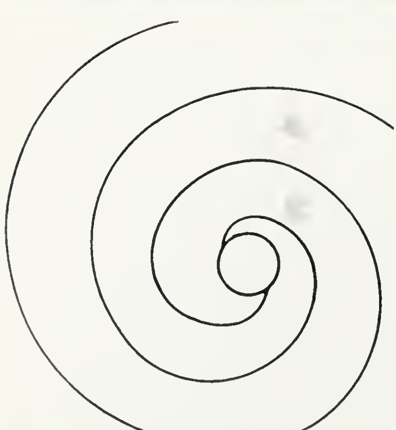


FIG. 3

The Character of Biological Form

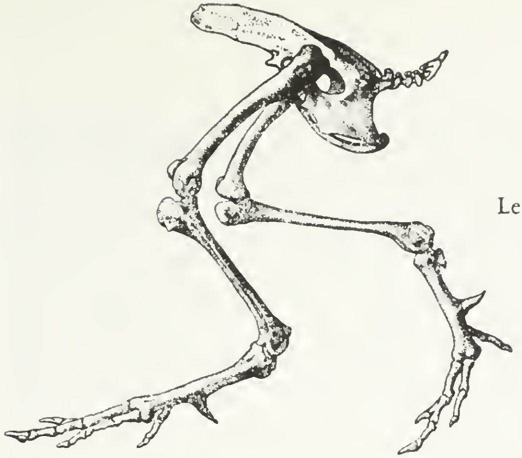
by C. H. Waddington

IT IS HARDLY TOO MUCH TO SAY that the whole science of biology has its origin in the study of form. The foundations which support the elaborate superstructure of modern experimental work—the description of living things, the anatomising of them into separate and discrete organs, and the comparison of related types which led to the development of the theory of evolution—are all essentially concerned with the shapes assumed by the living organism and its parts. Thus all biologists, in their elementary training even if not in their later more specialised interests, have been immersed in a lore of form and spatial configuration. Most of them would probably admit that there is some general character which pervades the whole realm of organic form. If one found oneself walking along the strand of some unknown sea, littered with the débris of broken shells, isolated bones, and odd lumps of coral of some unfamiliar fauna, mingled with the jetsam from the wrecks of strange vessels, one feels that one would hardly make any mistakes in distinguishing the natural from the man-made objects. Unless the churning of the waves had too much corroded them, the odd screws, valves, radio terminals, and miscellaneous fitments, even if fabricated out of bone or some other calcareous shell-like material, would bear the unmistakable impress of a human artificer and fail to make good a claim to a natural origin.

What is this character, which the naturally organic possesses and the artificial usually lacks? It has something, certainly, to do with growth. Organic forms develop. The flow of time is an essential component of their full nature, and the spatial objects we can hold in our hands and examine, with eyes or microscope, during a short few minutes is only a single still out of a continuous sequence of forms which continuously unfolds, sometimes quickly, sometimes more slowly, throughout the life of the organism of which it is a part. All scientific consideration of organic form must start from this point. Science is essentially concerned with causal relations; and causal relations cannot be expressed unless there is change. It is therefore in the changes of form—during individual development, during evolution, or under the influence of function—that the biologist is mainly interested.

It is not, however, the change of organic form which, at our present level of technique, is the prime feature for those who observe it from a non-analytical point of view. When, or if, the cinema becomes the most important technique of artistic creation, and movement one of the fundamental raw materials out of which beauty is created, then, perhaps, we shall have to turn our attention to the aesthetic characteristics of the developmental processes. At present, there is interest enough to be found in the instantaneous objects, frozen at some moment of their developmental career, in the bone or shell whose growth is arrested by the death of its owner, or the living creature snap-shotted while about the business of its living. How do such shapes compare with those of machines, or of painting or sculpture?

In the first place, the forms of living material have some quality of completeness. There are no ragged edges, nothing obviously lacking or merely and irrelevantly added. The form is, to use the embryological word, "individuated"; it is a recognisable individual whole. This is most fully true of the form of the total living entity. A skeleton from which the shin bones and feet had been removed at the knee could not be a completely individuated form, since the knee-joint end of the thigh bone comes to no natural termination; it is like a tune which breaks off in the middle. But by the same token any natural division of the body, such as an isolated thigh bone, has a certain degree of completeness, though one which carries some implications about the other parts to which it is attached, as one phrase out of a tune



Legs and pelvis of a goose.

implies something about the rest of it. It is for this reason that we can call such natural parts organs.

The quality which we recognise as organic wholeness—individuation—is the symptom and expression of an underlying order; an internal order which endows the organ with such unity as it possesses and an external order which relates it to the rest of the organism. Crystals, among inorganic forms, are also pre-eminent in the possession of an internal order. But they are distinguished from organic forms in that they are ordered according to a single or very few relations. Each unit is composed of atoms arranged in a definite and specific way according to their mutual attractions and repulsions, and the units, grouped in some simple relation of symmetry, are repeated indefinitely to build up the crystal, which is, as it were, the solution of a single equation. Organic forms must be compared to solutions of a much more complicated system of simultaneous equations. The forces which hold the elementary parts in a certain orderly relation to each other are not derived from the affinities of just a few kinds of units, but arise from the interactions of very numerous active entities. Only in the simplest unicellular organisms do we commonly find some approximation of organic form to the simplicity of crystals, systems of bubbles, or other relatively pure mechanical arrangements. Most organic forms are built up from very many cells, each of which contains and is controlled by a whole host, several hundreds at least, of hereditary factors.

Again, man-made mechanical forms, such as screws, cogs, propellers, are usually designed to serve one single function, or at most two or three, and their unity is correspondingly blatant and single-minded. The requirements of general living, for all but the simplest animals, cannot be reduced to performance of any one series of actions. The shape of a limb-bone has to be adapted to walking, running, jumping, sitting, leaping sideways or backwards, and this multiplicity of actions requires it to have a more subtle and less immediately perspicuous unity. It is only in those human artefacts whose form, perfected over centuries, is designed to be an appropriate extension of the human or animal body or to meet the exigencies of some ever-variable medium such as the sea—in the handle of a scythe, the saddle of a horse, or the hull of a boat—that we meet an approximation to the character of the natural forms of life.

Organic form is, then, the resultant of the interaction of many different forces. The wholeness of the form indicates that this resultant is always in some sense an equilibrium. The internal tensions are balanced against one another into a stable configuration—or rather, nearly balanced, since the configuration is destined slowly to change as development proceeds.

But it is not this slight degree of ill-balance which strikes us, not the remaining elements of arbitrary and unresolved peculiarity, but rather the connectedness and unity. It is instructive to compare the character of the variations from the ideal form in an organic and in human creation. The shell of the minute unicellular organism *Aulonia hexagona* is one of those animal structures whose functions are simple enough for it to approximate to a simple mathematical figure, that of a sphere covered by almost regular hexagons (Fig. 1). It will be seen that the hexagons are in practice not quite regular; they do not make up a rigidly defineable pattern, but rather a rhythm, in the sense of Whitehead, who wrote: *"A rhythm involves a pattern, and to that extent is always self-identical. But no rhythm can be a mere pattern; for the rhythmic quality depends equally upon the differences involved in each exhibition of the pattern. The essence of rhythm is the fusion of sameness and novelty; so that the whole never loses the essential unity of the pattern, while the parts exhibit the contrast arising from the novelty of their detail.

**The Principles of Natural Knowledge.* Cambridge 1925, p. 198.

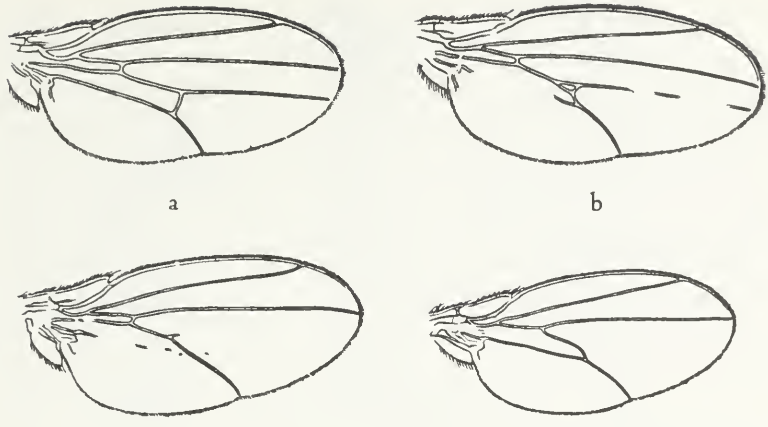
A mere recurrence kills rhythm as surely as does a mere confusion of detail".

Look, again, at the fragment of bone from a vulture's wing (Fig. 2), which D'Arcy Thompson rightly compares, in the mechancial principles which it exemplifies, with a Warren's truss, a well known engineering construction. The natural form deviates somewhat from the rigid repetitive pattern of a man-made steel structure. Some of these deviations are, as D'Arcy Thompson also points out, improvements on the normal form of the truss, since by being arranged in three instead of merely two dimensions they stiffen it laterally as well as vertically. Other departures from the regular pattern are less functional, chance variations in thickness or angle; but they are not completely arbitrary, a variation affects a member as a whole, the diagonal strut leading upwards to the left, just near the middle, is thickened throughout its length, and its junctions with the over and underlying horizontal bones are correspondingly solider. Each variation is, we may observe, resolved and brought into harmony with the whole.

Compare with these two examples an unsophisticated human product, a native textile decoration from Nigeria (Fig. 3). There is again a basic pattern, which is given with variations; but here the discrepancies and irregularities seem merely fortuitous. The lines waver, even within each unit. We are approaching, not a variation of elements each of which is internally controlled and resolved, but Whitehead's "mere confusion of detail".

We come then to conceive of organic form as something which is produced by the interaction of numerous forces which are balanced against one another in a near-equilibrium that has the character not of a precisely definable pattern but rather of a slightly fluid one, a rhythm. It is perhaps easiest to appreciate the character of forms of this kind by considering some of the variations which may be produced when the normal balance of forces is upset. The genes, or hereditary factors which are contained in each cell, are the most important determinants of the developmental processes, and, since abnormal or "mutant" genes are known, we can observe the structures which arise when the normal delicately adjusted complexes of genes, selected during evolution because they produce a well-equilibrated development, are altered by the introduction of such a foreign element. One example is shown in Fig. 4, which shows the wings of the fruit-fly *Drosophila*. The introduction of a mutant gene, *cubitus interruptus*, causes breaks in the third and fourth longitudinal veins, counting from the top downwards. The resulting pattern gives an impression of incompleteness, of disequilibrium; and indeed we find that it is highly variable, as between different individuals, and even between the two wings of the same fly. A slightly different mutant gene, *cubitus interruptus Wallace*, tends to produce larger breaks, and here the veins may assume a configuration which, although different from the normal, nevertheless appears more inherently stable (Fig. 4*d*). One would not be too surprised to find that natural selection had seized on a pattern like this, and stabilised it as the normal form developed in some other species of fly related to *Drosophila*, but it would be more unexpected if one of the unresolved variants of Figs. 4*b* and *c* were to be so singled out and equilibrated. Again, the legs of the same animal usually end in a series of five tarsal segments, whose relative lengths vary rather little; and there are some mutant genes (such as *aristopedia*) which merely disrupt the normal balance, producing irregular, variable, and "unnatural" legs, while others (such as *dachs*) cause the appearance of a new pattern, four-jointed, regular, and more or less invariable legs, which might well be natural, although they do not actually occur in wild strains of the fly, but are known only in the laboratory.

In organs of more complex form, the natural qualities of equilibrium, of internal resolution of conflicting forces, may be more difficult to recognise. Fig. 5*a* shows a normal thigh bone of a mouse, Fig. 5*c* is a rather extremely abnormal one from a mouse bearing the mutant gene *luxate*. Probably any biologist with some familiarity with bones would be able to say that the latter must be an abnormality and could not be a part of the normal skeleton of some species unknown to him; its knobbly, uncertain lumpishness betrays it. But Fig. 5*b*, which is also from *luxate*, though a less extreme one (note the variability of these unequilibrated types) is more deceptive; a practised anatomist would suspect it of being "pathological"; but those not versed



a b

c d

FIG. 4. Wings of the fruit fly *Drosophila*. *a* is normal, *b*, *c* in the mutant type *cubitus interruptns*, *d* in the mutant *cubitus interruptus Wallace*.

in this particular vocabulary of form might allow it into the category of normal biological structures.

It is interesting to enquire how far the special qualities of organic form, which have been described above, have been realised in the works of artists. The development in recent years of abstract sculpture and painting allows one to examine aesthetic forms unprejudiced by the complicating requirements of representation. In my opinion certain of these works have a "biological" quality; they might conceivably be bones of some unknown animal, patterns on a butterfly's wing, or the hide of that romantic Swiss Family Robinson beast, an animal unknown to science, while others lack this particular character. Not that they are necessarily any the worse for that, as works of art; there is no reason why an abstract creation should be modelled on even the most general laws of organic nature.

Consider, from this point of view, the Picasso drawing (Fig. 6), which is a project for a monumental piece of sculpture, which, in the optimism of the 1920's, the artist would have liked to have seen erected along the Croissette at Cannes. It bears a superficial resemblance to an articulated series of bones; but it lacks altogether the quality of a skeleton, either in the nature of the articulations

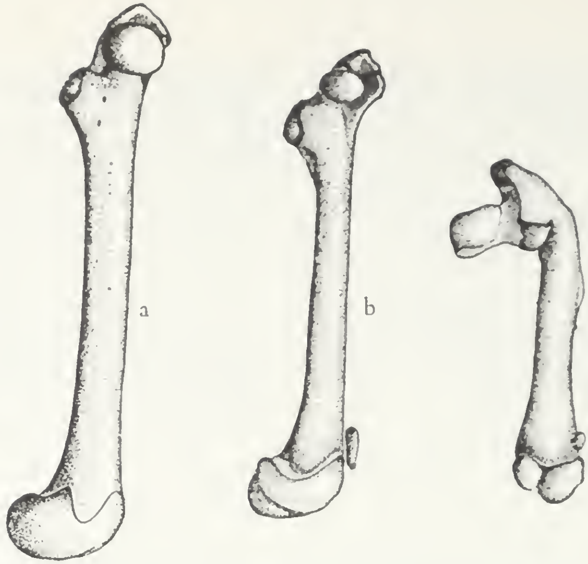


FIG. 5 Thigh bones of mice: *a* normal, *b* and *c* in the mutant type *luxate.*

or in the details of each separate element. The rods are too simply rod-like, the sphere too spherical, the cone with its prolongation has no internal logic of its own, and the large block at the bottom right introduces another type of form which needs to be distinguished from the organic, although the distinction is not always easy. It is a typical pebble. That is to say, a mass which has been moulded, like an organic one, by a very large number of forces, but in this case by forces which are external and unco-ordinated. It represents not the equilibration or balancing of many conflicting tendencies, but the chance outcome of a series of random and unrelated events; in fact, Whitehead's mere confusion of detail. But there is a complication here. If the number of detailed events is large enough, and if they are all of approximately the same magnitude, a certain statistical regularity will emerge, and there will be a tendency for the production of some reasonably definite shape, which may perhaps simulate an organic shape produced by an internal equilibrium. Thus the artistic developments of the pebble form may be very similar to those derived from a knee-cap or knuckle bone.

Usually, however, the organic character or the pebble character are fairly easy to distinguish. The two forms of Moore's ironstone Sculpture of 1934 (Fig. 7) are clearly inscribed pebbles. The general form of the Cyclades Idol (Fig. 8), on the other hand, might well be that of a bone, at least in side view, although the front view, which is not reproduced here, shows that the junction of the neck and body is too abrupt, and the depression separating the legs too sharp, to be altogether natural. But the curves and ridges of its profile flow into one another as though controlled completely by their own internal logic of construction, and look as though they might well endow the form with a particular fitness for some function or other; whereas the swelling undulations of Moore's surfaces appear related in an aesthetic, but not in a constructional or functional manner.

In some other examples of Moore's abstract sculpture, an organic quality is much more apparent, as it is in much of Barbara Hepworth's. In the double construction, carved in wood (Fig. 9), with a pierced form leaning over a smaller oval, there is to my eye the implication of internal tensions balanced and resolved which allies it with such a shape as a kidney. This is absent from, for instance, Brancusi's Leda (Fig. 10), which seems to be derived neither from the pebble nor the organic, but to be a wholly human conception. Again, of the two works by Arp (Figs. 11 and 12) the Torso might be a self-sufficient biological form, a bone or other solid organ which can maintain its shape, while the Concretion Humaine could only find a parallel in the living world if we looked among the semi-fluid structures whose shape is largely determined by the external forces acting at the moment.

Primitive man was surrounded by organic forms. So nowadays is the agriculturalist or anyone who lives in the country. It might be expected that the specific biological character would impress itself by mere familiarity on artists who lived in close contact with nature, and would be particularly apparent in their works. But it is only to a slight extent that this is true. The most primitive paintings of the European Stone Age and of African Bushmen indeed often express the qualities we have been describing, but most folk art lacks them. Man, it seems, when he begins to create, is usually more single-purposed than living Nature. The inner logic of his constructions is simpler; or he is concerned more with an externally imposed logic, of representation or symbolism. There is, in a human work of sculpture, no actual multitude of internal growth-forces which are balanced so as to issue in a near-equilibrium of a rhythmic character. We should therefore not expect that works of art will often arrive at the same type of form as we commonly find in the structures of living matter. Much more can we anticipate an influence of man's intellectualising, pattern-making habit of simplification, diluted perhaps by an intrusion of unresolved detail. Only the extremely simple, or the extremely sophisticated, are likely to stray into the realm of form which is the proper outcome of the blind but complex forces of life.

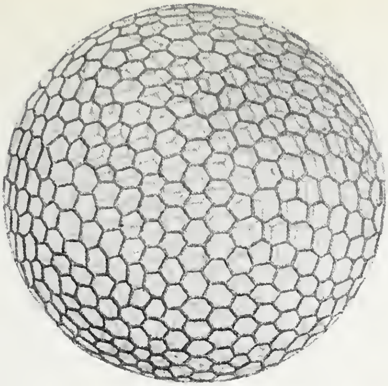


FIG. 1 The shell of the minute Radiolarian, *Aulonia Hexagona*

FIG. 2 (*below*) Bone from a vulture's wing, to show internal structure

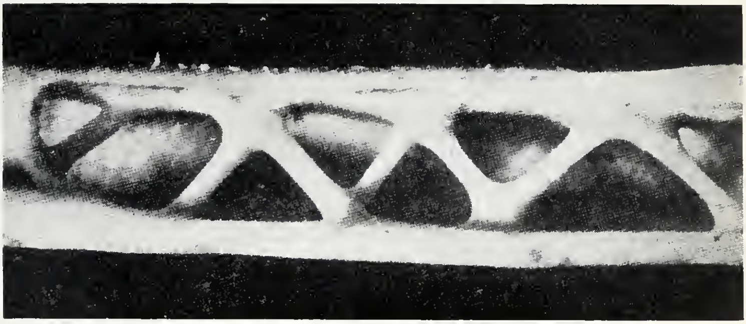
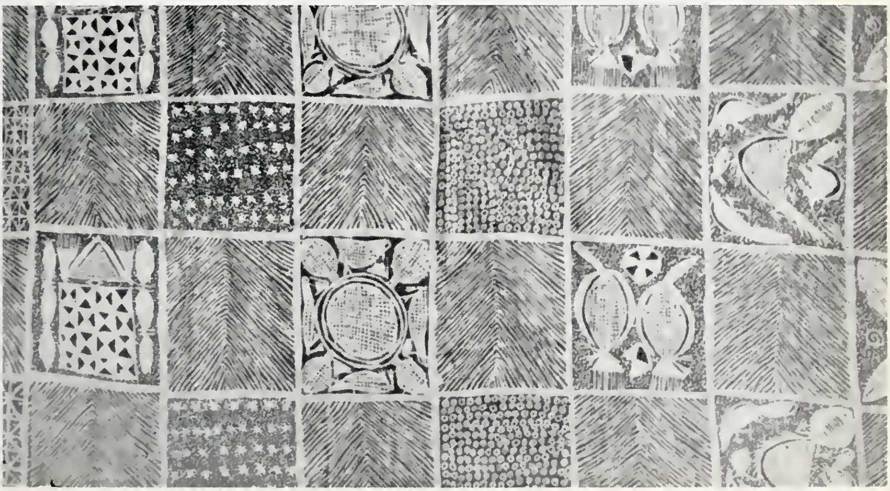


FIG. 3 Native dyed textile from Nigeria



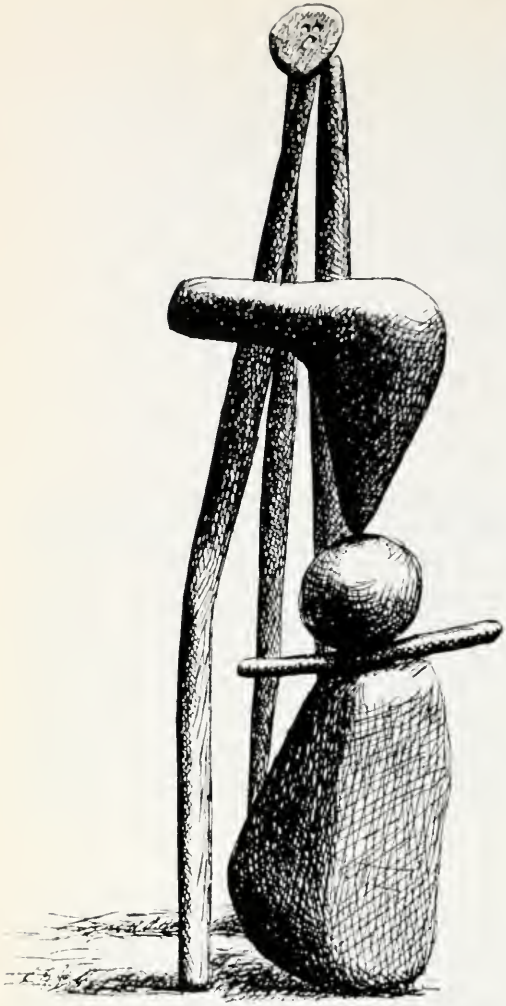


FIG. 6 Project for sculpture by Picasso from *Cahiers d'Art* 8–9, by courtesy of Christian Zervos

FIG. 8 (*right*) Idol from the Cyclades from *Cahiers d'Art* 6, by courtesy of Christian Zervos

FIG. 9 (*above*)
Sculpture by Henry Moore

FIG. 7
Two forms, by Henry Moore

FIG. 11 (*left*) Torso, by Arp
FIG. 12 Concretion Humaine, by Arp

FIG. 10 Leda, by Brancusi
(by courtesy of Miss Katherine S. Dreier)

Form in Plants *by F. G. Gregory*

The appearance of symmetry is an invariable characteristic of growth whether it be of a living or non-living system; this is true both of the simpler organisms consisting of single cells and of higher organisms composed of multitudes of such cells. We recognise this symmetry as the characteristic shape of the living organism, and this feature is so constant that it enables us to classify the myriads of living organisms into a comparatively few species; and so enduring is the shape that successive generations of individuals covering vast periods of time may remain substantially unchanged. It must be stressed that the external form of the organism bears no relation to the form of the individual cell, but is dependent upon the mode of aggregation of cells in the tissues and organs.

The study of form in organisms goes by the name of Morphology, a term introduced into biology by Goethe in 1827. He regarded plants as variants of an "archetypical" form, his "Urpflanze" consisting of an axial structure (the stem) bearing lateral appendages, the leaves. Development he regarded as a reiteration of successive parts, thus a "time pattern" constituting the life history of the plant, in the course of which modifications of the fundamental repetitive unit occur—essentially a "metamorphosis" of the leaf culminating in the organs of the flower, which Goethe regarded as modified leaf structures. It is not easy in post-Darwinian days to recapture the notion of the archetype in its essential simplicity; what to us appears artificial is the divorce of a pure form or shape from any functional consideration. And yet the notion of a pure morphology exerted a powerful influence over biological thought in the early part of last century. The morphological categories of leaf, stem, and root were generally accepted, and the notion of metamorphosis was transferred from the purely abstract realm to the realm of reality, in that the functional aspect of the plant organs became the dominant consideration. The categories of leaf, stem, and root of the higher plants are the seats of essential functional activities; thus the leaf syntheses organic constituents of the plant; the stem tissues conduct the essential materials, water and nutritive elements, to the leaf and translocate the final products to the various parts of the plant, and in addition provide the mechanical support for the effective display of the leaves to light and air; the root absorbs nutrients and water from the soil and provides the necessary anchorage for the plant.

Regarded functionally the various plant parts are organs consisting of tissues composed of cells all engaged in specific activities. From the morphological standpoint the category to which an organ is consigned is determined by its spatial relations to other organs, although the function may not be that usually attributed to the organ in question, e.g. the leaf may be reduced to a vestige and the stem carry out photosynthesis. Such functionally substituted organs are regarded as "analogous", whereas two organs such as a tendril and a normal leaf similarly situated but diverse in function are "homologous". Comparative morphology concerns itself with such considerations, and its formal nature is self-evident. From the functional standpoint the pre-eminent rôle of the leaf is justified in view of its synthetic activities.

The most obvious function of the plant, however, is growth, and it is not possible to discuss the origin of the symmetry of plants without enquiry into this fundamental process. Plants, in common with all organisms, can originate from a single cell resulting from a sexual union. By a process of cell division the fertilized egg cell gives rise to an embryo (in the higher plants enclosed in a seed) in which the "growing points", later to develop the aerial and root portions, are determined from the outset. These localised centres of growth in the plant persist as "meristems" at the apex of the stem and its branches, and of the root. At the junction of the leaf stalk with the supporting stem further localised centres are laid down as buds, from which branches may develop. The plant thus differs from the animal in that these localised regions (meristems) persist in the embryonic condition throughout the life of the plant. The final form of the plant thus does not arise by a process of "folding" of cell layers as in the animal embryo, but by a continual production of appendages within growing points. Multiplication of cells in the meristems goes on without intermission, and thus reproduction is the essential feature of plant growth. Normally the process of cell division in the various organs ceases at an early stage, indeed at the time when new leaves are unfolded from the bud division of the cells is reaching completion, and the very rapid increase in size which subsequently occurs is due to extension growth of the individual cells already formed. Normally in the mature organ cell division permanently ceases, but it is characteristic of most plants that by removing a portion of organs a "wound reaction" occurs, whereby the cells undergo a process of rejuvenation and "de-differentiation" and cell division again begins, and the wound is healed in the case of the injured leaf, or as in the case of the stem or root a new "growing point" may be organised, and the whole plant re-established. It is clear therefore that "regulating factors" must exist in the intact organ maintaining an equilibrium between the various cells and inhibiting further division. The capacity for isolated portions of the plant body to regenerate when supplied with the necessary nutrients and growth regulating hormones is the basis of the method of tissue culture, whereby the factors concerned in the establishment and maintenance of the organised structure of plants are being studied.

The symmetry of the structure arising from the division of a single cell will clearly depend upon the direction of cell divisions. These may be confined to a single dimension yielding a thread structure found in many of the algæ (fresh water and sea weeds) and generally in the fungi (moulds); to two dimensions leading to the formation of a frond (thallus); or to three dimensions. In the last case the resulting structure will depend upon the relative number of divisions occurring in the different spatial directions, and the final form of the plant or organ may be approximately spherical as in some succulent plants. If two directions predominate a frond-like structure results as in normal leaves; or a cylindrical structure as in stems and roots.

In the growing points the cells are all of extremely minute size and the cell divisions occur in all three directions except in the surface layers which constitute a true epidermis. In many of the lower plants (ferns, horsetails, mosses, and liverworts) the meristem is dominated by a single apical cell which may be of a pyramidal or lenticular shape, and in such cells divisions take place in regular succession parallel to the faces, and the new cells thus formed add to the mass of dividing cells in the growing point. The rate of cell division is however not everywhere the same in the meristem, but at discrete regions of the meristem the rate of division is greater than the average, and at such points swellings arise laterally and these become the rudiments of the leaves. It is important to note that the final arrangement of the leaves on the stems is determined by the spatial arrangement of these localised areas in the growing points, and this symmetry of leaf arrangement is one of the characteristic features of plant form. It needs stressing here that in those cases in which a single apical cell exists the symmetry of leaf arrangement is not related directly to the symmetry of this cell.

The form of the plant apparent to the eye is determined in the main by the following factors: the size and arrangement of the leaves, the degree of development and branching of the stem. Contrary to the speculation of Goethe on the fundamental status of the leaf the evidence of fossils indicates that in primitive plants the leaf was subordinate to the stem; indeed in the earliest land plants it appears probable that no leaves at all were present. The tree-like plants from the coal measures were all small-leaved types, the stem being densely clothed with leaves as in the modern club-mosses, their diminutive lineal descendants; or with whorls of comparatively small leaves as in the modern horsetails. These plants were none the less true trees with well developed woody stems increasing in girth by addition of "annual rings" arising from a persistent embryonic region of the stem, the cambium, as is found in modern trees. Only with the ferns did the large leaf type of plant appear, and in these plants, which may reach very large size (tree ferns), there is no cambium in the stem so that no increase in girth (secondary thickening) can occur. This columnar structure is found also in the modern palms which again have large leaves, and also are without massive development of wood and show no increase in girth, as these plants are also devoid of a cambium. The predominant development of the stem, with dense clothing of leaves or leaf bases, give the archaic appearance to such plants as the monkey puzzle (*Araucaria*) and is in fact a primitive characteristic.

The tree, including shrubs which are in fact diminutive trees, is thus characterised by the massive stem development with compact woody structure which supplies the needed mechanical rigidity to carry the wide spreading crown of leaves. As the leaves are individually small, profuse branching is needed to expose a sufficient area of leaf surface to the light. The characteristic form of trees, easily identifiable when bare of leaves, is due to the degree of branches of various orders which are produced. The branches arise from buds on the main axis and assume various characteristic angles, attaining in different species varying degrees of development relative to the trunk.

The plant body thus consists of a series of axes each terminated by a centre of growth, and bearing along its length a series of subsidiary meristems, which may grow out and repeat the pattern of the main axis or may remain dormant, unless the growing point of the main axis is destroyed. Meristematic regions may also occur at regular intervals along the stem and their activity leads to the production of jointed stems as in the bamboo and other grasses.

The plant differs from the animal in the great variation of form encountered in plants of the same species. Since the whole process of development is dependent upon multiplication of cells in the meristems and their subsequent extension growth factors affecting the rate of multiplication of the cells or their rate of extension must inevitably affect also the form of the plant. Such factors may be associated with the environment (external factors) or are inherent in the plant itself (internal factors).

The effect of external factors

Of the external factors the most important are water supply, light, and temperature. Water is essential for the enlargement of the individual cells, and thus plants inadequately supplied will tend to remain stunted. Plants adapted for existence in arid regions display striking modifications in form: the leaves may be much reduced so that the blade is represented only as a woody midrib and appears as a thorn, so well seen in the cacti and euphorbias of desert regions. In these cases the function of the leaf is taken over by the stem or leaf stalk which may become flattened and leaf-like; a familiar example is the butcher's broom (*Ruscus aculeatus*) in which the apparent leaves are flattened shoots subtended by minute leaves. Alternatively the stems become approximately spherical with well marked ridges to increase the surface exposed to light. In some cases, as that of the gorse, when grown in a humid atmosphere the spines normally present revert to more normal leaf form. The tendency to spherical or cylindrical forms of stems and leaves may also be induced by high salt content of the rooting medium, as in the case of salt marsh plants.

Plants growing in shallow water may display two types of leaves (*heterophylly*), as for example the "Arrowhead" (*Sagittaria sagittifolia*), in which the submerged leaves are strap-like and the aerial leaves arrow-shaped. Experiment has shown that in some plants displaying heterophylly the effect is due directly to the influence of water on the terminal growing-point, for if the extreme apex alone is kept above water the leaves laid down are of the aerial type (entire blades) though they expand under water, whereas if the apex is covered with water the much divided submerged type of leaf only is formed. Modification of leaf form in many of these amphibious plants can however also be induced by varying the quality and intensity of the light; in red light the submerged type may be formed in air, whereas blue light always induces the aerial form.

Four characteristics of light exert direct effects upon the form of plants: intensity, quality, duration, and direction. When grown in complete darkness the form of plants of the most diverse kinds is completely transformed; this phenomenon of etiolation is associated in green plants with the absence of chlorophyll so that the plants are entirely devoid of green colour and are thus incapable of synthesis of organic substances. It is not the lack of nutrients however which is the immediate cause, for when tubers such as the potato rich in storage material are allowed to germinate in darkness the typical symptons of etiolation appear. Under these conditions rapid extension of the stem occurs, but in the absence of any mechanical tissues this growth is very weak; meanwhile the leaves remain undeveloped. The flowering plants (*angiosperms*) fall into two classes in this respect; the *monocotyledons* (grasses, bulbous plants, etc.) in general in darkness are capable of expanding their leaves, which indeed are longer but narrower than normal, whereas the *dicotyledons* (with few exceptions) show arrest of leaf expansion in darkness. It is interesting to note that in the former class, plants with long narrow leaves having parallel venation, these grow by a meristem at the base of the leaf, which is either below ground or enclosed in the sheaths of older leaves, whereas in the latter class the young leaf is fully exposed to light when the bud opens. In darkness the leaves remain in this stage of development unless exposed to light. A very short exposure to light (1/5th sec.) is sufficient to begin the process of leaf expansion which has been shown to be due to the stimulation of cell multiplication by light. In certain monocotyledons with net-veined leaves (thus resembling dicotyledonous leaves) expansion does not take place in darkness, but the stem or leaf stalk elongates excessively. The cause of this difference in behaviour of the two classes of flowering plants is not known.

.The excessive elongation of the stem in darkness is seen even in plants such as the "house leeks" in which the stem is normally so telescoped that the crowded leaves constitute a rosette. In darkness the leaves are reduced to minute scales on the elongated stem. Plants with flattened leaf-like stems revert to radial symmetry in darkness.

With increasing intensity of light the etiolation symptoms give place to normal form, though for each species an optimum intensity exists (its level however depending upon the prevalent temperature) beyond which injurious effects occur associated with destruction of the chlorophyll. The red end of the spectrum (6000—6500Å) is primarily concerned with leaf expansion with a less effect in the blue (4000 Å); all other wave-lengths are ineffective.

The effect of duration of light and darkness in the daily cycle of day and night expresses itself mainly in the onset of the reproductive phase of the life cycle with the appearance of flowers and other reproductive organs. Three types of plants can be distinguished: those requiring no dark period or short dark periods (long day plants); those requiring long dark periods which fail to flower above a critical day-length (short day plants); and those which are indifferent to day-length and merely require a minimum of total light energy. In general flower induction is due to the longer wave lengths, with a minor effect in the blue, though some plants (*Cruciferaw*), appear to be more sensitive to blue than red light.

Here it should be mentioned that the formation of storage organs such as tubers of the artichoke, found on modified underground stems, is much encouraged by long dark periods, i.e. short days.

The direction of light as a formative factor is associated with the unsymmetrical illumination of the tissues, resulting in unequal distribution of extension growth and the consequent bending of the plant or organ either towards or away from the source of light (*phototropism*). The wave-length of the light is again important, but here it is the blue end of the spectrum which inhibits extension growth. The leaf in general tends to assume a posture at right angles to the direction of light, thus securing maximum illumination, and this is achieved either by transmitted effects leading to curvature of the leaf-stalk, or to variation in the angle of posture of the blade by flexion at the junction with the leaf-stalk. In regions of very high light intensity the leaves of some plants on the other hand assume a vertical posture. Such changes of posture are secured by local variations in the turgor of the tissues, similar to the so-called "sleep posture" of leaves.

So far as temperature is concerned the rate of cell multiplication is largely controlled by this factor, and many of the effects of light, particularly of duration of light, show complex interactions with the ambient temperature.

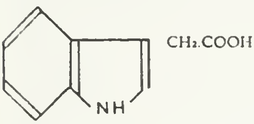
The formative effects of temperature have been studied exhaustively in connection with the temperature of storage of bulbous plants, in which both the subsequent vegetative growth and the flowering may be radically affected. Thus storage of the bulb of the hyacinth (Queen of the Blues) at a temperature of 35°C for five to eight weeks in July followed by a lower temperature (18°C) until planting, leads to the maximum development of leaves in the following spring, this being due to the increase in the number of cells formed in the growing point at this temperature. At this temperature of storage, however, inflorescence formation is entirely prevented, and a similar result is obtained by storage below 13°C—only within this range of temperature does flower formation occur with a marked optimum around 25°C. This is a striking example of an "after effect" of an environmental factor. Even more striking is the phenomenon of vernalisation in which the subsequent time of flowering of winter varieties of cereal plants is determined by the temperature prevailing during germination of the grain. Unvernalised grain of winter cereals (germinated above 10°C) when planted in the spring fail to produce ears, whereas the fully vernalised, by maintaining the germinating grain to temperatures near freezing point, produce ears at the normal time. Duration of day-length plays a part in this phenomenon also, for with continuous light even unvernalised grain comes into ear. Even more remarkably, if for the first six to eight weeks at the start of growth short days are given, followed by normal summer day lengths, flowering is much hastened. Similarly effects of low temperature have been found in the Chrysanthemum and the henbane (*Hyoscyamus niger*) on the time of initiation and development of the inflorescence, but whereas in the henbane and the cereals the effect of low temperature can be reversed by immediate exposure after cooling to high temperatures—this is not so in the chrysanthemum. The unvernalised cereals sown in spring retain throughout the summer the "rosette" habit, the elongation of the stem failing to occur; the appearance of the plants is thus very much changed.

The effect of internal factors

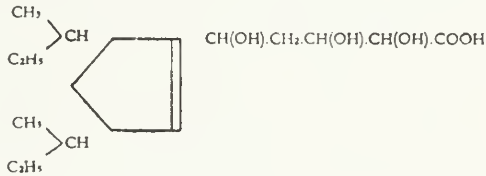
A regular sequence of leaf form is very often found during the development of annual plants or within the annual cycle of perennial plants. The later formed leaves are generally larger and more complex in form. The first leaves formed on the embryo (*cotyledons*) are often modified as storage organs and fail to expand into normal leaves. In plants, such as some species of acacia, in which the leaf blade is suppressed and its function taken over by the flattened leaf-stalk, the first formed leaves are of the usual pinnate form. The transition from the vegetative to reproductive phase is generally accompanied by a reduction or simplification of leaf form, and the floral organs (*carpels and stamens*) although of foliar origin show, except in abnormal cases, no obvious resemblance to leaves.

As long ago as 1865 Sachs postulated a mechanism controlling organ development depending upon the formation of specific substances—thus he postulated specific leaf, stem, root, and flower-forming substances. At the time this was dismissed as idle speculation, but the discovery of hormones in animals and their far-reaching effects on development has led to a search for hormones in plants. The recognition of the most important growth regulating substance in plants and its final isolation has been the culminating point of over a hundred years of research. It was the effort to analyse the reactions of the oat and other grass seedlings to light and gravity which led to this triumphant conclusion. In the grasses the cylindrical first leaf to appear above ground, enclosing the stem growing point, and known as the coleoptile, is particularly sensitive to light and gravitational stimuli, executing bending movements. These were early attributed to differential extension growth of the two flanks of the organ. By removal of the extreme tip all response ceased so that very soon its predominate rôle as receptor of the stimulus was recognised. It was also shown that removal of the tip led to cessation of growth of the organ, and further that the effect of the tip could be transmitted to the lower extending region through a layer of gelatin.

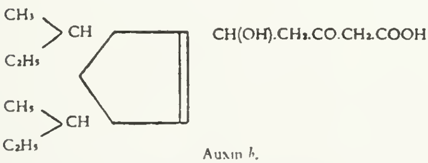
Went in 1928 finally proved that an active substance could be collected by diffusion from the tip of the coleoptile into gelatin, and a portion of this gelatin then acted like the normal tip when placed on a decapitated coleoptile. Placed symmetrically on the stump, straight growth of the organ was resumed but when placed on one side bending took place due to greater extension growth of the flank below the artificial tip. First attempts to extract the active material from coleoptiles failed owing to the extremely small quantity present. It has been estimated that one milligram of the pure substance would occasion a curvature of 10 degrees in 50 million decapitated coleoptiles. However, from the rate of diffusion in gelatin, Went concluded that the molecular weight was not much greater than that of cane sugar. Growth-regulating substances were first isolated and characterised by Kögl who extracted two substances from urine. One of these "heteroauxin" was found to be indole-3-acetic acid ($C_{10}H_9O_2N$, molecular weight 195) and identical with a growth-regulating substance first obtained from the medium on which the mould *Rhizopus suinus* had been grown. The second substance obtained from urine is Auxin *a* (auxentriolic acid, $C_{18}H_{32}O_5$, molecular weight 328). A third substance, Auxin *b*, was isolated from malt and maize oil and other vegetable oils. It is very similar in structure to Auxin *a* ($C_{18}H_{30}O_4$: molecular weight 310). The structural formulæ of these "auxins" are shown below.



Heteroauxin



Auxin *a*.



Auxin *b*.

The activity of all three substances is primarily concerned in extension growth of the cell. Thimann has elucidated the relation of the activity of these substances to their structural configurations. The five membered ring is common to all, and the presence of the double bond in proximity to the side chain is essential. The side chain needs to comprise at least two carbon atoms. The molecules from their structure are of a strongly polar character and would therefore tend to orientate themselves as monomolecular films at cell surfaces. A very large number of synthetic substances have now been prepared which behave similarly to the naturally occurring auxins, and have found wide application in horticulture and agriculture, some in the propagation of cuttings, others as weed killers.

The behaviour of the auxins in growth regulation is of immediate importance here. The quantitative method of biological assay devised by Went using the angle of bending of the oat coleoptile as index has enabled the distribution of auxin in various plant organs to be assessed. It appears that wherever rapid growth is occurring auxins are present in stems, leaves, and roots. By extraction of the growth substances in organic solvents (sometimes in water), first employed by Thimann, their wide distribution has been proved. In the plant gradients of auxin concentration have been shown, the maximum occurring either at the stem apices or immediately below in the region in which leaf expansion is actively taking place: thus distribution of the auxin corresponds with the spatial distribution of extension growth in the developing organs. The auxin is actively transported in the tissues of the plant at a rate of round about 1 cm. per hour, a much greater rate than could be accounted for by physical diffusion. The rate depends upon the temperature, reaching a maximum at about 25-30°C. At temperature above 35°C the auxin is rapidly destroyed. The most striking fact in auxin transport is that normally the tissues are "polarised", so that auxin readily passes from the apex towards the base but not in the reverse direction.

The tissues of the stem and roots also differ greatly in their sensitivity to auxins, for whereas in stem tissues maximum elongation occurs at a concentration around one part in ten thousand, this concentration will inhibit the extension growth of roots for which dilution must be increased a million times to obtain a stimulation. In this connection it is interesting to note that very little if any auxin can be obtained by direct diffusion from root tips.

The reaction of plants to light and gravity can to a large extent be explained by the action of auxins. In a stem illuminated from one side the tissues become "polarised" and auxin passes to the shaded side, and a similar movement occurs to the lower side of both stem and root tissues placed horizontally. In light, beside the active movement of auxin across the tissues a reduction in total free auxin is found indicating that light will destroy auxin in part. This effect has been attributed to two possibilities: with Auxins *a* and *b* a molecular change of structure occurs due to the formation of an inactive lactone. Auxin may also be destroyed by a photo-chemical reaction. This is due to the effect of short wave-length light, and as already stated the blue end of the spectrum is active in inhibiting extension growth. The energy of the light is absorbed by pigments either carotin or riboflavin and leads to photo-oxidation of the auxin.

The varying response of stem and root to gravity can also be explained by the movement of auxin. In the stem, where extension growth is accelerated by auxin, bending upwards will therefore occur by greater growth on the lower flank, whereas in the root the opposite effect occurs and bending downwards results.

Auxin has other effects also on plant growth. Thus, the buds other than the terminal bud are inhibited by auxin. The terminal bud thus exerts a dominant effect, the phenomenon of "apical dominance", which controls the branching of the stem. In a plant such as the sunflower in which no branching normally occurs, on removal of the terminal bud branches arise, but by replacing the absent bud by auxin this branching can be prevented. The normal shedding of leaves in autumn in deciduous trees is also explicable on the basis of auxin action. Thus if the blade of a leaf is removed the leaf-stalk is very soon shed by the activity of a special "abscission layer" normally found at the base of the leaf-stalk. This layer of cells, although present from the start, is not active until the day-length becomes reduced in autumn, and that its activity is controlled by auxins is proved by the fact that if the blade of the leaf is replaced by gelatin containing auxin the leaf-stalk is not shed. Keeping the plant in continuous light in autumn has a similar delaying action on leaf-fall.

Again, the activity of the cambium, the meristematic region of the stem responsible for the production of "annual rings" of thickening, is controlled by the auxin produced in the terminal buds. In the spring this activity of thickening begins in the end of all the branches and passes as a wave downwards throughout the plant to the roots. The posture of the leaves is also effected by auxin; with increased auxin supply the leaves bend downwards, assuming an even vertical position and it is probable that the angle between the branches and the main stem is controlled by an auxin mechanism. As already stated gravity affects the distribution of auxin in tissues, and the intensity of the gravitational effect depends upon the angle to the horizontal. A further effect of auxin is in the control of root production. Cuttings taken from the stem and planted in a suitable medium produce adventitious roots and this tendency can be greatly augmented by the application of natural or synthetic auxins: hence its use in propagation in horticultural practice.

Finally, auxin has been shown to lead to fruit formation even when normal fertilisation is prevented: in this way seedless tomatoes and other fruits have been produced.

It will thus be seen that auxin is concerned in both the process of cell multiplication and extension and is without doubt one of the regulating factors in plant growth. As our knowledge of the factors regulating the production of auxin in growing points increases no doubt our understanding of development in plants and the control of organisation will be greatly extended.

Auxins are by no means the only growth hormones which have been found in plants. Some of the vitamins which have profound effects on animal growth are produced by plants and these act as growth hormones. Thus the growth of roots is stimulated by at least three vitamins of the B type, namely thiamin (vitamin B_1); nicotinic acid; and pyridoxine (vitamin B_6).

It has been shown that the apex of the root removed from the plant can be grown in aseptic solutions of nutrient salts and sugar so long as the necessary growth hormones stated above are provided, and an isolated root system can be grown in this way. Plants differ in their requirements; thus whereas isolated roots of pea require thiamin and nicotinic acid, flax roots need pyridoxine in addition and nicotinic acid has no effect. In the tomato thiamin and pyridoxine are essential and nicotinic acid has a less effect. Evidently various plants differ in their capacity for producing these hormones.

The requirements of lower plants (*fungi*) differ from those of the higher plants; thus cultivated yeasts require beside thiamin and pyridoxine the addition of pantothenic acid and biotin. Among the fungi the requirements differ; the moulds (*Phycomycetes*) require thiamin only; some toadstools (*ascomycetes and basidiomycetes*) require also biotin. Thus *Polyporus adustus* is very sensitive to thiamin but can synthesise for itself biotin to the addition of which it will not respond. *Nematospora gosypii* (a parasite of cotton) responds to biotin alone and thus can synthesise thiamin. When grown together these two fungi thrive as they provide for each other the necessary hormones. In this way "symbiosis" can be established, a phenomenon occurring in nature and best exemplified in the lichens which are compound organisms consisting of the union of a fungus and an alga. Mention should also be made of "wound hormones" associated with the repair of damaged organs. One such hormone has been isolated and is known as traumatic acid of formula $HOOC \cdot CH = CH \cdot (CH_2)_8COOH$. Sach's original suggestion of specific organ-forming substances has thus been verified, but so far the evidence for a specific leaf-forming hormone is not very convincing. It has been suggested on experimental evidence that adenine and certain amino acids, particularly proline and asparagine, may be active in leaf-growth.

Auxin is certainly present in developing leaves but does not promote growth in mature leaves. Finally it should be stated that growth inhibitors have also been extracted from plants, and it appears probable that growth regulation is brought about by the mutual control of activators and inhibitors, but at present our knowledge does not carry us very far in the analysis of this regulation.

The facts presented certainly show that the categories of stem and root are absolute. By no means so far employed can the stem meristem be converted directly into a root meristem or vice versa, and this fundamental difference is established by the first division of the fertilised egg-cell. The polarisation of the tissues also establishes the reality of the upper and lower poles of the plant, and the varying sensitivity of the tissues of stem and root as shown in their reactions to light and gravity indicate a profound difference in their nature. Again the leaf is quite different in its hormone requirements from the stem and root tissues. All this lends support to the morpholigical categories established on quite other grounds.

The relation of form to reproduction

In the most primitive plants the slime fungi (*Myxobacteria*) there is no visible structure. They consist of a fluid which has no inherent form. When reproduction begins, however, a very definite structure appears, of very varied and sometimes complex nature, in which the spores are borne. Again in the fungi during the vegetative phase growth takes place by formation of branched threads (*hyphae*) so that the whole plant consists of an expanding circular mycelium on the surface of the medium. These threads show no response to gravity, though they may be affected by light, and certainly show growth responses to variations in concentration of nutrients. When reproduction is about to begin certain of the hyphae react to gravity and grow upwards. By a process of continual branching and inter-weaving the complex fructification is produced with a highly symmetrical structure with well defined stalk and spreading cap on the lower side of which the spores are borne on the gills. This organ now displays active responses to light and gravity, shows etiolation in darkness, and has marked powers of regeneration and healing when wounded.

In the mosses and liverworts and the remaining higher plants, two phases of the life history are found displaying entirely different symmetry. There are in fact asexual and sexual individuals, the former producing spores, the latter egg-cells (*ova*) requiring fertilisation. In the mosses, for instance, the germinating spore gives rise to a branching thread-like green plant (*protonema*) from which the familiar moss plant with stems and well developed leaves arises. This is the sexual generation (*gametophyte*) on which later reproductive organs are produced. The egg cell borne on this plant after fertilisation grows out *in situ* into the asexual generation (*sporophyte*) consisting only of a stem bearing a capsule in which spores are produced, thus completing the cycle. It is true that normally the asexual phase arising from the fertilised ovum has double the number of chromosomes in the nuclei of the cell as compared with the sexual phase, but this difference in chromosome numbers is not the cause of the difference in form. It has been shown that from the capsule by regeneration processes a new individual may arise which in form resembles the sexual generation although it has not the normal but double the number of chromosomes. Indeed by this means even further reduplication of chromosome numbers can be achieved without change in the form of the plant in either phase.

With all other plants this "alternation of generation" of sexual and asexual phases occurs, but now it is the asexual generation (*sporophyte*) which is the familiar plant with stem and leaf structure, whereas the sexual generation (*gametophyte*) is of much simpler construction—in the ferns, for instance, it is a small heart-shaped frond (*prothallus*) closely adpressed to the soil and bearing the reproductive organs. In the flowering plants the gametophyte is not capable of independent existence but is represented only by a few cells or even nuclei within the embryo sac. The flower is thus part of the asexual generation (*sporophyte*) and is in fact a specialised portion of the stem bearing modified leaves, some of which are green and leaf-like (*sepals*), some highly coloured (*petals*), and the sexual organs which are highly modified appendages.

Since we are concerned with problems of form it is not apposite to raise the question as to the presence of special sex hormones in plants, but since the flower and fruit display very characteristic differences in form from the vegetative parts, the question as to whether there are special flower forming substances as Sachs suggested must be mentioned. We have already seen that external factors, particularly daylength and temperature, exert control over the passage from vegetative to reproductive phases in the flowering plants. At the time when flower initiation takes place marked changes occur in the growing points. The flower consists of a modified stem apex, and the flowers may either be borne singly on the apex of the stem or in the axils of leaves, or a complex inflorescence of many flowers may be produced. A great variety in structure of these inflorescences appear depending upon the degree of branching of the inflorescence axes and their spatial relations, the relative developments of the main axis and of its branches, and the degree to which individual branches display limited or unlimited growth.

In the most primitive flowers the symmetry is radial, the organs of the flowers are spirally arranged on a much compressed axis, and large variations may occur in the numbers of the floral organs. In more advanced types the number of parts is greatly reduced and appear as whorls; concrescence of the organs also occurs to varying extents. Bilateral symmetry is very frequent and may be extreme, e.g. in the snapdragon. Functional modifications are found related to the mode of fertilisation, whether by wind or insects.

The origin of the symmetry in plants

The leaves are arranged on the stem in a spiral and generally are separated by internodes. In plants of rosette habit in which the stem is much compressed the leaves are crowded together, and in such plants a number of spirals are apparent running round the centre of symmetry in opposite directions. Such spiral lines are also very evident in crowded inflorescences such as the sunflower, and in the scales of pine cones. The number of intersecting spiral lines running in the two directions generally conform with two adjacent members of the series 1, 1, 2, 3, 5, 8, 13 . . . . the so-called Fibonacci series in which each member is the sum of the two previous members. In the apical bud of the stem, in which the rudiments of the leaves (*primordia*) are being formed, cut transversely the geometrical centres of the leaves in section again lie upon two sets of spirals running in opposite directions and conforming numerically with the Fibonacci series. This geometrical arrangement of leaves is called phyllotaxy. The leaf-primordia are formed (in the simplest case) in succession and under uniform conditions at regular intervals of time: this time interval is called a plastochrone, and is specific for different species of plants. In the interval between the formation of successive primordia the apical meristem continues its cell devisions and enlarges, and thus each successive leaf-centre in a transverse section is more distant from the centre of the system. The symmetry of the whole system is dependent upon the angular divergence between the points of origin of the successive leaf-primordia with reference to the centre of the system.

It has been shown by actual measurements on sections of buds that this divergence angle closely approximates to the mean value of 137.5°. In complex systems with many intersecting spirals, such as is found in sunflower heads with 34 and 55 members, the mean angle of divergence must not deviate by more than a few minutes of arc from this value of 137.5° if symmetry is to be maintained. This particular angle of divergence is capable of giving rise to all systems of phyllotaxy conforming with the Fibonacci series. The complexity of the system depends upon two factors, namely the rate of growth of the whole apical meristem and the plastochrone period. We cannot discuss here how this angle of divergence is achieved, but the problem of phyllotaxy has recently been treated by F. J. Richards and M. & R. Snow in the "Symposium of the Society for Experimental Biology" II (1948). In this volume there is also an excellent account of recent work on experimental morphology in ferns and its bearing on the problem of organisation in these plants by W. C. Wardlaw.

The crux of the problem of phyllotaxy is the effective factor determining the position of each localised centre of cell division in the meristem leading to the formation of a new leaf. It appears possible that the primordia of the leaves produce a specific substance of hormonal nature which diffuses out into the meristem so that a "diffusion field" is set up, the position of the new centres of growth being thus determined by intersection of lines of diffusive flow, pre-existing primordia thus playing a dominant role. Experiments by M. & R. Snow have indeed shown that the application of auxin to the surface of the apex results in displacements of primordia and alteration of the phyllotaxis. Other possibilities present themselves; thus the field might be due to diffusion of a substance into the meristem from below and flowing into the developing primordia of the leaves. These problems await further experimental work for their elucidation.

In the cases dealt with in which growth is centred in a single cell or a group of cells the organisation of the structure of the plant—the internal anatomy—can in theory be accounted for by interchange of hormone-like substances between neighbouring cells. This is facilitated by the circumstance that in the meristems the cells are not enclosed in the normal cellulose envelope which appears during the course of extension growth and therefore below the meristem; and even in the mature parts of the plant it is known that the cell walls are traversed by threads of living cell contents so that all the cells are in organic continuity. Indeed, in many lower plants (fresh water and sea weeds) no cell walls may be formed at all and the whole living content of the plant is continuous. Definite form can arise under other conditions, as is best seen in the fructifications of the fungi. In this case the whole plant organ consists of individual threads arising as branches from the formless mycelium and each thread is enclosed in an envelope of chitin. In this case, therefore, it is at least doubtful whether interchange between neighbouring threads can readily take place, and although fusion of neighbouring hyphæ may occur, there is no regular connection between individual cells as in the higher plants. How in this case the growth of the individual hyphæ is regulated and what controls the degree of branching of the threads and the varying directions of their growth in the stalk and cap of the fructification is quite unknown. It is certain, however, that very precise regulation must occur, particularly in the gills; for the whole mechanism of spore shedding, on which the successful functioning of the organ depends, is contingent upon the exact spacing of the gills and the precise horizontal orientation of the cap. There are therefore many problems presented by these facts for which no adequate theory has been presented.

In conclusion the salient characteristics of development, and hence of form, in higher plants in contrast to those of higher animals may be stressed. These are first, the persistence of the embryonic condition in the meristems in which the production of new cells continues throughout the life of the plant; and second, the extreme degree to which the form of the plant is capable of modification by external factors located in the environment. Although the apical meristem exerts a dominant influence over the development of the plant this is a matter of degree only, and the independence of the parts is best seen in their power of regeneration when separated from the parent body. Thus from severed buds, roots, and stem a new plant may arise: only the severed leaf is in general incapable of such regeneration and can do no more than produce an adventitious root system.

Biochemical Aspects of Form and Growth

by Joseph Needham

One of the inspirations of the present symposium has been the life work of d'Arcy Wentworth Thompson, that truly remarkable man who occupied the chair of biology at St. Andrews' University for nearly half a century. His *magnum opus* "Growth and Form", which first appeared in 1917, and was revised as a second edition in 1942, remains one of the two or three most brilliant and original books in the life sciences which this century has seen or is likely to see. D'Arcy Thompson's approach was fundamentally mathematical; he saw in the myriad manifestations of living form a wonderful opportunity for mathematical analysis. I always remember one particular demonstration of his, that the spirals in fir-cones and other plant structures involve the famous Fibonacci series (named after the 13th century Italian mathematician) which corresponds to a continued fraction and has very far-reaching implications. D'Arcy Thompson studied, in this 1,100-page book of his, all conceivable aspects of the mathematics of living forms—the shapes of cells, in isolation or association; the shapes of concretions, spicules, and skeletons; the twists of horns, teeth, and tusks; the characters of eggs and hollow structures. His final chapter deals with the interesting theory of transformations. If certain animal or plant bodies are plotted upon Cartesian coordinates, it is found that when these are systematically distorted in various ways, forms characteristic of species related to the original species plotted appear. While d'Arcy Thompson often examined the engineering problems which living organisms have had to face, his primary interest was the mathematical description of their forms.

So purely was d'Arcy Thompson's approach restricted to mathematics, indeed, that many have been tempted to see in him the last of the Pythagoreans. The lyrical concluding pages of his book invite us to see in Number the why and the how of all things, and the keystone of the universe. But, as has been pointed out by Edmund Mayer among others, this Pythagorean mysticism tended towards taking mathematical descriptions as explanations, no matter what level of physico-chemical analysis has been reached in the study of the biological objects concerned. While this vigorous Platonism was perfectly justified as the contribution of a single worker of genius, it was bound to seem unsatisfactory to a not inconsiderable class of persons, the biochemists, whose main preoccupation had always been, since the days of their Founding Fathers, Paracelsus and van Helmont, with the "matter" rather than with the "form" of life. While no one could possibly underestimate the magnitude of the task performed by d'Arcy Thompson, it was nevertheless, in spite of all its mathematical profundity, less difficult in a way than the problem of finding some relation between the gross morphological forms manifested by living things and the specific molecular constitutions which they possess. It is the purpose of this contribution to touch briefly upon some of the recent advances which seem to point the way towards the bridging of this terrifying intellectual gap.

The name of Alfred North Whitehead, though a contemporary, makes no appearance in the index of d'Arcy Thompson's book. Yet the famous aphorism that biology is the study of the larger organisms and physics the study of the smaller ones, has profound relevance to this situation. The old controversies about the reducibility or irreducibility of biological facts to physico-chemical facts are now seen to be unnecessary if we realise that we have to deal with what are different levels of organisation. The task of science is to elucidate the regularities which occur at each of these levels, the larger, higher, or coarser, on the one hand; the smaller, lower, or finer, on the other. At any particular level valid generalisations may be made applicable only to that level; such is the way in which sciences such as genetics or experimental morphology have been built up, and this is why the approach of d'Arcy Thompson in terms of mathematics and even engineering has its inalienable validity, no matter what chemical and physical discoveries may later be made. But until we can find the links between the superimposed levels of organisation, there remains a certain meaninglessness about the genetics of size and shape or the mathematics of spirals or polyhedra. A unified science of life must inevitably seek to know how one level is connected with the others. For the body contains organs, the organs cells, the cells nuclei and mitochondria, these structures are built up of colloidal particles which in turn consist of molecules large and small (proteins, carbohydrates, fats, steroids, etc., etc.), within which again are the atoms with their different kinds of valencies and bonds.

It was precisely because d'Arcy Thompson considered morphology the last stronghold of irrational views that he devoted his life to the mathematisation of it. But pure geometry was quite compatible, in the true Platonic tradition, with mystical vitalism and animism. The numerous devils of vitalism find a congenial abode in mansions of empty *forma*, swept and garnished by mathematical treatment. The biochemist is likely to have more sympathy with the tradition of Aristotle, who was much more conscious of the importance of *materia*. It is true that he held that there could be form without matter, but this only applied to the divine prime mover, the intelligent demi-urges responsible for the rotation of the spheres, and other factors in which modern science is not compelled to take an interest. But he maintained that there could never be matter without form, since however pure the matter was it was always composed of a certain mixture of the four elements, and so had a minimum of form. This standpoint is quite in accord with that of modern science. Form, as has often been said, is not the perquisite of the morphologist alone. It exists as an essential constituent of the whole realm of organic chemistry, as any passing visitor may see from the collocations of little coloured balls which the chemists keep in their glass-fronted cupboards; nor can it be excluded from "inorganic" chemistry or nuclear physics. Eventually it blends, we might say, into order and organisation as such, so that perhaps we might characterise the only two components required for the understanding of the universe in terms of modern science as Organisation on the one hand and Energy on the other. Only with this background in mind can we hope to see how the laws of each different level of organisation combine into a single structure the natural and the living world.

When I was an undergraduate in the years immediately after World War I, it could still be maintained, with Ostwaldian scepticism, that the structural formulæ of organic chemistry were pure constructions of the imagination and had nothing in common with the real nature of the molecules. Hence the great importance of the pioneer experiments of Langmuir and Harkins with monomolecular films, in which the dimensions of molecules could be accurately calculated, and in which it was seen that they took up positions exactly in accordance with their presumed structures, the acidic groups of fatty acids being "dissolved" in the water, and the hydrocarbon chains standing out away from it. During the past thirty years a wealth of new methods has been added to that of surface phenomena, by which we know that the structural formulæ of chemistry correspond to true spatial relations. Particularly notable is that of X-ray crystallography. If the crystallographers were not often able to suggest a true formula, they were certainly able to say that some formulæ were wrong, as Bernal did with the early representations of the sterol ring skeleton, thus laying open the way for the immense advances in steroid chemistry which have been so important for endocrinology and other biological fields.

Already in 1912 a bold application of the idea of fibrils or anisometric elongated molecular chains had been made to the problems of the living cell by the Russian biologist N. K. Koltzov, a man whose life work was hardly less inspired than that of d'Arcy Thompson, and who deserves to be much better known than he is. All he had to go on at that time was the polypeptide chain theory of protein structure enunciated by Emil Fischer in the nineties of the last century, and then unconfirmed by the modern results of surface chemistry and X-ray analysis. Elongated protein fibrils were pictured by Koltzov as essential building-stones in the labile "cell-skeleton". Striking extensions of this hypothesis have been made in very recent months by Lorch and Goldacre. But the first advances in X-ray crystallography of components of living organisms were made on polysaccharides rather than on proteins, in the work of Sponsler in California in the early twenties; this led to a series of studies which has thrown much light on the building up of cellulose walls of plant cells. In some cases, such as that of certain spherical hollow algal structures, we possess remarkably detailed information as to the way in which the cellulose fibres are laid down.

For animal cells and organisms, however, it was the proteins which needed investigation, and as is generally known, this arose in the needs of textile technology, from which support was derived for the epoch-making work of Astbury and his school at Leeds on the X-ray crystallography of animal textile fibres, and hence all kinds of fibrillar material of animal origin. Meanwhile the classical work of von Muralt and Edsall had established that the molecules of the characteristic protein of muscle fibres, myosin, were anisometric; in this they made use of another powerful experimental method, that of the study of anomalous viscosity. Later, during World War II, an even more elongated muscle protein, actin, was brought to light by Szent-Györgyi. It must not be supposed, however, that such structure-proteins are confined to muscle; on the contrary it is probable that they occur in all cells, as the pioneer investigations of Bensley indicated. There is here some connection, as yet unclear, with the cytoplasmic nucleoproteins.

In the twenties of the present century our knowledge of muscular contraction was hardly more advanced than it had been at the time of the *De Motu Animalium* of Borelli (1684). But the researches just mentioned are indicating that the contraction of an acto-myosin fibre involves a change of intramolecular configuration. Some believe that this is analogous to the shrinking of a fibre of the protein of wool. Others think that the contraction involves some sliding of the molecules upon one another, or a randomisation, as in rubber. But while in dead fibres the contraction is generally not reversible, that of the muscle proteins in living cells is readily reversible, as we know from every movement that we make. One might contrast "inert springiness" with "ert springiness". Parallel with these discoveries, a large amount of information had accumulated, as the result of the work of the schools of Meyerhof and Embden in Germany, Parnas in Poland, and Dorothy Needham at Cambridge, about the cycles of phosphorylation; in which energy from the breakdown of carbohydrate fuel is used for the building up of energy-rich phosphate bonds in the substance adenosine-triphosphate, whence the energy passes directly to the muscle-fibril itself. Still, however, there was no clue as to the relation between the chemical energy-transferring reaction chain and the physical contracting-relaxing function of the fibrils. But in 1937, Engelhardt and Ljubimova in Moscow, looking for the enzyme in muscle which breaks down adenosine-triphosphate and so liberates its energy, found that this enzyme was none other than myosin, the contractile protein, itself. It is still an unsettled question whether the myosin and the enzyme are absolutely identical or whether the enzyme is another protein bound so intimately to the myosin that it is almost impossible to separate it. But the theoretical consequences are not much affected by this uncertainty. More recent work has been devoted to the behaviour of actin and myosin in presence of adenosine-triphosphate *in vitro*, whether as artificial threads or in colloidal solution; and striking effects have been obtained the analysis of which is as yet by no means complete. We thus approach the conception of a "contractile enzyme". The substrate being once present, the enzyme-protein has no choice but to act upon it, yet in doing so its own physical configuration is fundamentally changed. With the disappearance of the substrate, the configuration-change may reverse.

It would seem that this state of affairs in muscle has extremely important implications for morphology in general and morphogenesis in particular. Here our fundamental principle must be that the protein or carbohydrate polymers which are directly connected with the gross form of cells, organs, and organisms, are not isolated or immune from the normal processes of metabolism, but on the contrary are closely connected with it. This originates from the thought of another man no less great than d'Arcy Thompson, namely Frederick Gowland Hopkins, the instaurator of modern biochemistry in Britain. Hopkins was possessed of a particularly penetrating gift of imagination, which enabled him to visualise the protoplasm of the cell as a kind of chemical factory, where a large number of reactions were able to proceed in close contiguity without becoming disorganised. But it was a factory the roofs and girders of which were broken down and re-formed; the latter process predominating, of course, during embryonic growth and differentiation. How true this metabolic vision was did not become clear to us until the development of the techniques of labelling individual atoms by the use of isotopes permitted estimates of the speed of metabolic scrapping and replacement. This powerful method, associated with names such as those of Schoenheimer in New York and Hevesy in Denmark, has rendered enormous services to the tracing out of complicated paths and cycles in the flowsheet of the cell's industrial processes.

Attention was devoted by d'Arcy Thompson, as it could not but have been, to the fundamental embryological phenomenon of gastrulation. His treatment of it was not one of his most successful forays. The rather naive models of a Rhumbler or an Assheton are not very relevant when we know as much as we now do of those strange directed cell-streams revealed by Vogt. One of the chief factors in the process is an enormous expansion of the outer ectodermal layer, and it is this which gives rise to invagination with its concomitant organiser phenomena where the newly-formed mesoderm acts upon the uninvaginated ectoderm. The expansion process, known as epiboly, is in need of a hypothesis which would explain the mechanism of what is going on inside the cells. Changes in cell shape are seen again in that primary example of histogenetic differentiation, the great lengthening of the cells of the neural plate when the mesoderm exerts its influence upon the presumptive neural tissue lying above it. The suggestion has been made that such processes are analogous to the relaxation (but in this case active extension) of protein fibres similar to those in muscle. It will be seen that one of our most urgent requirements is to know more about the structure proteins present in the cells of embryos. In my belief the conception of structure proteins as enzymes, bound to act upon substrates of small molecular size, but liable to have their physical spatial configuration irreversibly changed in so doing, is likely to provide a fertile field for experimentation in the immediate future.

The application of biochemical concepts to morphological form is difficult enough when this form is static, but the most challenging problem has always been their application to the changing form seen during embryonic development and differentiation. Up to 1931 the biochemists had done little more than study the chemical processes going on contemporaneously with development, and the vast majority of the facts available concerned precisely those late stages when the biochemist can get enough material to analyse conveniently, but when the most interesting events of embryonic determination are already over. But in that year a number of embryologists (especially the school of Spemann in Germany, and Waddington in England) made the revolutionary discovery that the agents of determination, (that is to say, those parts of the embryo which exert an "organising" action upon other parts, determining them to engage upon a path of histogenesis and differentiation which otherwise they would not pursue), were in some cases stable to boiling and denaturation by organic solvents. This brought into being a new phase of chemical embryology, in which the nature of what might be called "morphogenetic hormones" was assiduously pursued. Here again the chief theoretical point to be made is that morphogenesis itself was seen to be intimately connected with the normal running of the metabolic processes of the body; if these are deranged in the slightest way, deviations from normal morphogenesis will follow. After a number of years it became clear that this line of advance was much more difficult than had at first appeared, for (at any rate in the animal forms which were most convenient for experimentation) the active substances were found to be present in masked form even in those tissues upon which alone their activity can be tested. This has led to some disillusion among biologists without biochemical training, who have tended to fall back upon that last resort of baffled minds, the "unspecific stimulus". Biochemists are however entirely willing to agree that we need much more knowledge about the responding cell proteins as well as about the substances or surface configurations or whatever they are, which mediate the determination stimulus. Here the position has been greatly helped by the invention of methods of ultra-micro chemical analysis by the Danish school of Linderstrøm-Lang, and it is to be expected that great advances will be made by their use in the coming decade.

In this connection reference may be made to two contributions which open up very fascinating avenues of thought, one by the veteran American experimental morphologist Ross G. Harrison, and one by the most brilliant inheritor of the German tradition of "Entwicklungsmechanik", Johannes Holtfreter. During recent years Harrison has devoted exhaustive study to one of the strangest and most significant phenomena in experimental embryology, namely the determination of the axes of vertebrate limb-buds and ear-vesicles at different points in time. Here is a dimensional difference. The axes are determined at successive stages, the antero-posterior before the dorso-ventral, and the dorso-ventral before the medio-lateral. Thus a limb-bud ceases to be able to regulate its development (with the formation of a normally oriented limb) at three successive moments, not all at once. It seems impossible to conceive of this in any other way than by some analogy with liquid crystalline states, such as those known as nematic, smectic, etc. where crystallinity or rigid arrangement of particles occurs successively in the three dimensions. The contribution of Holtfreter to which I wish to allude is one in which the great importance of the lipo-protein structures of the surfaces of cells was brought out. In a long series of operations on very young embryos, he combined together the different germ-layers in all kinds of ways, and found that they exhibited affinities and repulsions varying with the stage. At first two such layers might cling together, but afterwards separate, while conversely others might originally be loth to combine, but later become mutually adhesive. Here again the doors have been thrown wide open for physico-chemical analysis of the mechanisms involved in terms of the configurations of protein and lipin molecules, with progressive changes in their various bonds and arrangements.

By way of summary, then, it may be said that neither the old-fashioned treatment of the systematic morphologist, nor yet the mathematisation of morphology in d'Arcy Thompson's great work, nor yet the traditional biochemical studies of purified substances or enzyme systems, are adequate for the present opportunities which we see before us in the unification of morphology and biochemistry. The problem has to be approached on all levels simultaneously. Biochemists are more and more coming to study "teams" of enzymes, linked energy-transfer mechanisms, and characteristic cell-inclusions such as mitochondria and the granules of Claude, or the cytoplasmic nucleins. And if the keynote of this mode of thought were to be summarised in a single sentence, it would be that the foundations of morphological form are to be sought in the proteins responsible for cell-structure, and that these are inescapably connected with the normal metabolic processes of the living cell as a going concern. The names of Koltzov and Hopkins as well as that of d'Arcy Thompson must be inscribed upon our orders of the day.

FIG. 1

Electron-microscope photo of cellulose structure of *Valonia* wall by courtesy of Dr. R. D. Preston and *Nature*

FIG. 2 Electron-microscope photo of collagen fibrils
by courtesy of Professor W. T. Astbury, F.R.S. and *The British Journal of Radiology*.

FIG. 3 Electron-microscope photo of earthworm cuticle collagen fibrils
by courtesy of the Elsevier Publishing Company, Inc. Amsterdam

FIG. 4 Electron-microscope photo of toad muscle fibrils (*Bufo marinus*)

FIG. 5 Electron-microscope photo of sarcolemma with overlying fibrils

Figs. 4 and 5 by courtesy of Dr. Draper and *Australian Journal of Experimental Biology and Medical Science*

FIG. 2

FIG. 3

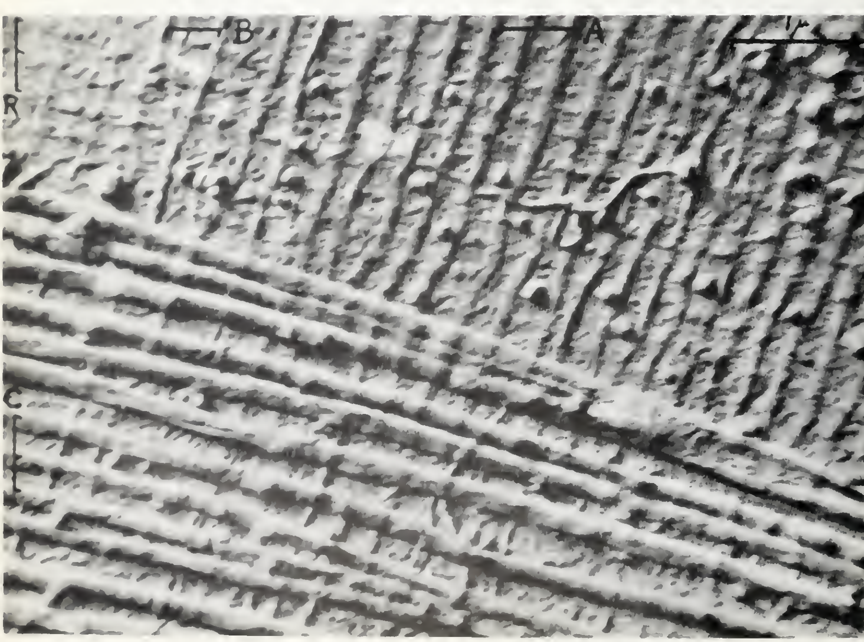


FIG. 4

FIG. 5

FIG. 6 Electronmicroscope photos

a nucleus from muscle cell of psoas muscle of rabbit

b formed elements of muscle cytoplasm: mitochondria and microsomes

c glycerol-ext myofibril showing regular filamental structure

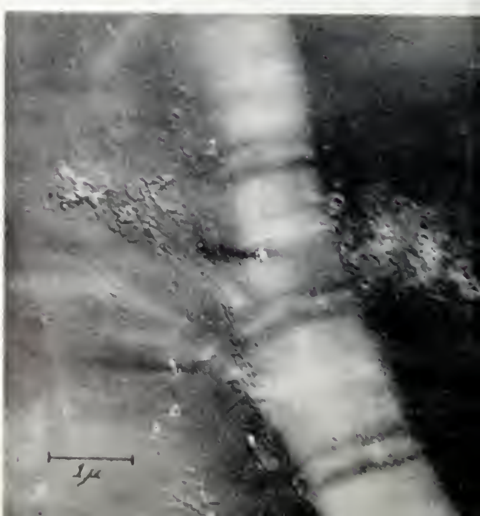
d myofibril shortened after treatment with adenosine-triphosphate

by courtesy of Dr Perry and Dr Horne (Biochemical and Cavendish Laboratories, Cambridge)

a

d

b



c

Form and Modern Embryology

by Albert M. Dalcq

The volume to which the present essay is a contribution testifies to the everlasting fascination exerted by Form. Form is both deeply material and highly spiritual. It cannot exist without a material support; it cannot be properly expressed without invoking some supra-material principle. Form poses a problem which appeals to the utmost resources of our intelligence, and it affords the means which charm our sensibility and even entice us to the verge of frenzy. Form is never trivial or indifferent; it is the magic of the world.

Ordinary Conceptions of Form

In the realm of our immediate perceptions, especially during their acquisition, form is primarily linked with things in a solid state. Soon comes the observation that liquids and gases do not have a form of their own, that they are moulded by their recipients thanks to gravity, cohesion, surface energy, etc. However, a new step is accomplished with the recognition that liquids and even gases show form if submitted to propulsion: waves on the surface of pools or of the sea, jets of water, of vapour, clouds, etc. In our western methods of education the acquisition of a sense of abstract form is based on literary, mathematical, and æsthetic teaching. By studying verse and prose, geometrical relations, sculptural cannons, and musical rhythms, sufficiently gifted minds gradually acquire a growing sense of form. Later, if their mental development attains its full maturity, they may become capable of penetrating the modern views on the structure of the universe, or, conversely, on the intimate structure of matter and energy, and thereby recognise that, at both levels, form rejoins order and is best translated by mathematical relations.

Perhaps, if inclined to philosophical generalisations, the same young intellect will eventually be struck by the kernel of truth contained in the hylemorphic theory, the scholastic doctrine of matter and form. Its distinction between Power, Form, and Act is far from being out-dated, even if it no longer answers to an actual necessity. In any definite situation offered by a real system, we have still the right to consider that its material and energetic elements can be combined in numerous ways (Power), but that a certain set of definite relations has been adopted (Form), resulting in the actual situation (Act). The only advantage of these considerations is probably to attain the conviction that no formulation of reality can be satisfactory if it does not imply some concept related to form.

Form in the living realm, and development

The orientation of the mind towards form as present in the living realm is a slower, and generally less complete process. Quite frequently it seems to start with aesthetic impressions invoked by external aspects of flowers, insects, birds, human beings. It may very well develop considerably on that superficial level, without any desire being felt for a deeper analysis.

Two "banal" reasons explain that more or less frivolous attitude. The first is that, for most people at least, the charm evoked by the shape and colours of vegetal or animal organisms immediately subsides, or even vanishes, if their internal structure comes to be considered. Anatomy has some background of ugliness, which the uninitiated tend to exaggerate. Moreover, the aspects provided by the various tissues of a leaf or of a flower, by the organs included in a limb—which was so graceful when surprised in its movements—are deprived of any aesthetic nimbus; they are like the words of a poem, once scattered.

The second reason which habitually limits the comprehension of form in the living realm is that it can only be understood through the development of organisms, and such a preoccupation is decidedly outside the ordinary trend of our thoughts. Except for some vague ideas, most persons do not realise all that is implicated in development. Our social organisation has been conceived primarily by and for adults. Even the consideration granted to children is founded on their quality as future adults. Conventions of respectability and tendencies in education combine to cast a veil over our representation of all processes connected with reproduction. Naturally upon the slightest reflection we become conscious that any living being must proceed from the sequence of events that science designates as *ontogenesis*. But even then we see it as a process of fabrication, as a necessity imposed from outside, while ontogenesis implies the whole intimate reality of the organism. We strive to reduce it to a nearly negligible preparatory phase, which will soon give place to the true activities of our destiny, while in fact development is the essence of ourselves and contains, potentially, our whole existence.

Morphogenesis and vital organisation

From this unquestionable fact results the true formulation of the problem offered by biological forms and by the concepts linked with that fundamental reality. Let us leave aside, for sake of clarity, the lowest levels of vital organisation: viruses, bacteriophages, and simple bacteria. All higher beings are evidently endowed with a typical form. It does not only characterise their external features, but also their internal structure, so far as this is not considered under the aspect of *disjecta membra* but in its relation to the other parts and to the whole. Evidently also each new existence begins with the construction—*de novo* and, in most current cases, *ab ovo*—of all general and special characters inherent in the "morphe". This happens to such an extent that "morphogenesis" is currently used for ontogenesis or development. Consequently, all that we think or that we feel about form is rooted in our most intimate nature; it can only be better understood by the accurate consideration of some fundamental, really creative activities of life.

One principle must be set forth from the start. Life does not imply any kind of matter or energy which is not present, to some extent, in the inanimate realm. This assertion may not conform to our impressions, or to our more or less avowed wishes. It is, nevertheless, a certitude. But yet something establishes the difference which allows us to recognise life, with its characteristic triad of associated properties: assimilation, reproduction, autonomy. Altogether, this is simply what we call, using a term with a psychological and social background, *organisation*. This means the whole complex of relations between the particles at a given moment—let us say of the atoms and molecules—which enter into the composition of the system. Let us suppose that we suddenly stop all functions—but in a reversible manner, as is now made feasible by the use of certain cautious devices of refrigeration—and assume that we are to describe the exact relations of all the stabilised elementary particles included in the specimen. That description would be, in a concrete case, organisation. Consequently, our very concept of life, in its most general acceptation, necessarily implies some definite, always elaborate structure or order: that is, an abstract translation of form.

Hierarchy in manifestations of form

But let us turn our attention towards concrete, observable forms, as we can draw or photograph them either on the ordinary scale, or under the light microscope, or with the help of electronic devices. Forms are generated by limits, that is by separation of phases, either in the cytoplasm or in the nucleus, either between organs or, finally, between the organism and its surroundings. Well, in that collection of forms, some hierarchy can be perceived. At the lowest level, forms do not seem to be intrinsically significant; they are merely expressions of multiple physico-chemical contingencies, which are probably not, in themselves, important to the organism of which they are part. That microbes are spherical, ovoid, rod-shaped, comma-like, etc., does not apparently affect their power of proliferation and their success in the struggle for life. The particular shape of organites present in the interior of cells, mitochondria or chondriom, microsomes, protein fibres, fat vesicles, chromosomes, has not any special bearing on their way of playing their part in the cellular workshop. But, at a somewhat higher level, structures are encountered, the definite shape of which has an intrinsic importance for the welfare or the future of the organism. Such is the case during the successive cleavages of an egg, with the architecture of the spindle and astrospheres of the transitory mitotic apparatus, necessary to the completion of division. The same can also be said for the typical features of the successive stages passed through by the embryo, the shape of its blastopore or of its primitive streak, the form of its neural plate, of its optic vesicles, and innumerable other features indispensable to the building up of the young organism. These are the significant forms, as opposed to the accessory ones. (Figs. 1 to 6).

General events of ontogenesis

The characteristic of these significant forms is their constant progression until attainment of a certain equilibrium typical for adult specimens of each species. Incessant transformation and complications evoke the impression of an unfolding, like that to be observed in vegetal buds; morphogenesis displays a continuous activity, apparently striving towards a definite end. For a long time that wonderful process was studied under its aspect of shape, by a kind of accurate contemplation. Nowadays, embryologists have learned to scrutinise the process from the inside. Indeed, they are less concerned with the forms in themselves than with the functions which cause the orderly re-shaping, stage by stage, from the egg to the embryo. Now that the development of a sufficient number of animal groups has been carefully explored, the main problem faced by these scientists is to attain a rational explanation of morphogenesis.

How far have they already succeeded in that task? No more and no less than in the case of other explicative sciences. Like astronomers, physicists, chemists, etc., modern embryologists have coined some hypotheses, the exploitation of which affords a fairly coherent view of developmental events. Especially during the first half of this century description and experimental data have combined to afford at least a general picture of germinal organisation. At the start, the germ is practically deprived of any significant form. It is also established beyond any doubt that it possesses in itself the means of creating forms—"l'œuf, créateur des formes", said the late Pr. Albert Brachet—and does not receive them from its milieu. The environment only affords the general, basic conditions for life: moisture, oxygen, a convenient equilibrium of ions, a favourable level of osmotic pressure, etc. What can be perceived in the fertilised egg as its morphogenetic endowment, as precursors of forms, is extremely subtle. In the nuclei—for there are at first two, one of paternal, the other of maternal origin, which soon fuse together—is a ball of threads, the so-called chromosomes, of a complex chemical constitution. Each of them has a definite form and structure, and its successive parts, usually called genes, present striking functional differences and are disposed in a given order. In the cytoplasm the ordinary constituents, proteins, fats, sugars, salt, and more elaborate special molecules, are not mixed haphazard as they are most probably in an amœba, a myxomycete, or certain cells in tissue culture; no, they are disposed in a given spatial arrangement which can only be expressed in terms of gradients and fields. In a certain sense, the more or less conscious aim of embryological research has always been to disclose and express in increasingly precise terms that germinal organisation.

Causal Embryology, its main results

The introduction of the experimental methods around the eighties, by the Frenchman L. Chabry and the German W. Roux, has resulted in an extended enquiry bearing on the eggs and embryos of the various types presented by the actual animal kingdom. A huge amount of painstaking work has been devoted to that task, for which many minds feel a singular and significant attraction; is not the whole enigma of life condensed therein? Thanks to that broad investigation, we begin to know, for each main Order, which are the constituents of the cytoplasm especially involved in the realisation of the gradients and fields, and what is the localisation of such truly morphogenetic materials. It would be too technical to enter here into a detailed description of the various cases, the more as that there still reigns some disagreement among the embryologists on that topic.

I personally feel justified in believing that the fundamental and probably primary state of germinal organisation in Metazoa is the co-existence of an internal polarisation (a simple gradient) of the cytoplasm and of some progressive tri-dimensional variation in its cortical (external) layer, in other words, a cortical field. From fertilisation onwards, some interaction takes place between the bio-chemical materials integrated into the internal gradient and the cortical field, which results in regional graded activities of metabolism—disintegrations, oxidations, syntheses, etc.—which represent the morphogenetic field. This field is directly responsible for the building of forms; it must naturally be conceived in an entirely dynamic, not static manner. But, in some Classes, evolution has achieved another, perhaps more skilful, formula of germinal organisation. The specialists of the sea-urchin egg admit that it is essentially endowed with two inter-penetrating gradients, each one being probably represented, at each level, by two different systems of biochemicals, in varying proportions (Fig. 7). In Mammals I have found that, even from a very early stage of its formation in the ovary, the egg is already endowed with a symmetrical organisation: a set of important macromolecules and granules, including mitochondria, all correlated with the turn-over of nucleic acids, is not distributed equally all around the polarisation axis; but these materials are present at a higher concentration, one might say crowded, at one side of that axis (Figs. 5, 6). In my opinion, it can be assumed that this type of organisation represents a refined simplification. The devices encountered in other eggs may be held to result, after some preliminary steps, in the same or a similar distribution of nucleic* materials in the cytoplasm. The eggs of Mammals, man included, should excel by their efficiency.

There exists certainly some disagreement with these views. Scientists frequently differ in their final appreciation of data according to their method of approach. This can be seen in the case of morphology, which can be studied in two ways. That mainly adopted by embryologists is the direct one, which may be descriptive or experimental. But there is also the possibility of manipulating the composition of the fertilised egg by controlled crossing: that is the basic method of genetics. Its results have been so astonishing, so far-reaching, that geneticists are tempted to

* The evolution of biochemical terminology has been such that "nucleic" has only a biochemical meaning and does not necessarily refer to materials included in the cell nucleus.

correlate any morphological manifestation with those tiny units they call genes. They are inclined to think that all specialised materials appearing in the cytoplasm are elaborated under the control or even the impulsion of genes, or of groups of genes. Especially, when geneticists are led to consider the morphogenetic organisation of the cytoplasm in the ovarian egg, they tend to assume that it is provoked by activities of the nucleus at that early stage, that is by the so-called germinal vesicle, which is certainly a remarkable and unique type of nucleus. Embryologists do not contest that, in that decisive incipient period of morphogenesis, nuclear processes are of extreme importance. But they observe that a definite and constant *spatial* organisation has so far not been detected in the germinal vesicle, while it can often be observed in the cytoplasm. Therefore, some embryologists maintain that the concepts arrived at by genetics are not sufficient to account for the fundamental aspects of morphogenesis. In my opinion, hereditary patterns of form are not satisfactorily explained by the sole continuity of gene units. In their transmission these are never wholly independent of cytoplasm. Neither can the significance of the undeniable continuity of cytoplasm between generations be ignored. Cytological data and experimental analysis converge, according to my own experience, to demonstrate that some structural character, of a very general type, is transmitted by the cytoplasm, or, maybe, by its cortical layer. To recognise this fundamental property seems indispensable to a rational explanation of morphogenesis.

However this may be, if the existence of gradients, fields, nuclear equipment, is accepted from the start, the course of events in morphogenesis can be deduced in an ever more satisfactory way thanks to the results of recent investigations. If the presence of a spatial configuration is conceived in the fertilised egg, a four-dimensional representation is then mentally grafted on it by considering, step by step, the intimate developments of cellular life, forcefully aroused by the impetus of fertilisation. The clue to an understanding of these delicate and intricate processes is to remember that, here more than anywhere else, small causes may result in considerable effects, to be attentive to the multiple possibilities of cumulative actions, of competition, of reinforcement, and never to neglect the prevalent fact that we have to do with the "organism as a whole".

General re-shaping in the early stages

That fine and famous expression of J. Loeb is the more justified in that, apparently, embryonic morphogenesis cannot be accounted for simply by a kind of summation of internal and regional events. During the first steps, which are the most significant, some eggs show a modification of their general form not due, it appears, to the activities awakened inside them. The hen's egg, that classical material, shows this during the first hours of its incubation. The same fact is also evident in a Reptile egg (Fig. 4). A characteristic re-shaping also takes place in the rat's egg during cleavage, in that of the frog and sea-urchin just after gastrulation. We have only very fragmentary information concerning the cause of that general process. Most probably it originates from properties inherent in the whole cortical layer of the system. I personally judge it to be really important, and perhaps obscurely connected with that impression of beautiful harmony displayed by most living embryos, and also with that special distinction which strikes us in certain thoroughbred specimens of adults.

Morphochoresis

Naturally, development is not only, even in its first steps, a general re-shaping. If the egg progressively abandons its initial shape, which is spherical or nearly so and corresponds essentially to a state of quiescent equilibrium, this is mainly due to co-ordinated internal reactions appertaining to the most refined and complex processes of cellular chemistry. Part of these give rise to movement. At first, particular constituents of cytoplasm and nuclei are systematically mobilised, in a cyclic manner, for cleavage (Fig. 5). When the materials of the germ have been distributed in this way in a sufficient number of cells or blastomeres, movements of a higher type make their appearance. They are extremely difficult to sketch, owing to their subtle nature. They are not restricted to a given region, but appear simultaneously in all groups of cells integrated in the germinal system. Although these groups have no definite boundaries, at least at the beginning, each of them has its own law of displacement, relatively to other areas. A certain "regiment" tends to migrate inside, while another one stretches itself to the utmost on the surface, and a third one also dives, while stretching itself along one main axis, and so on (Figs. 3, 4).

There are, in the various Classes, numerous variants of that *kinematics*. More than any other process, it gives one the impression of a deliberate, preconceived operation. One of its consequences is, amongst others, that the initial continuity between germinal materials becomes attenuated, if not broken, and that the system can now be dissociated into a certain number of layers or, somewhat later, of primary rudiments of organs.

These displacements and regional re-shapings are caused, naturally, by definite cellular activities which culminate in a modification of surface energy and, by their summation, acquire a somewhat mechanical aspect. But, since the great discovery of H. Spemann in 1923, we have learned that, during that highly constructive period, the various territories of the germinal system are not working only for themselves. Some of them elaborate products of an enigmatic nature (see *infra*) which are transmitted to an adjacent layer of sister cells and entirely change its destiny. This is the phenomenon of embryonic induction. Its rôle is different in various types of eggs, but in all members of our own Phylum, that is in all Ascidians, Fishes, Amphibians, Reptiles, Birds, and Mammals, it is extremely important as an indispensable step in the formation of the nervous system.

The processes we have just tried to picture in perhaps too general and imprecise terms are decisive for morphogenesis. They take place very early, immediately after cleavage. In Amphibians of our regions, for example, they happen during the second and third day of life. In Birds, during the two first days of incubation. In Mammals, they find their equivalent during the second half of the first week. In general, they are referred to as gastrulation but, for reasons not to be exposed here, I prefer calling them: *morphochoresis*. Indeed the formation of an internal pouch, announcing the digestive tract, is not the predominant feature of that period, contrary to the impression of the pioneers in descriptive embryology. What is really primary is the mobilisation of cellular elements, their arrangement in groups of distinct destiny, all in obedience to the severe rules of some ceremonious dance, typical for each type of creature. Development, from its very beginning, strives towards animation.

The field—threshold concept

If we now try to withdraw our minds from the details of particular events and problems, so as to get a panoramic view of the mental activities implied in the modern explanation of incipient morphogenesis, the leading idea appears to be that of an intrinsic order. At each successive stage, the aspects we have to interpret arise from spatial and numerical inter-relations existing during the preceding period. Quantitative relations are primary; apparently new qualitative situations appear according to the existence of thresholds, a concept of general importance in the whole physical realm and especially in living systems.

We are consequently led to a kind of Pythagorean conception. If we should find it necessary, and if the convenient methods were available, we could establish the physical diagram of an egg at a deliberately chosen starting point. This should indicate the biochemical nature, the exact amount—in a statistical sense, and the precise location of all molecules and atoms—milliards of them!—implied in the configuration. If the views of modern physicists are rightly founded, that chemical representation could be finally reducible to spatial and numerical relations between immense hosts of the elementary particles constituting matter, protons, electrons, neutrons, etc., with the intermingled quanta of energy.

Modern research has not afforded any argument seriously opposed to that kind of conception, and causal embryology constantly progresses and attains new positive results on the basis of that general working hypothesis. Therein would lie, consequently, the origin of organic form. In that sense, it is, undoubtedly, intimately connected with a material substrate, but, far from emerging out of chaos, it surges from the mathematical relations, the statistical laws inherent to organisation.

The building up of the embryo

To advance a step or two further, let us now try to discover how animal forms attain their full realisation. If the first steps of morphogenesis are difficult to scrutinise and still more to express adequately in their intimate refinements, the consecutive transformations are not much easier to disclose. Very fast, indeed, we are confronted with intricate complications, for which it is impossible to account without the technical and iconographic apparatus of a regular treatise.

Our sole purpose here must be to examine how far morphogenesis can be considered as logically intelligible and which are the principles appropriate to its explanation. According to the premises just sketched a distinction must be traced, for the convenience of analysis, between the parts of the germinal system which proceed by their own forces and those which have received the impulsion of induction.

As to the first, one could expect to see their system of continuous gradients and fields proceed to a series of graduated activities; one would hope to find everywhere the same type of transformation, but graduated from a maximum to a minimum. To take a simplified example, if the important step was a swelling of the cells, we should be able to observe in a given region all the stages of swelling from a huge to an imperceptible one. Such is not the case. Very soon the four or five types of rudimentary organs vaguely modelled by the morphochoresis, and at first undifferentiated among themselves, each take a strikingly definite aspect. The notochorda, that axial rod, the somites, in which future muscles are embedded, the pronephros, first excretory organ of the embryo, have each their pertinent personality. This is so definite that all morphologists were deeply moved when, thirteen years ago, the Japanese research worker T. Yamada showed that, nevertheless, the young anlagen of these primary organs could be, by appropriate operations, converted the one into the other. The sudden appearance of such quite distinct organs is an essential step in the realisation of morphogenesis.

Its causes have been and are still difficult to disentangle. There are at this time sufficient data to suggest that the primary morphogenetic field inherent to the cytoplasm implies differences of cytoplasmic constitution among the cells resulting from cleavage; that their nuclei echo, so to say, these differences, noticeably by synthesising different amounts of nucleic acid, as recently demonstrated, in the sea-urchin egg, by my Brussels colleagues J. Pasteels and L. Lison; that, in this way, some genes or sets of genes are awakened to new activities, these factors being different according to the concentrations of the various chemicals present, in each cell, in the cytoplasm, and the nucleus; that this change provokes, by a snowball effect, new syntheses or desintegrations, and so on . . . If this view is correct, embryonic development could be compared to a kind of symphony in which, after the general exposition of a main theme, various instruments successively enter and solicit genuine answers, each definitely creative, until the whole orchestra comes into play.

Correlations—growth—differentiation

So far we have only considered what the cells of the various layers, or of the various regions, can perform according to their own constitution. But that does not happen without some movements, although more moderate than in the preceding period. In particular, migration intervenes. It causes new contacts, and, in many places, cells of different origin intermingle intimately to settle the definitive rudiments of primary organs. The most various possibilities of such combinations seem largely to intervene in order to lead each organ to its characteristic maturation. The processes of that achievement are always complex, at least two being involved.

First, the mode of growth, with its particular rhythms and rates in the various directions; its causes are far from clear, but certain arguments point to the rôle of nuclear activities, both general and genic. Second, the type of intracellular differentiation, due to the production of special cytoplasmic structures such as fibrillas of muscles or of nerves, secretory vacuoles, etc. From these and other factors result the final functioning of each organ, its physiological integration into the whole, and, what interests us mainly here, its definitive shape. When the young organism is constituted, its form is the resultant of these multiple regional events and also of the general patterns of growth. These will still change during maturity and even senility, under the combined influence of hereditary factors and of the environment.

The origin of the nervous system by induction

Some remarks are now necessary concerning this extremely important part of the embryo, which depends on induction for its formation. Let us restrict our field to the Vertebrate embryo, and assume that what has been established in favourable species of Amphibians, Fishes, Birds, Mammals is also true in the development of man. Let us also neglect here inductive processes other than those connected with the building up of the nervous system (Fig. 8).

That this system is of primary importance needs not to be emphasised. It is not only the regulator and co-ordinator of functions and actions but also a predominant element in morphology. The impression we receive from the sight of an animal is largely influenced by its head, which is essentially its brain-container, and its eyes, which are originally an expansion of its brain upon its face. The physical personality of a human being depends on its demeanour when standing or walking, on the proportions of its face, the mobility or fixity of its eyes, the control of its mimic muscles, and such-like everyday observations. All these features are related to the fantastically complex system of neurones and neurites, that is, the nervous cells and their threadlike expansions into the whole organism. Without entering into any illusory description of the central nervous axis—that huge organisation of specialised and hierarchised centres, with an incredible luxury of connections—nor of the peripheral sensory organs and nerves, with their afferent and efferent paths, it is necessary to point out that consciousness is far from being a general attribute of nervous functions. A considerable part of these are performed "à notre insu". This is true for the whole set of so-called inferior centres of the brain, for the automatic centres of the medula and spinal chord, and for the nervous ganglia of the viscera, some of which, e.g., the splanchnic plexus, are of considerable size.

One main characteristic of the nervous system is its perfect continuity, which points to an unity of origin. Curiously enough, at the start that unity is not so much spatial as functional. I mean that the nervous system does not really originate from a unique and continuous layer of cells. There is indeed a principal "anlage" and several accessory ones. But the common property is that all these parts, large or small, are induced according to some specific and localised modification of the external layer.

Intimate nature of induction

As already mentioned, embryonic induction is one of the great discoveries of this century, and it has, naturally, excited considerable interest. As is usual in science, especially in biology, more problems have been opened up than have been effectively solved. All things considered, two ideas emerge out of that exploration, but in spite of their probable value, they have not yet a full scientific validity. Nevertheless, I find it advisable to expose them briefly, for if they are an approximation to the truth, as I believe, they may have far-reaching consequences.

The first of these notions concerns the kind of transfer implied in the inductive process. In spite of extensive research, its biochemical aspects remain really puzzling. It does not seem possible to account for it simply by the passage, from cell to cell, of one or more sets of molecules. The suddenness, extension, durability and transmissibility of the effects observed impose upon us the impression of a kind of *contagium vivum*. The hypothesis has again been recently expressed by my colleague, J. Brachet, one of the best qualified specialists in that field, that the agent of induction could consist of "granules" capable of auto-duplication. This means, that the process would be linked with one of the basic properties of life: the reduplication of these fundamental units that the Swiss embryologist F. E. Lehmann has recently proposed to call *biosomes*.

The second notion which I believe to be important for the general meaning of neurogenic induction is its sub-ordination to quantitative relations. As everybody knows, the central nervous axis is a continuous organ with striking regional differences: cerebral and cerebellar hemispheres, olfactic lobes, optic nerves and eyes, spinal chord—to enumerate only some macroscopic aspects. The explanation of these regional specialisations poses an arduous problem. Actually, embryologists agree that there are certainly not as many special inductors as there are characteristic structures. But some hold for a certain plurality, others for an original unity modulated in relation with chronological conditions and thresholds. However that may be, in both systems of interpretation the decisive role of quantitative relations is admitted. They cannot yet be interpreted by numerical measurements, but the effects of reinforcement or weakening cannot be denied nor the resulting establishment of discontinuous levels in nervous organisation. Consequently, it may be said that for induction, as for more simple aspects of morphochoresis, the final result of actual studies is a sort of Pythagoreanism.

The role of induction in morphogenesis

What is the part played in morphogenesis by these induced structures? In my opinion this ought to be examined on two different levels, the one strictly embryological, the other far depassing the accepted limits of that science.

From the purely structural point of view, it is remarkable indeed that the embryonic nervous system does not only contribute to the form of the organism by the bulk of its massive part, the rôle of which is evident, especially in the head conformation. It also intervenes in a more discreet, insidious manner. At first sight, the neural plate, when it makes its apparition at the end of gastrulation, seems to be limited by an exact boundary from the rest of the external layer (Fig. 8*a*). In fact a closer inspection shows, all around the plate, a transitional structure, caused by an induction of intermediate strength, and, accordingly, endowed with intermediate morphogenetic properties. These cells generally begin by forming the peripheral part of the neural plate (Fig. 8*a*,*b*), but soon—they migrate outwards, as a delicate fringe, the neural crest (Fig. 8 *d*, *e*). Their subsequent fate is complex. Some will remain almost where they are, and become genuine nervous, ganglionic cells. Others will migrate somewhat farther, near the limit of the head and trunk. There they will take an active part in the construction of the branchial arches, that archaic component of any Vertebrate head. A third and fourth group will acquire a still broader distribution, migrating either inside towards the rudiments of the digestive tract, or spreading superficially into the future subcutaneous tissue.

The visceral part will build up a large amount of the vegetative nervous centres and associated organs, such as the abdominal sympathetic and the adrenal glands. The surface elements will, in many cases, elaborate pigments; their proliferation will afford the black and coloured patches or stripes which, under the intervention of certain accessory factors, are distributed according to the various patterns of pigmentary spots, scales, feathers, hairs, observed in the different Vertebrate groups. In a word, large parts of these organisms are, so to say, stuffed with derivatives from the neural crest in various amounts, and some of these invaded regions are indeed important for the morphological aspect of an animal. The complex transformations of the branchial arches are decisive for the shape of the face, while the patterns of the skin are among the most characteristic features of the animal. Again, their discussion could be taken further by explaining the modulating rôle of sexual hormones, the production of which is evidently linked with the development of the ovaries and testes, that is with the sources of the next generation! But it suffices to emphasize how remarkable is the fact that a derivative of our primary nervous system plays such a rôle in the secondary modelling of the form in any Vertebrate, man included.

From neurogenic induction to psychism

By these considerations we have perhaps fairly well covered the field of embryonic morphogenesis, as it is daily realised in any being coming into existence. At least we have tried to disclose the main principles of that eternal great adventure. Is the lesson of causal embryology limited to that? Does it leave plainly inaccessible an enquiry into that most remarkable achievement of nervous centres, consciousness? Could not the way by which the nervous organisation originates throw some dim light on its highest performance? Is there a possible transition, or an irrevocable hiatus, between biological and mental morphogenesis? Is the superior realm of abstract forms, of their perception, their consciousness, their invention, enigmatically superimposed on the prepared canvas of neural structures, or does it surge out of them as their natural fruit?

In the course of development the nervous system acquires, in all animals, but especially in higher Vertebrates, a particular importance. It condenses all properties of irritability and memory common to all kinds of living substance; it becomes the specialised instrument of perceptions, transmissions, instantaneous co-ordinations. It seems to be the one organ in which most refined micro-chemical and micro-physical devices are produced—even electronic, as recent works of cybernetics suggest! Consequently, if we admit that any animal endowed with a somewhat elaborate nervous system, including brain ganglia, experiences that permanent sensation which is the consciousness of being alive, can we not admit that such a sensation is nothing else than the perpetual rustling of that ever-vibrating system?

But if we imagine in this way the functional substrate of psychism, this does not explain to us why the nervous apparatus is capable of performing the double set of its precise functions. That is, on the one hand constantly to co-ordinate the most varied internal activities, on the other to exert for the profit of the organism the survey and the regular domination of a certain vital space. We shall make this ever-puzzling problem easier, if we remark, again in opposition to current ideas, how much these two apparently different functions of the nervous system are intimately linked together. To isolate intelligence or instinct as autonomous abilities is an artificial procedure, which can only be upheld by neglecting the vegetative substrate on which they are built up and from which they never liberate themselves completely. In fact, whichever aspect of nervous functions we consider, it implies a kind of *knowledge*—of which the organism is not necessarily conscious, and which may attain many graded levels. At the basis of nervous activity there is always an appreciation, a discrimination, an aptitude to distinguish the identity, the difference, the relative proportions of two situations. This ability to estimate is not exclusive to neurones; all living cells possess it to some extent, but the nervous centres have amplified and brought it to a high degree of perfection. A noticeable progress would probably be accomplished if we could perceive, even vaguely, whence comes that capacity for more or less distinct knowledge.

This is the point where the position attained by the analysis of induction can eventually be articulated with the nature of mental activities. As we have seen, the rational explanation of development in general, and of the neurogenic induction in particular, seems to be best approached on a Pythagorean basis. If this view is valid, a relation, in itself remarkable enough, becomes apparent: a close similitude exists between the conditions which cause the formation of the nervous system and the nature of the services it is called upon to render. On both sides, we find the capacity for differential reaction, the ability to compare, to evaluate some external influence which characterises the situation. Naturally it is permissible to retort that our human comprehension is itself based on that very principle, and that our mind therefore cannot find anything else when it applies itself to ontogenesis. However, since this manner of understanding leads to predictions and verifications, as happens in general morphogenesis and notably in the case of neurogenic induction, and since also, it makes the existence of psychism and of its multiple manifestations less enigmatic, the fear of a vicious circle must not restrain us too much from this unusual trend of thought.

Considering the situation from another angle, the unfolding of psychism is an everyday fact appearing as the normal prolongation of morphogenesis. Logically, the basic principle of psychism may already be present in the morphogenetic processes, or it may be derived from outside, or result from a combination of intrinsic and extrinsic causes. The first and third of these possibilities are both in agreement with the solution advocated here. The second amounts to taking psychism for a kind of incidental graft. Confronted at a given moment with its environment, the organism might prove itself capable of adjusted answers, somewhat as the configuration of certain valleys gives rise to an echo. Such a regular encounter does not seem very likely; is it not more satisfactory to admit, as proposed above, the link between morphogenesis and psychism, even if the connection still remains rather vague and to some extent subjective?

Complementary arguments in favour of that thesis come from the light thrown by it on otherwise enigmatical aspects of our mental experience. In obviously gifted individuals operations of the intelligence attain an exactitude of insight, often including the prediction of data, which attests a secret correspondence with reality. Without admitting it, our capacity for inductive synthesis cannot be understood. It is remarkable enough that a close consideration of the recent achievements of microphysics may lead to similar views. E. Huant, in 1946, spoke of "a property of contact, of spiritual adhesion, a kind of permeability of the Universe to human thought."

Again, the same approach affords us an evident clue to a general understanding of our capacity for invention and for aesthetic creation. In this immense field, over which all the sources of our civilisation are scattered, formal relations of all kinds appear everywhere. As the great immunologist J. Bordet likes to proclaim: "living matter is ingenious". In this marvellous property is rooted our whole pragmatic, scientific, and æsthetic power to create forms of manifold kinds.

Life, creator of forms, and evolution

As shown by these considerations, the morphogenetic power of life, as actually at work in multitudes of creatures, opens up and throws light on some of the most fascinating problems offered for our reflection. But that power has not suddenly attained its present status; it has developed gradually: evolution.

Life, heredity, evolution are the three most general concepts to which the biologist has access. He must necessarily start from the notion of Life, so far irreducible, save to translate it, as we did above, in terms of organisation. As this property inevitably implies decay and death, heredity is necessary to insure continuity of the lineages. But, if life had only been endowed with that essentially conservative function, it would have been condemned to stereotyped repetition. It could never have attained that perennial character, that ubiquity that we admire in it, granted a certain range of physico-chemical conditions. The extraordinary expansion of living beings necessitates more than the ordered repetition of events. It has been attained through their gradual alteration, the superposition of changes on regularity, the introduction of discontinuities in the conformist course of heredity; all that is, properly speaking, evolution.

Accordingly, heredity and evolution have combined with the most intimate life processes, especially in sexual reproduction, to confer on the living realm its complex and multiform aspects. The depth to which we penetrate these mechanisms increases constantly with the progression of the whole biological science. Evolution is not a classical, mummified topic. It is an ever-changing problem, which has recently gained much thanks to impressive advances in genetics, paleontology, and causal embryology.

This is not the place to enunciate and discuss the modern interpretations of evolution. Nevertheless I cannot leave the problem of form, as it now appears to a morphologist, without at least a birds-eye examination of the historical aspect of morphogenesis. Facing such an immense riddle, our attitude can only be tentative, and must be cautiously eclectic. There is certainly a large amount of truth in the system of ideas presented by neo-Darwinism as a coherent interpretation of evolution. Mutations, conceived according to the results of genetics, and selection, understood in the light of population problems, studied both in field and in the laboratory, probably hold the key to many processes occurring at the present time. These are also recognised by palaeontologists as true events of the past. However there is a current of opinion that such a theory is not capable of providing a complete interpretation of the whole process of evolution.

Three kinds of arguments are put forward to sustain this critique. One originates in the consideration of the general evolutionary process. It distrusts the idea that evolution should have happened haphazard, by the action of forces as blind as those which call forth a hurricane or a volcanic eruption. It insists on a general orientation, on some purposefulness, on the adaptive character of many structures which amount to practical tools. This last point of view has been defended magnificently by the great French biologist L. Cuénot—a pioneer in Genetics and a first rate zoologist—who died some months ago. His book on "Invention et Finalité dans le règne vivant" will remain, in my opinion, as a milestone in modern biological thought.

A second argument is presented by some of the geneticists who have devoted themselves to the difficult study of natural populations. In France, Albert Vandel—an eminent zoologist, a specialist on the humble group of Isopods (wood-lice) and a thinker formed by the best philosophical training—insists on a parallelism between ontogenesis and evolution: the ascension of lineages appears to him as a kind of long range development. In my country, the young geneticist M. J. Heuts, a clever student of natural and artificial populations, has come to think that mutations and selection leave unexplained a considerable residue, which is, in fact, the core of the problem.

The third argument comes from the study of development. Generally speaking, embryologists have rarely been warm advocates of an interpretation which exclusively, or nearly so, considers mutations of genes or similar chromosomal changes as the *primum movens* of evolutionary processes. They are, professionally, conscious of the important organisation of the cytoplasm, and do not feel obliged to subordinate it entirely to the nucleus. The recent advances in causal embryology only render this position stronger. They make it possible to formulate more clearly the problem of the initial evolutionary steps in the animal kingdom, that is, how the main types of morphogenetic organisation have diverged from one or more simpler primary patterns. In a recent essay I discussed that crucial aspect of evolution. I felt entitled to draw attention to the drastic transformations which must have taken place in the eggs at the start of a new Phylum, and must have been viable from the first. I showed how difficult it is to imagine that these advances have been achieved gradually, by small successive steps, progressively stabilised by selection. I even proposed the new concept of *onto-mutation* to designate the sudden appearance of a new type of egg organisation, with all the logical implications necessary to insure the successful beginning of a new Phylum. And, finally, I suggested that the power of *morphogenetic regulation*, which is now recognised to exist in every kind of egg, explains that the pattern of gradients and fields could be repeatedly submitted to such a thorough re-organisation. Evidently these views are speculative, for these imaginary processes lie buried in the most remote past. But is it of no importance to awaken our imagination to the possibility of such events? They concern intimate but ordinary activities of cellular life and it is not excluded that appropriate experiments could imitate them with more or less exactitude.

However this may be, a causal embryologist reaches much the same conclusion as do some of the best students of evolution under its other aspects: some discovery has still to be made to render really intelligible the history of life and of morphogenesis.

General impression

This essay does not lead to a firm conclusion. Its sole justification lies in the attempt to show how a specialist of development sees the place of his activities in the general realm of modern thought. But the author is acutely conscious of his limitations, of his inability to master problems to which a whole life could be devoted. The general idea which again strikes him, after this new survey of living forms and of their genesis, is that nowhere are matter and spirit so intimately linked together. Neither the doctrine of Mechanism nor Vitalism can afford an adequate translation of the situation before us. Mechanistic ideas can only seem satisfactory if one forgets the human mind which has built up and which defends the theory. Vitalism invokes factors or principles which are not demonstrable and which are not even necessary hypotheses. Consequently, the author wishes to finish by asserting his scientific faith in Organicism, which reconciles the struggle for objectivity with a full respect for life. And from a broader, philosophical point of view, he desires to underline that whatever aspect of form is examined, be it in the most general sense, or in morphogenesis, in evolution, or in mental achievements, the primacy of an Order, of an Idea, can always be asserted.

Literature

An introduction to the bibliography of these problems can be found in the following papers:

DALCQ A.—1949—La Pensée moderne devant le problème de la Forme. Arch. Inst. Intern. Sc. théor., S.A. p.7 à 32.

DALCQ A.—1949—La Morphogénèse dans le cadre de la Biologie générale. Actes de la Sté Helv. des Sces Nat., Lausanne p.37 à 72.

DALCQ A.—1949—L'apport de l'Embryologie causale au problème de l'Evolution.—Livr. Jub. Pr. Goldschmidt.—Portug. Act. Biol. Sei. A. p.367 à 400.

HEUTS M. J.—1951—Les théories de l'Evolution devant les données expérimentales.—Rev. des Quest. Scient., Extrait, 20 janv. 1951, p.1 à 32.

VANDEL A., 1941—L'Homme et l'Evolution.—Paris, Gallimard.

VANDEL Albert—Les modalités de l'Evolution dans le genre Porcellio (Crustacés Isopodes).—Cptes Rdus Ac. Sc., 230, p.1691 à 1693.

Illustrations: *explanatory notes*

FIG. 1. General view of the fertilised egg of a Fish, *Coregonus macrophtalmus*. If this is stained by the addition of cresylviolet, the bulging mass of animal cytoplasm (An) becomes red, and the yolk globe on the vegetal side (Vg) becomes blue. This makes the polarity conspicuous—an example of significant form. The larger circles, mainly round the neck, are oil globules—their size and shape are an example of non-significant form. (Redrawn from J. Spek, *Protoplasma*. 13. 1933).

FIG. 2. General view of a segmented egg of the brown frog, *Rana temporaria*. The egg is seen from the vegetal or vitelline pole. The dark pigment covering the animal half is visible along the equator. Between the dark ring and the whitish vegetal pole a delicate grey crescent can be observed. Its broader part corresponds to the dorsal aspect (D) of the embryo, its left (L) and right (R) horns to the corresponding sides of the embryo. On the vegetal side (V) yolk and dark pigment are adjacent. All these details are relevant for morphogenesis: examples of significant form.

FIG. 3. Gastrulation in a *Discoglossus* egg. Three successive photographs of the same egg at about 6 hours intervals, seen from its vegetal pole. In the upper one, the blastoporal lip is just appearing at the limit of the grey crescent (not very distinct here) and of the big vitelline cells (12h. earlier, this egg was almost identical to that shown in Fig. 2). In the middle picture, the blastoporal lip has surrounded the yolk region and the blastopore tends to close. In the lower picture, the blastopore has become circular and the yolk plug disappears inside; lines drawn by the pigment granules reveal the movements. This is an example of morphochoresis under its kinetic aspect and also of transitory forms which are highly significant for morphochoresis. (Photos of Pr. J. Pasteels).

FIG. 4. Gastrulation in a tortoise, *Clèmmys leprosa*. At four different stages, eggs have been opened, their embryogenic region dissected, fixed and then photographed.

(*a*) the embryogenic region at the end of cleavage. It appears as a clear area (the limits of the small blastomeres are not visible) surrounded by yolk platelets; a plane of symmetry is perceptible in the up-down direction of the picture.

(*b*) the embryonic shield has become distinct (dark semi-circular line light), the yolk platelets are condensed all around, a blastoporal lip has appeared in the posterior part of the shield; bilateral symmetry is quite evident.

(*c*) the blastopore is nearly closed hindwards, the anterior limit of the shield is covered by the incipient amniotic fold.

(*d*) gastrulation is practically at an end, the longitudinal neural grove is quite distinct, the anterior part of the embryonic shield is covered by the amniotic fold (limit slightly oblique on the main axis). A yolk condensation has formed ahead of the shield. An example of significant forms, with general reshaping of the embryogenic material. (Photos Pr. J. Pasteels).

FIG. 5. Photographs of two living rat eggs at the two cell stage. In both of them, especially in the right one, the clearer nuclear areas are partly occupied by spheres, the nucleoli; an example of non-significant form. In the left specimen, a darker area is to be observed in the cytoplasm of both blastomeres, up and somewhat right. This is a feature significant for morphogenesis, for it points to the material forming the embryo itself.

FIG. 6. A section of a human oocyte still located in an ovarian follicle. A piece of healthy ovary, which had to be surgically removed from a 25-year-old woman, has been fixed, embedded, sectioned and coloured with a method revealing true basophily, that is, the distribution of ribonucleic acid in the cytoplasm. The polarity is shown by the excentric position of the big nucleus (with its chromosomes in a cluster). *Right of the axis, the cytoplasm is darker than on the left.* The egg is surrounded by a clear membrane, the *zona pellucida*, and by follicular cells of the *corona radiata*. The distribution of the basophily is an example of a most delicate proto-morphology.

FIG. 7. A tentative representation of the double gradient system in the sea-urchin egg. The animal tendency is represented by stripes, the vegetal tendency by horizontal hatchings. It is suggested that both decreasing properties are somewhat intensified on one side of the polar axis to account for bilateral symmetry. *An.*, animal; *Vg.*, vegetal; *D.*, dorsal; *V.*, ventral. Largely hypothetical.

FIG. 8. *Aspects of the neural crest. a* and *b. General dorsal views of a Discoglossus embryo at two successive stages*; in *a*, the neural plate (N.P.) is formed and the neural crest (N.C.) is expanding on both sides of the future brain;

in *b*, the plate is closing and the neural crest appears as two distinct ridges. *c, d, e, aspects concerning the Salamander. c.* general dorsal view of a neurula stage, with the neural plate (N.P.) and the location of the neural crest material (N.C.) all along the neural ridge. *d, e,* right lateral views of reconstructions showing the nervous system of young embryos at two successive stages, to demonstrate the migration of the neural crest material (N.C.). *Sp. Ch.*, spinal Chord; *S*, solerotome. (*c, d, e*, redrawn from Sv. Horstadius, The Neural Crest, Oxford University Press, 1950).

FIG. 1

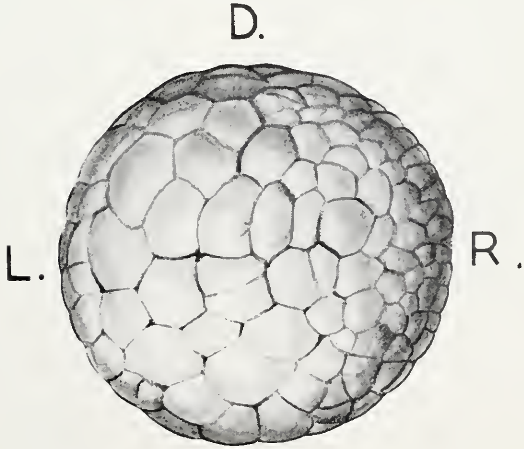


FIG. 2

FIG. 3

a

b

c

d

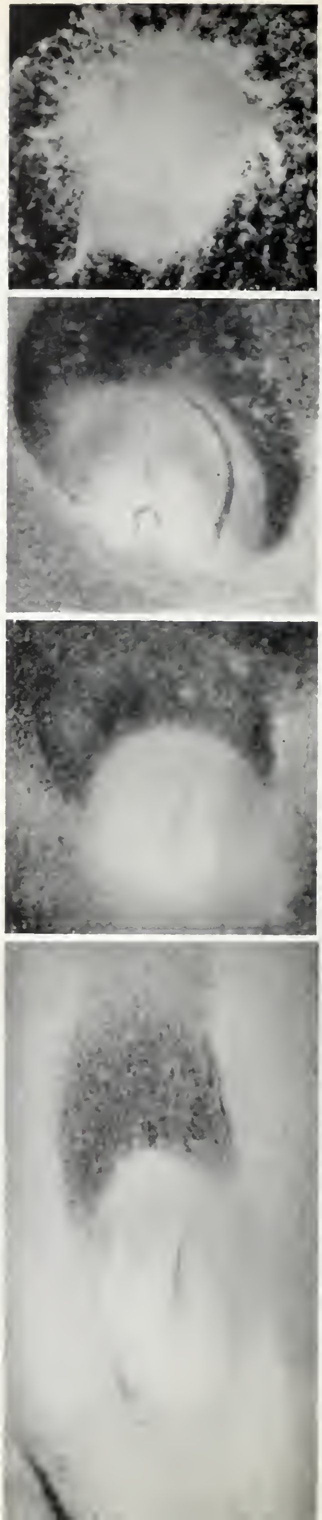


FIG. 4

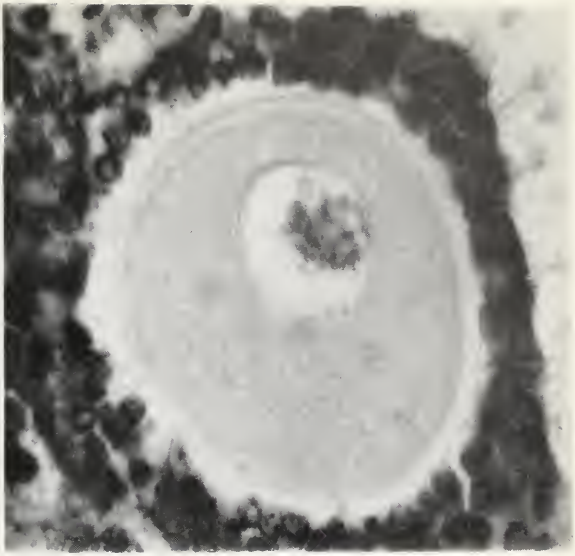


FIG. 6

FIG. 5

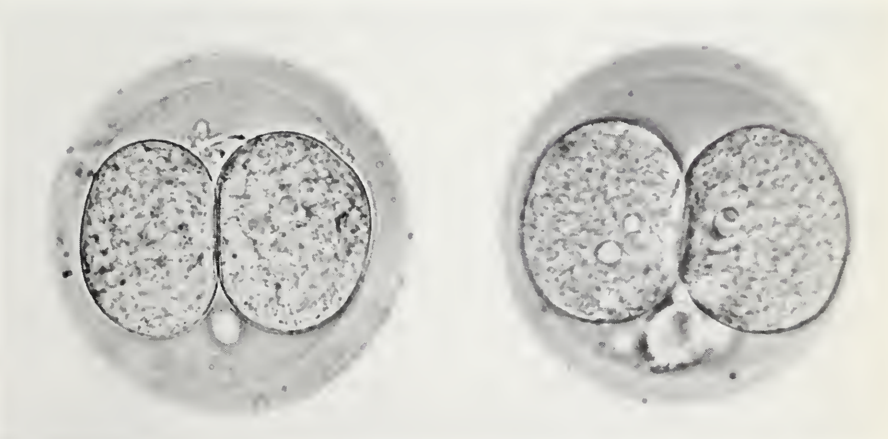


FIG. 7

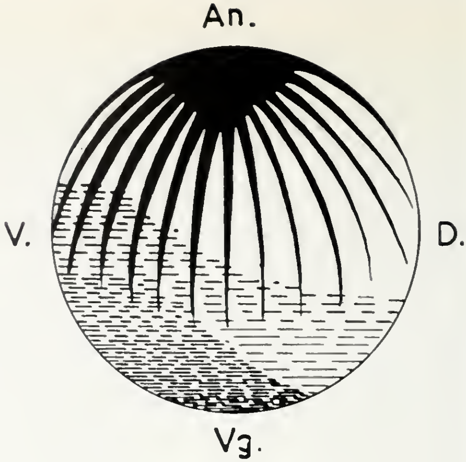
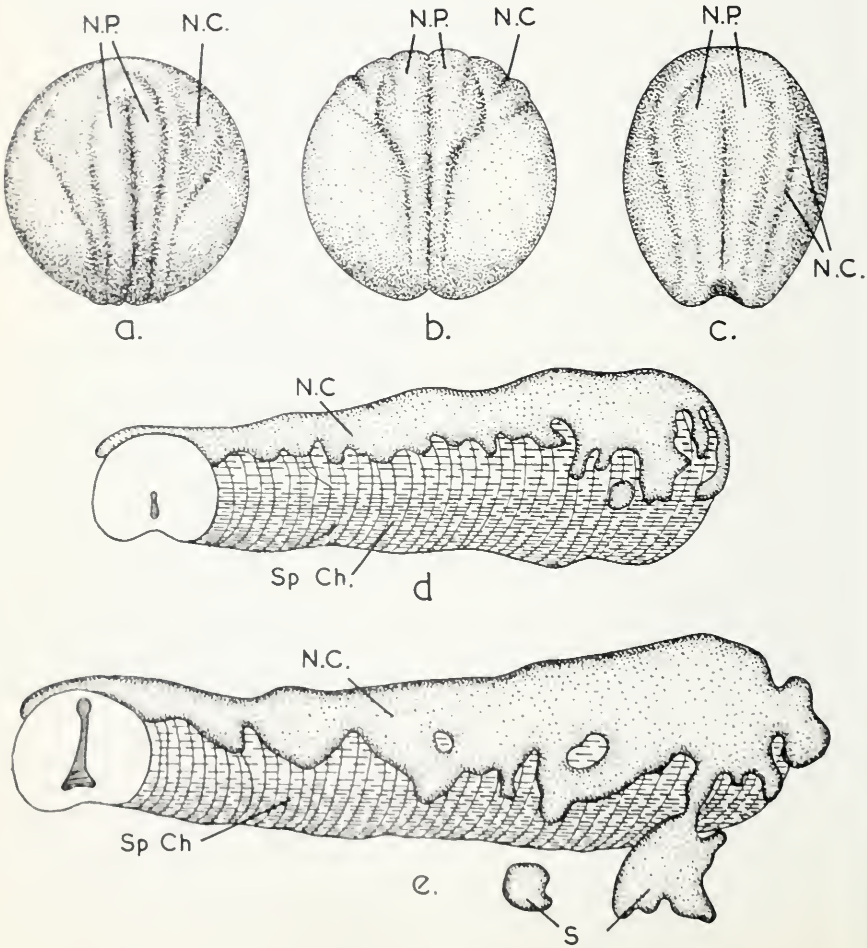


FIG. 8



Animal Form in Relation to Appearance

by Hugh B. Cott

The evolution of form in animals is closely associated with their mode of life. We may note briefly in the first place, that three main ways of life are open to them: they may be free-living and active, a habit characteristic of the great majority of species; they may be sedentary or inactive; or they may exist as external or internal parasites upon or within the bodies of other animals. These diverse conditions of life exert a strict control over the general organisation of the body. In free-living forms, such as a lobster or a lizard, where the environmental conditions are different for the upper and under surfaces, and where in locomotion one end goes in front, we find dorso-ventral and antero-posterior differentiation, associated with bilateral symmetry. In sessile or passively-floating forms, such as a sea anemone, jelly fish, or sea urchin, where active movement becomes unimportant to the mode of life, the differentiation is mainly between upper and lower surfaces, associated with a tendency towards radial symmetry. In parasites and especially those living within the body of their hosts and which are out of contact with the external environment, adaptations are mainly physiological, sometimes involving loss of symmetry, and generally, degeneration of nervous and other systems of the body, but with complex development of the reproductive mechanism.

Again, if we confine our attention to the free-living forms, we find these—even if different members of a limited group of animals—exploiting many types of habitat for a livelihood. For example, air-breathing creatures have many worlds to conquer: they may live on the surface of the ground, and develop speed; they may return to the water and become amphibious or secondarily aquatic; they may exploit the advantages of a subterranean habitat; or they may live above the surface of the earth, becoming adapted to life in the trees; or finally, like the insects, pterosaurs, birds, bats and man himself, they may master the air by true flight. Life in each of these habitats in turn demands varied specialisation in locomotary organs—whether developed for running, leaping, swimming, digging, climbing, swinging, gliding or flying. Moreover, in each environment widely different modes of feeding may be evolved, so that we find further wide radiation in habit—filter-feeding, carnivorous, piscivorous, insectivorous, herbivorous, frugivorous, omnivorous or scavenging—each requiring special modifications of teeth or tongue, beak, jaws or other organs associated with capture and manipulation of the pabulum.

A third factor influencing form, and that with which we are concerned in the present essay, is an animal's appearance, considered in relation to the visual perception of other animals, whether of the same or different species. In the struggle for existence, two primary necessities for life are security and sustenance. If an animal is to survive, it must in one way or another obtain food and at the same time avoid being eaten. A third basic requisite, which relates to the species rather than to the individual, is reproduction. The devices by means of which animals achieve these three ends are almost infinitely various. Many, themselves bewildering in their varied modes of action and application to the day-to-day needs of survival, fall into a class by themselves—in that they exert their influence upon other animals from a distance, by sound, by sight, or by scent. To such characters the term "allaesthetic" has been applied.

The nature of allaesthetic characters, and the "public" in relation to which they have evolved, vary widely: on the visual side, the phenomena fall broadly into three main categories—

namely, concealment, disguise, and advertisement; on the functional side, these elusive, deceptive or attractive features are variously concerned with other organisms of the habitat—whether predators or prey, mates or rivals, parents or offspring. Through reduced visibility, they may facilitate the capture of food or escape from an aggressor; through deceptive or mimetic effects, they may mislead the observer as to an animal's whereabouts, attitude or identity; through increased conspicuousness they may serve as a warning to enemies or a threat to rivals, as a courtship display, or a recognition mark. In the following pages, we shall consider briefly some of the expressions of visual adaptation—which involve not merely modifications of form (actual or apparent) and coloration, but elaborate associated changes of posture, and habit—all of which can be seen in true perspective only when viewed in relation to the animal's natural environmental background.

Obliterative Shading

In the visual interpretation of form, effects of light and shade, or relief, take a prominent place. The great importance of relief as a clue to recognition may easily be demonstrated. If we take three cylinders of paper, three half-cylinders and three flat paper strips, and fix them horizontally so that the eye is presented with a series of convex, concave and flat surfaces, their real form, when they are illuminated from above, is readily made out. But if we colour each of these forms in three ways, namely (*a*) with graded tones ranging from black above to white beneath, (*b*) with graded tones ranging from white above to black beneath, and (*c*) with a uniform half-tone—then, on viewing the shuffled objects from a distance, it is impossible to pick out all those which are convex, concave and flat respectively. Now for our present purpose, one of these nine combinations of form and coloration has a particular interest. It is the cylinder which has been graded from dark above to light beneath. When this is seen under diffused top-lighting, the more highly illuminated upper surface is darkened, and the shade of the under surface is lightened, by paint. The effect of this graded pigmentation is to neutralise relief, and thus visually to flatten the cylinder.

This optical device is one very widely adopted in the animal kingdom. In innumerable animals, belonging to groups as diverse as caterpillars and cats, mackerel and mice, lizards and larks, countershading forms the basis of their coloration. Such animals are coloured darkest above, lightest beneath, with graded tones on the flanks; or, as in certain zebras, civets, genets and guinea-fowl, a similar result is produced by patterns when they become blended with distance. Described in print, this principle of obliterative shading may not appear very remarkable. But these effects, like many of those treated in the following pages, are of course visual, and they need to be seen in nature to be appreciated. Viewed under diffused lighting from the sky such animals seem to lack solidity, and when, as often happens, they also wear a superimposed disruptive pattern, their bodies are easily overlooked, being accepted by an observer as mere incidents in the background. It will be noted that in achieving such results, nature goes to work in the opposite way to an artist—who by the use of light and dark pigments produces the illusion of solidity and relief on a flat surface.

Countershading is typical of cryptic animals living in a well-illuminated environment. It is significantly modified or absent under special conditions where its use would be ineffective. Thus, in the larva of the Eyed Hawk Moth (Plate V, 1) the gradation from dark to light is reversed—the insect's back being light and its belly dark: but this reversal is correlated with the habit of resting in an inverted position. Again, while countershading is extremely common in surface-swimming fishes, in deep-sea forms living in the darkness of the abyss it is not found. Similarly, it is absent in cave animals, and in subterranean burrowers. In other cases its absence is connected with the biological advantage to be derived from a round appearance—as in some stick insects, twig-like caterpillars (Plate II, 1) and stick-like spiders, which rely for disguise upon their resemblance to natural objects of no food-interest to their enemies.

Disruption—the Rôle of Pattern

In the previous section we have seen how the visibility of form, as revealed by graded effects of light and shade—to which is mainly due the appearance of solidity—may be modified or even obliterated by countershading. A countershaded but self-coloured animal nevertheless tends to be revealed as a continuous patch of colour in the visual field, differing more or less from the background against which it is seen, and bounded by a characteristic contour. For effective concealment, it is essential that this tell-tale shape or silhouette should be destroyed. The difficulty of doing this is met, often with extraordinary success in nature, by the use of patterns (*see* Plates I; III; VIII; VI, 1).

Differential Blending

A simple but highly effective use of pattern is seen in animals having the surface of the body broken into two colours, light and dark in tone, and of hues dominant in their background. When the form of any animal, such as a moth, is uniformly coloured, and seen against a background from which it differs in tone and colour, it presents maximum conspicuousness to the eye of an observer, and is readily recognisable by its shape (Fig 1, 1). If the surface-continuity is broken by a pattern of contrasted tones, a step is taken towards concealment, even when the whole surface is differentiated from the background (Fig 1, 2). The effect of the disruptive pattern is greatly strengthened when one of its component colours resembles and blends with the background, while the other component differs strongly from it: under such conditions only certain parts of the form can be recognised and these in no way suggest, but rather tend to contradict and distract attention from, the animal exhibiting them (Fig 1, 3). Finally, the concealing effect will be further enhanced when the animal is exposed at rest against a broken background of the same coloration as itself. Ideally, such an animal when motionless becomes virtually unrecognisable (Fig 1, 4). Such differential blending is commonly seen in nature, as for example, in the eggs of the Lapwing or Golden Plover (Plate I), where the olive-brown and black pattern of the shell blends with the surrounding broken chiaroscuro of earth or dead vegetation and shadowed interspaces.

Maximum Disruptive Contrast

Differences of tone, as opposed to those of hue, play a most important part in the visual concealment of form. Since the optico-psychological effect of a disruptive pattern is to break up what is really a continuous surface into what appears to be a number of discontinuous surfaces, it follows that the most effective patterns are those whose components show the maximum tonal contrast. Such patterns actually attract the observer's eye to themselves; but since they contradict the structure of the form wearing them, they tend all the more to confuse judgment and distract attention, just as a conjuror deflects the attention of his audience by actions which are intended to be seen. A homely example of this principle is provided by the familiar white net curtain—so effective as a visual screen against the passer-by in the street. On looking at the window from outside, one's vision is arrested by the curtain on account of its brightness in relation to the dark room interior. But the curtain merely distracts the eye: that it does not intercept the view like an opaque screen is evident, for if it be dark or dirty, or if it is viewed at night when the room-interior is illuminated, then the principle of tonal contrast no longer operates, and the curtain ceases to be an effectual visual barrier.

Thus it is that the greater the contrast in tone between elements in an animal's pattern, the greater will be its distractive function. With this principle in mind, a glance at many members of the animal kingdom, whether mammals or birds, fishes or frogs, snakes or insects, will show how widely it has been exploited in nature. The effect is greatly heightened when there is a build-up of tonal contrast along the adjacent boundaries of the dark and light elements, as seen in the patterns of the Copperhead Snake (Fig 2), Puff Adder, and of many birds, grasshoppers, moths and butterflies.

Coincident Disruption

We have seen in the foregoing section that the success of a disruptive design depends upon the obliteration of visual form by means of superimposed patterns, and that when any object like an animal bears upon its surface a pattern of contrasted colours and tones, so arranged as to contradict anatomical features, they serve to mask its real form, which is replaced by an apparent but unreal series of separate shapes. These forms tend to be interpreted as representing a number of separate surfaces—none of which suggests, by shape or arrangement, the body which bears them. In short, such patterns are successful because they break up surface continuity. Similar optical devices are carried even further in the case of many animals where the pattern has precisely the opposite effect, in that it serves to unite discontinuous surfaces.

Important visual clues to recognition are afforded by the several component parts of the body—such as legs, wings, fins, mouth or eyes. If seen as specific units, such organs tend to reveal their owner. This difficulty has often been overcome in nature by the use of coincident patterns, which sweep, unbroken, across adjacent but anatomically distinct parts. The principle is beautifully illustrated by the East African tree frog here figured (Fig 3). This animal is coloured brown and silvery-white. A broad stripe of the latter colour runs down the side of the back, and again along the median segment of the hind-limb. The meaning of these markings only becomes apparent when the frog, a nocturnal form, is seen in its diurnal attitude of rest. When in this position, the stripe on the exposed part of the hind-limb exactly coincides with and forms a continuation of the similar stripe on the back. In nature such a pattern effectively masks the identity of the animal wearing it. Various other frogs carry patterns on the hind-limbs which are so disposed that bars of contrasted colours run right across the three folded segments of foot, shank and thigh. Their appearance is as though an artist had passed his brush across the folded leg, and thus produced an effect which is, of course, in absolute contradiction to the morphology of the limb (Fig 4).

Such coincident patterns are too widespread in nature, too complex in detail, and too closely associated with their wearers' resting attitude, to be explained away as mere accidental effects. In many fishes these patterns sweep unbroken across the root of the tail on to the dorsal fin above and the anal fin below; in many grasshoppers they form continuous transverse bands of colour extending from the folded wing covers on to the adjacent femur of the hind-limb, or in others a longitudinal leg pattern is continued along the side of the insect's body; in various butterflies, such as the Comma (Fig 9) the pattern, often extremely complex in detail, extends from the exposed under surface of the fore-wing on to that of the hind-wing; while again in certain moths such as the Blood Vein and Scalloped Oak (Fig 5) they sweep without interruption across the exposed upper surfaces of all four wings.

Concealment of the Eye

A special and highly interesting application of such patterns is seen in the concealment of the eye in many fishes, frogs, reptiles, birds and mammals, and again even in some grasshoppers. Unmodified, the eye of a vertebrate, with its black pupil surrounded by a circular coloured iris, is a veritable target, which tends at once to attract attention. Few natural objects possess greater inherent conspicuousness. If, however, the eye, with its staring black pupil, can be made to appear another shape, then its significance for the observer will be altered. In theory, such an illusion could be created by covering the eye with a black mask of irregular shape, so designed as to blend with and pass for part of the patterned background. In practice, this is achieved by the inclusion of the pupil within a pattern of black pigment which sweeps across the whole or part of the iris and continues on the scales, skin, feathers or hair of the head, as in the frog (Plate III, 2 and Figs. 6, 7). In this way the target is obliterated. Anyone interested in ornithology will realise how frequently disruptive patterns are closely associated with the birds' orbit. The Woodcock has a dark strap of colour which passes from eye to eye transversely over the head (Plate III, 1). The Snipe has a stripe, similar in function, but passing horizontally along the side of the head and including the eye in its sweep. Cream-coloured Courser, various plovers and many other birds illustrate the same point.

Contour Obliteration

Disruption of surface is not the only concealing function of patterns: a special problem is presented by the continuous outline, often of charactistic shape, which bounds the visible surface and which is of great significance as a factor in recognition. Pattern can be used to break up a continuous contour just as it can to break up a continuous surface. Essentially, outline obliteration is induced when contrasted elements in the pattern cut across and are arrested by the margin. This principle is well illustrated by a comparison of the two rectangles in the accompanying figure (Fig 8). In one (left) the pattern follows the boundary; in the other (right) it cuts across the boundary. If this figure is viewed from increasing distances, a point will be reached when the black and white patterns blend as a grey half-tone which is lost against the background; but this critical distance for the left-hand figure is nearly twice as great as that for the right-hand figure. In nature, such secant patterns are of frequent occurrence, and are well seen in the Zebra, whose stripes everywhere are so disposed as to break out against the contour—of ear, muzzle, neck, withers, back, belly, buttock and leg.

A functionally similar device, but one which is anatomical rather than optical, involves the actual modification of the contour itself, as in the irregular wing-contour of the Comma Butterfly (Fig 9), in the bizarre excrescences on the legs of some tropical mantids, and in the weed-like outgrowths of the Australian sea-horse *Phyllopteryx*.

Shadow Elimination

Another important aid to visual recognition is provided by the shadow which an object casts upon its background. Everyone with experience in reading aerial photographs will appreciate how significant is this feature. In the patchwork configuration which the eye sees in nature, shadows take a prominent place—indeed, the shadow of a cryptic animal may well be far more conspicuous than the body that throws it. Hence it is not surprising to find in the animal kingdom various modifications, both of habit and of structure, whose function is directed towards shadow elimination.

When at rest, certain animals orientate the body in relation to the sun, and thus reduce their shadow's size. Such behaviour is, of course, especially effective in the case of laterally-compressed forms, and it is well seen in various butterflies which alight on the ground with the body orientated, so that the shadow cast by their uplifted wings is reduced to a mere inconspicuous line. Other butterflies, like the Grayling, tilt the wings over in a more or less pronounced "list", so that their cryptic undersurface screens the shadow which they cast.

Dorso-ventrally flattened animals are of course pre-adapted in this respect, since the length of a shadow is directly proportional to the height of the object casting it. Nevertheless many such creatures attain yet more effective concealment by crouching low —either habitually when at rest, as in the case of flat fishes and skates and various bark-dwelling bugs, moths and geckos; or instinctively in times of danger, as in the case of young Stone-Curlews (Plate VI, 2), Ringed Plovers, Oyster-Catchers and other birds, and of various tropical shore crabs.

Perhaps more remarkable than the above instances of cryptic posture are those animals which have in addition evolved special flaps or fringes or frills that serve most effectively to fill in the space between the lower edge of the body and its substratum, and thus to mask any tell-tale furrow. Such structural modifications are found in many stick-like Geometrid caterpillars, such as those of the Early Thorn, Brimstone and Pepper-and-Salt Moths (Plate II, 2), which carry a number of light-coloured fleshy tubercles between the posterior clasping legs: this frill neutralises the shade between the insect and its food-plant so that the animal —itself wonderfully twig-like—appears to grow out of the branch upon which it rests. In other species, such as the larva of the Red Underwing, which lie with their whole length closely applied to a twig, the frill extends the whole length of the body. Thus the structures are in each case distributed where, in terms of vision, there are needed.

Such devices reach their climax in various tree geckos and fishes. A highly cryptic, bark-like and bark-living gecko of Malaya has the fingers and toes webbed and a frill of skin projecting on each flank, while the tail is broadened like the handle of a spoon: all these structures cause the creature to melt into its background. Even more striking is the Angler Fish, with its irregularly-shaped cryptic frill extending all round the margin of the huge mouth, and along the sides of the body. When these bottom-living fishes come to rest, they habitually flop down in such a way that the frill is spread outwards by the out-flow of water, and thus the fish becomes optically united with and part of its background.

Background Picturing

We now pass to a visual device, one aspect of which is the very opposite of that just considered. For while, as we have seen, actual shadows may be effaced, so too spurious ones may be suggested. It frequently happens that the dark elements in a disruptive pattern are so shaped and disposed as to suggest the irregular shadows or interspaces of the natural habitat. Such fake shadows are seen in hawk moth larvae (Fig 10), where they variously represent or suggest the shade beneath a curled-over leaf-edge or the shadow of midrib and lateral veins. They occur again in innumerable creatures which rest on bark—whether bugs or moths, lizards or tree frogs. Thus it comes about that such animals exhibit on the exposed surfaces of their bodies a replica of their natural habitat—whether of bark, lichen, heather, coral or sea-weed. It is as though a picture of their background had been painted upon themselves: and in effect that is what has been achieved.

Not only do such animals habitually rest in the surroundings which they resemble, but in many cases special postures are adopted which serve to bring the pattern into conformity with the background configuration (Fig 11). Thus, many moths with horizontal wing-markings, such as the Willow Beauty and Scarce Tissue (Plate VIII), rest with the body turned sideways, so that the pattern of the wings is aligned with the vertical pattern of the bark on which the insect rests. Similarly, when disturbed, the nesting Bittern raises the bill and presents towards the observer the vertically-striped plumage of the upstretched neck and breast, which then harmonises in configuration as well as in coloration with its background of tawny reeds and dark shadows.

Disguise and special resemblance

Instances like those mentioned above intergrade with others in which protection from attack or capture of prey is facilitated by special resemblance to some seemingly innocuous object—such as a leaf or patch of lichen, a flake of bark, a twig or thorn, a stone or piece of sea-weed, a flower, or the dropping of a bird. This expression of the principle of disguise reaches a wonderful degree of perfection among various spiders, grasshoppers, Geometrid caterpillars, butterflies, praying mantids and leaf-insects, and is even found among vertebrates: and we have to note that the visual deception is perfected not merely by modifications of form and coloration—remarkable and extravagant as these may be—but also by the adoption of special and appropriate habits and postures, which in turn are correlated with particular types of habitat and background.

These points are well illustrated by certain members of the Acridiidae or short-horned grasshoppers. For example, in East Africa the slender grass-haunting *Certacanthacris tatarica* (*Plate* V, 2), has the tegmina or wing-covers and thorax decorated with a disruptive design of dark brown, pale buff and green which exactly assimilates with the natural habitat. Living in semi-desert of the Canary Islands, *Acrida turrita* in form and coloration resembles a sprig of the sun-burnt grass with which it is associated. In this species the antennae are flatttened and taper to a point and are held erect and diverging from one another: this gives them the appearance of young blades at the end of a grass-shoot. On the other hand, *Omura congrua*, a stick-like species from British Guiana, perfects the resemblance by stretching the antennae forwards and holding them together, so that they continue the linear form of the body. Even more remarkable is the desert-dwelling *Eremocharis insignis* of Algeria, which bears a close likeness both in form and texture to a rough and weathered rock fragment; its hind femora are flattened and fit closely and inconspicuously against the sides of the body; while the tell-tale antennae, much reduced in size and thread-like, are lowered and laid flat against the front of the face, where they disappear against the simulated stone.

The above-mentioned animals illustrate the principle of adaptive divergence or radiation—related forms being differentiated is relation to diverse modes of life. Conversely, it frequently happens that quite unrelated organisms, in taking on a deceptive likeness to some particular natural object such as foliage or bark, so incidentally come to resemble one another. Thus many animals of the most diverse groups which live amongst sea-weed closely resemble their environment: notable examples occur in the Sargasso sea, where various crustaceans, molluscs, annelid worms and fishes adopt a common uniform. Similarly, many of the most striking examples of special resemblance are found among leaf-mimics, which include butterflies such as the famous *Kallima* of

Ceylon (Plate VII, 1), various moths, caterpillars of several families, long-horned grasshoppers, leaf-insects (Plate VII, 2), and mantids, as well as certain tropical toads, chamaeleons and fishes. Among the last-named *Monocirrhus polyacanthus*, the "Peche de Folha" of the Amazon (Fig 12), both looks and behaves like a water-logged leaf, being extraordinarily flattened in form and having a "beard" which does duty for a leaf-stalk; and here the resemblance is aggressive rather than protective in function, enabling the animal to drift towards its victim undetected, until close enough to dart forward and engulf the unsuspecting quarry.

Adventitious resemblance

We must here briefly mention another device by which disguise is achieved—though in a strikingly different manner—namely, by the use of an adventitious covering of foreign objects. Many animals habitually masquerade in garments borrowed from their surroundings. In such cases the cryptic appearance depends absolutely upon highly specialised behaviour, such animals instincttively covering themselves with a clothing of leaf-fragments, sticks, or sea-weed—as seen for example in various beetles, caterpillars and dressing crabs. Such creatures often carry on the body hooked bristles or spines which do duty as clothes pegs. If the disguise is removed from a dressing-crab's carapace, the animal will at once begin to clothe itself again: and if it is removed into a new environment it will assume a new disguise to suit its changed surroundings.

Warning coloration and bluff

The coloration of many animals is the reverse of cryptic, in that it serves rather to reveal than to conceal. Coloration of this type, known as "phaneric", meets widely different biological needs, and may be utilised in various contexts, both interspecific and intraspecific. Among the first it serves such functions as warning, bluff, false warning, allurement or distraction; and in the latter, threat, sex- or social-recognition, and epigamic display associated with the reproductive cycle.

Everyone is familiar with the fact that many creatures, such as salamanders, skunks, hornets and ladybirds are highly conspicuous: moreover their behaviour as well as their coloration is advertising.

The theory of warning coloration—originally proposed as an explanation of the appearance of certain gaudy caterpillars, but now known to apply widely to a certain type of phaneric coloration in many groups, including spiders, frogs (Plate IV, 1), birds and mammals—is based upon the fact (well established by innumerable observations and experiments) that such advertisements are associated with distasteful or dangerous attributes which render their owners relatively unacceptable as prey. Since many predators such as birds learn by experience what is fit to eat and what is to be avoided, these advertisements serve to facilitate recognition and recollection, and thus favour the creatures exhibiting them.

A different expression of the warning principle involves the sharing of a common warning livery by two or more unrelated but distasteful species: for example, certain Lycid beetles with orange-and-black warning colours are resembled by a considerable assemblage of other insects, including various wasps, flies and moths. Such a similarity, known as Müllerian mimicry, provides a combined warning to enemies and tends further to promote their rapid education and thus to reduce the total number of casualties during the trial-and-error stages of learning—to the mutual advantage of the species in the Müllerian association.

Very different are the conspicuous advertisements and threatening attitudes displayed by certain animals which are not themselves protected by deterrent tastes or stings. Here the mechanism rests upon a principle of bluff, or false warning. Such displays often involve a sudden increase in size, either by the distension of the body, as in chamaeleons and toads, by presenting its maximum surface towards the aggressor, as in the familiar threatening posture of a kitten, or by the erection of frills, fans, wings or other organs. Often the deterrent character exhibited by insects such as the Eyed Hawk Moth and the East African Mantis *Pseudocreobotra wahlbergii* (Fig. 13) include a large ocellus or dummy eye: and sometimes the displaying animal takes on the appearance of a formidable adversary, as in a Brazilian hawk moth caterpillar (Fig. 14) which, when provoked, inflates the anterior segments of its body so as to expose two large fake eyes and assume the likeness of a snake. Such cases of bluff intergrade with those of Batesian mimicry, to be considered in a later section.

Allurement and Distraction Display

Again, advertisements may be used as lures or baits, which serve to attract unsuspecting prey towards a predator. Disguise for such an offensive purpose—depending upon the exhibition of some object attractive to the prey—is seen in angler fishes, star-gazers, and in the Brazilian "Matamata" turtle, all of which carry lures near the jaws; certain deep-sea angler fish have an elaborate mechanism including a fishing rod, line, hooks, and a photogenic organ serving as bait; while certain tropical spiders and preying mantids resemble, respectively, the dropping of a bird, or a blossom, and thus attract insect visitors to themselves.

Yet another use of self-advertisement is seen in the so-called "injury-feigning" or distraction displays, by means of which during the breeding season parent birds—by various grotesque and conspicuous actions—draw enemies away from the eggs or young, and towards themselves. It is interesting to note in passing that while this habit has been evolved by birds of many groups, including plovers, nightjars, buntings and others, it appears to be confined absolutely to birds as a class, and is not known elsewhere.

Courtship and Epigamic Display

When we turn to the uses of advertisement in the inter-relations between members of the same species, their variety and abundance is again almost bewildering, and it is only possible here briefly to mention a few relevant points of interest. Inter-specific display is found in many groups of animals, including insects, spiders, fiddler-crabs, newts, lizards and mammals; but it is amongst birds that the phenomena reach a climax. Most commonly, such displays serve, in one way or another, to promote successful reproduction—the ritualized postures of birds constituting a signal-language used particularly during courtship and in rivalry between males. They fulfil a variety of functions, at physiological and psychological levels—serving variously to threaten in inter-male visual combat, to advertise the presence of an unmated individual, to stimulate processes leading to ovulation, to synchronise the reproductive cycles of male and female or as an emotional bond throughout the prolonged period of mating, nest-building, incubation and parental care. They take many forms, including communal displays, mutual displays in which both sexes participate, nest-relief, recognition and greeting ceremonies. The main point which we have here to notice is that in the bird's world, signal-language plays a most important part; and that the display itself is made effective by modifications of coloration, structure and posture. In general, the display presents the bird in a striking or abnormal aspect; and where, as is usual, bright colours or specialised plumage or organs are found, these are typically made conspicuous to the observer by specific postures and behaviour-patterns.

Colour Conflict

The phenomena of allaesthetic coloration fall, as we have seen, into two main functional groups—cryptic and phaneric. Those in the first category, which tend towards effacement, operate exclusively in the interspecific struggle for existence, e.g. in the relations between predator and prey. Those in the second category, which tend towards advertisement, subserve on the other hand many diverse functions, both interspecific and intraspecific, e.g. in the relations between predator and prey (warning coloration, Müllerian and Batesian Mimicry, and distraction displays), in those between rival males (recognition and threat), in those between the opposite sexes (sex recognition and epigamic display), and in those between parent and offspring (feeding and recognition stimuli). Thus it will be observed that both concealment and conspicuousness carry biological advantages. Yet, for obvious reasons, these two types of coloration are antagonistic, if not mutually exclusive. This conflict between the rival claims of cryptic and phaneric coloration is met in various ways, and as an example we may here briefly consider how the problem has been solved by birds.

In many species, where the normal coloration is predominantly cryptic in the resting attitude, previously-hidden patches of conspicuous colour are exposed to view in movement, especially when the bird is in flight, or in particular display attitudes. Such are the group recognition marks on the secondary wing feathers, rump and tail feathers of many plovers and waders. A similar two-purpose system of coloration is seen in many animals which exhibit what are known as flash colours when they leap or fly—like the black-and-white seen in the otherwise highly cryptic desert-living Bifasciated Lark when in flight, or those momentarily exposed on the "wings" of flying lizards of the genus *Draco*, on the hind-wings of many grasshoppers, or on the groin and flanks of various tropical tree frogs. Such momentarily exposed patches—frequently red or yellow in hue—being visible only during rapid movement and suddenly eclipsed as the animal comes to rest, are believed to confuse a pursuing enemy. Also included in this group (though of course not found among birds) are the light-producing organs in fire-beetles, various deep-sea fishes, crustacea and other animals, which possess photogenic organs whose light is intermittent and under mechanical, nervous or humeral control. Essentially, all such characters have this in common—they are transitory, and the animals exhibiting them are quick-change artists.

A striking example is afforded by the newly-hatched young of the Lapwing, Egyptian Plover, and other related species. These youngsters carry a conspicuous white patch of down on the nape. When an intruder enters the breeding ground, the parents utter a warning note, and the highly cryptic offspring scatter and crouch motionless, with the nape-patch hidden. But when danger no longer threatens, at the return and "all clear" call of the parents, the young stand up or run, with the head bent downwards so as to expose the white patch on the neck, which doubtless acts as a recognition mark enabling the adult bird to reassemble her brood. Other familar transitory advertisements are seen in the brightly coloured and greatly enlarged gape of nidicolous nestlings—exposed to the parent preparatory to the feeding reaction.

The problem of colour conflict may also be met by the exhibition of these two rival sets of coloration by different groups of individuals within the species (rather than on different parts of the body in the same individual). In such cases the advertising coloration is generally worn by the less vulnerable or less valuable members, such as males, or adults; and the cryptic dress by the more valuable or defenceless members, such as females, or young. Among sexually dimorphic birds, like many game birds and ducks which nest in the open, it is typically the male that has utilised the biological advantages of conspicuousness, whether for purposes of display or to deflect the attention of enemies from the mate; while the female, upon whom devolves the duty of incubation, has been forced to take the evolutionary road leading to concealment. Parallel conditions obtain in the parent-child relationship: for example, the young of many ground-nesting species such as the Oyster-Catcher, and of gulls, terns and skimmers, in which adults of both sexes are conspicuous, are themselves highly cryptic.

Other conditions obtain with large birds, possessed of fighting strength or formidable powers of offence, and which therefore have little to fear from predatory enemies. Here the way is open for the untrammelled use of advertisement by both sexes—as seen, for instance, in the coloration of albatrosses, penguins, gannets (Plate IV, 2), frigate birds, swans, cockatoos, ravens, and many others. While conversely, many small and relatively defenceless species tend—like larks, pipits, partridges (Plate VI, 1), quails, and nightjars—to forego the advantages of conspicuousness and to take the opposite road, both sexes being typically cryptic, as is generally true of ground-nesting species in which incubation is shared by both parents.

Resemblances between Animals

We now come to a highly interesting aspect of the modification of form and appearance. Everyone is familiar with the fact that—though members of the animal kingdom show a vast range of diversity, whether of size, organisation, structure, or habit—different species nevertheless often resemble one another, as for example, a Willow Warbler and a Chiffchaff, or a Swallow and a Swift, or a Cuckoo's egg and that of the Meadow-Pipit in whose nest it is laid. When we study such resemblances, we find that they fall into various categories having widely different biological significance.

Firstly, the commonest and most familiar type is that in which the likeness is due to relationship—such as that seen between a

Lion and a Puma, or a Rook and a Raven, or between a Poplar and Privet Hawk Moth—resemblances, in fact, such as are used in the systematic or "natural" classification of members of the animal kingdom, and which indicate true affinity in the taxonomic sense.

A second type of resemblance, whose significance is perhaps less well appreciated by the layman, is that often exhibited by unrelated animals which have adopted, and are adapted to, a similar mode of life. For example, the Mole (*Talpa*) has a counterpart in the Australian Marsupial Mole (*Notoryctes*) and again in the Mole Rat (*Spalax*) of the Lebanon: all these animals are superficially alike (being blind, earless, having short sub-cylindrical bodies, reduced tails, and powerful broad and heavily-clawed digging fore-limbs): yet they belong, respectively, to the three distinct mammalian orders Insectivora, Marsupialia, and Rodentia. Or again, a Basking Shark, an Ichthyosaur, and a Porpoise all share in common the form of a "fish" (having a compact, neckless, spindle-shaped body, with stabilising fins or paddles and tails with swimming flukes); though the second belongs to an extinct group of reptiles, and the third is of course a mammal and more nearly related to a ferret than to a fish. A Humming Bird and a Humming-bird Hawk Moth again bear a general and superficial likeness when seen feeding at a flower, though here the relationship is still more remote. Such cases of superficial similarity between unrelated organisms are brought about by independent adaptation to a common mode of life, and are utterly distinct from the first group—being due, not to affinity, but to adaptive convergence.

In a third category are certain resemblances which, like those just considered, are independent of relationship, but which unlike them, so far from being adventitious, are believed to have evolved for their own sake: in other words, the likeness, as such, is the end that has been aimed at in their evolution. The Hornet and, the Hornet Clearwing Moth, or the Honey Bee and the Hover Fly may be cited as examples. In such cases, the resemblance is typically between a dangerous or distasteful, and a defenceless or palatable animal—the latter gaining a measure of protection from predatory enemies by its likeness to the former. Such resemblances are known as mimetic—the term in its zoological sense being of course descriptive and without any implication of conscious imitation.

Mimicry

The phenomena of false-warning, or Batesian mimicry, are extremely varied, and the subject has a large literature: it is only possible here to mention a few selected examples to illustrate points of interest. In the first place, such resemblances are, as we have seen, essentially independent of affinity, occurring between species belonging to different families, orders, classes, or even phyla: consequently, the mimic departs more or less widely from the usual appearance of its congeners. Thus, various Asilid flies bear a marked likeness to Xylocopid bees—being broad-bodied and hairy, with pigmented wings; while their non-mimetic relatives are slender-bodied and naked, with narrow transparent wings. Again, the eggs of non-parasitic cuckoos are typically white: but those of different parasitic species frequently bear the closest resemblance to those of the birds in whose nests they are deposited; and in the European Cuckoo they take on the appearance of different models in different countries—such as the Meadow-Pipit in Scotland, Great Reed-Warbler in Hungary, and Brambling in Lapland.

Mimicry also involves marked modification of behaviour. Most moths are crepuscular or nocturnal in habit; but species like the Lunar Hornet fly by day, when their models are active. The same applies to moths whose models are day-flying butterflies. Many insects use the stinging Hymenoptera as models, and typically they adopt not merely their appearance, but their mode of activity. A Brazilian grasshopper which mimics a fossorial wasp has the same curious habit as its model of running short distances with expanded wings. And among various spiders which simulate the appearance of ants, not only is the form of the body modified, with the evolution of an extra "waist", but the gait is indistinguishable from that of the ant: some species even employ the front pair of legs so as to simulate the model's antennæ.

Again, a superficially similar appearance may be produced by the most diverse methods. Thus in the ant-mimicking spiders, the extra body-constriction may be developed, in different species, either on the cephalothorax or fore-body, or on the abdomen; while in various other stout-bodied forms the appearance of a narrow waist and swollen abdomen of the ant is painted in pigment on the insect's back—such creatures having evolved a kind of optical slimming! (Fig. 15) and this last method has been variously and independently achieved by ant-mimicking bugs, grasshoppers, and beetles. Finally, it is significant that mimetic resemblances only affect superficial or visible characters; in other words, the effects are essentially external and such as can appeal directly to the eye of an observer.

Conclusion

We have given grounds in the foregoing pages for the belief that the biological needs of security, subsistence and reproduction have exerted, through the operation of natural selection, striking modifications in the appearance of animals—modifications which involve form, coloration, and behaviour. Moreover, it will have been noted that in producing such effects as concealment, disguise, or advertisement, the particular arrangements of colour and pattern, posture and habit, which for theoretical reasons are those best adapted to reduce, translate, or increase visibility, are those that have in practice been evolved.

Thus, we find solid surfaces made to appear flat by countershading, while simple flat surfaces are made to appear complex or curved; we see continuity of surface rendered as separate discontinuous surfaces by disruption, while discontinuous surfaces are given visual continuity by coincident patterns; we find real shadows reduced or covered, while false shadows of pigment suggest real ones; contours or silhouettes are masked or modified; real eyes obliterated; false eyes appear in the rôle of warning or display; again—we find animals imitating, or wearing adventitiously, inanimate objects of their habitat; or defenceless forms simulating the appearance and behaviour of dangerous ones; while various aggressive species advertise their presence, as a warning to enemies, as an allurement to prey, or as a stimulus to mates.

When we review the enormous range of such visual adaptive modifications, it becomes increasingly clear that they can only be interpreted in terms of the perception of other animals. Such allaesthetic characters have evolved in relation to, and are directed towards, a seeing public. In short, these highly specialised and widespread appearances and activities are of a kind which would be inconceivable or virtually impossible of achievement in a dark world where the faculty of vision had never emerged.

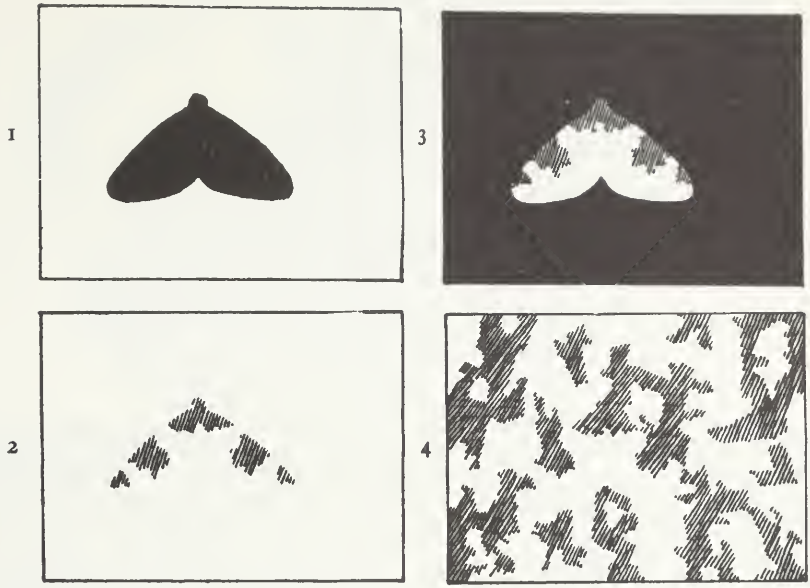


FIG. 1 Garden Carpet Moth—illustrating the principle of differential blending. (See page 125).

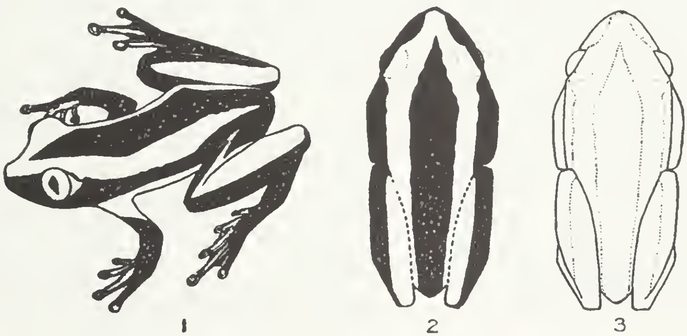


FIG. 3 East African Tree-frog (*Megalixalus fornasinii*)—illustrating the principle of coincident disruptive coloration. (See page 127).

FIG. 4 Hind limb of the Common Frog (*Rana temporaria*)—showing coincident disruptive bands. (See page 127).

FIG. 2. 1

FIG. 2 Copperhead Snake—illustrating the effectiveness of disruptive contrast in relation to background configuration. (See page 126).

FIG. 2. 2

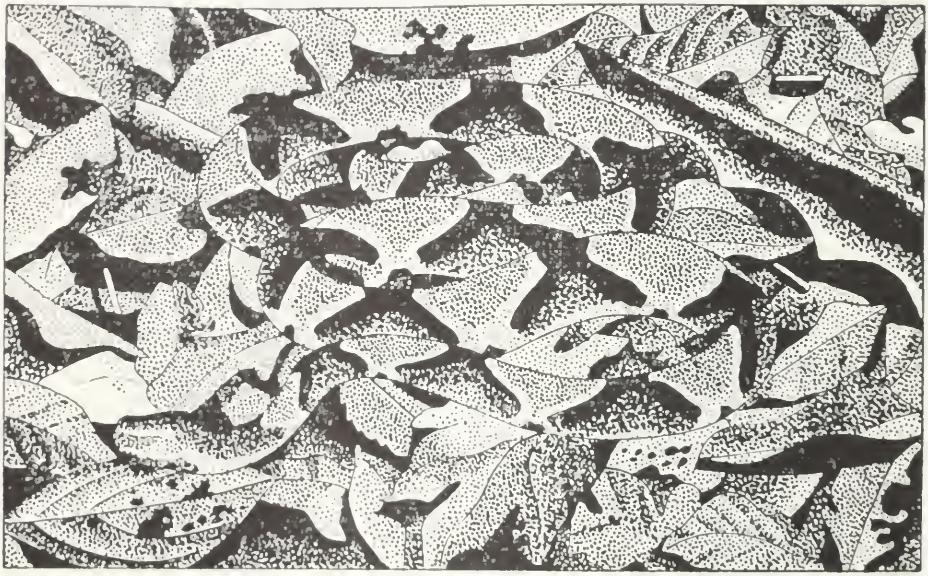


FIG. 5 Scalloped Oak Moth—showing coincident disruptive pattern: (left) wings opened to show disruptive elements; (right) appearance of moth in natural attitude of rest. (See page 128).

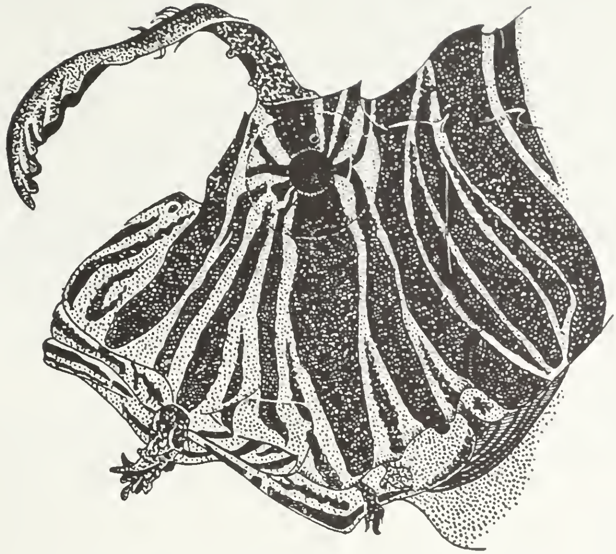


FIG. 6 Lion Fish (*Pterois volitans*)—showing camouflage of the eye. (See page 128).

FIG. 7 *Eques lanceolatus*—showing coincident disruptive pattern with maximum tonal contrast. (See page 128).

FIG. 14 The Hawk Moth larva *Leucorhampha ornatus*—showing (left) resting attitude; and (right) display attitude. (See page 134).

FIG. 15 Camouflage of the waist-line in stout-bodied mimics of Hymenoptera. (1) *Nabis lativentris;* (2) *Oberea brevicollis;* (3 & 4) *Myrmecophana fallax.* (See page 141).

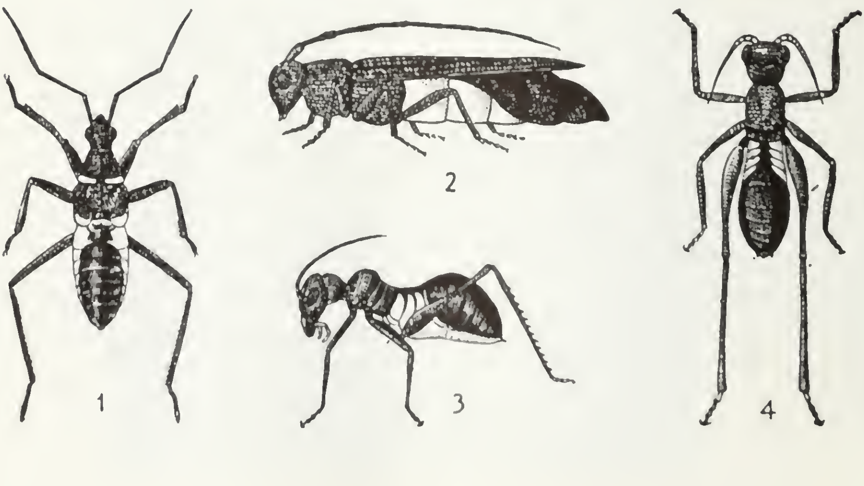


PLATE 1 Nest and eggs of Golden Plover. The eggs, like those of many ground-nesting species, are highly cryptic.

PLATE II. 1 Larva of Pepper-and-Salt Moth (*Pachys betularia*) in natural resting attitude; showing special protective resemblance to a twig of its food-plant.

PLATE II. 2 The same: showing the rear part of the body, with shadow-neutralizing screen between the grasping appendages.

PLATE III. 1 Woodcock at Nest: showing coincident disruptive stripe associated with the eye.

PLATE III. 2 The Frog (*Cana temporaria*) in natural surroundings. Colour-harmony, countershading, and coincident patterns combine to reduce conspicuousness.

PLATE IV. 1 The East African tree frog *Hyperolius marmoratus* wearing the advertising dress typical of species well-protected by poisonous skin-secretions.

PLATE IV. 2 Gannet and Young: example of a conspicuous species, well-protected by size and fighting strength.

PLATE V. 1 Larva of Eyed Hawk Moth (*Smerinthus ocellatus*). Note the combined effect of inverted counter-shading and inverted resting attitude.

PLATE V. 2 East African grasshopper: *Certacanthacris tatarica*. A striking example of the effectiveness of tonal contrast in a disruptive pattern.

PLATE VI. 1 Partridge: illustrating the effectiveness of disruptive coloration here enhanced by the superimposed chiaroscuro due to sunlight and shadow.

PLATE VI. 2 Young Stone-Curlew: showing the instinctive crouching posture which is adopted when danger threatens.

PLATE VII. 1 The leaf-like butterfly *Kallima*, in which the undersurface of both wings—those seen when the insect is at rest—simulate a leaf by their form and coloration.

PLATE VII. 2 The leaf-insect *Chitoniscus feedjeanus*: showing leaf-like modification of the fore-wings, including the simulated midrib and lateral veins.

PLATE VIII Scarce Tissue Moth (*Eucosmia certata*): showing orientation of body which is horizontal in position, thus bringing the cryptic colour-scheme into relation with the vertically-patterned background.

The Role of Gestalt Perception in Animal and Human Behaviour *by Konrad Z. Lorenz*

I. Introduction: The Concepts of "Gestalt", "Whole", and "System"

IT IS THE MERIT of Gestalt psychologists to have introduced the method of correlative analysis to the study of organic systems, at a time when the atomistic way of thinking was holding sway. They showed that the characteristic quality of the whole can be dependent on the universal interaction of literally all its parts, thus proving the naïvety of the current atomistic assumption that a part, though isolated experimentally, would behave exactly as it did in the context of the whole.

To a considerable extent the rules laid down by Gestalt psychologists can be applied to the treatment of other organic systems, for the simple reason that the central nervous apparatus, whose function is the perception of Gestalt, is nothing else but one such system. However, it must be borne in mind that this apparatus, so far from being a typically average example of an organic system, is a very special case indeed whose particular qualities and function cannot be attributed to organic systems generally.

One of the most important criteria of Gestalt, and one upon which Ehrenfels laid particular stress, is the fundamental independence from particulate elements. The Gestalt of a melody is independent of the question in what key and on what instrument it is played. Now it seems a rather silly truism to state that this independence of elements is characteristic of perceptory processes alone, that a spherical conductor cannot be charged with soap solution and that bubbles cannot be blown from electricity. Yet this very same error has been committed again and again by group and social psychologists who, under the influence of the Gestalt theory, totally neglected the particulate element, its structure, and its influence on the whole.

A whole, in our sense of the word, is a system in which every part influences every other part. The soap bubble, the spherical conductor, and the solar system are doubtlessly perfect examples of such a system. But organisms are not! There is not one organic system in existence in which the mutual causal coherence of all parts is as complete as in these examples, because every organic system contains unchangeable structures which, though certainly causally influencing the form and the function of the whole, are not appreciably influenced by it in turn. Skeleton elements, for instance the chitinous cuticle of insects, are, in the definitive state of their development, good examples of such fixated structures.

In analytical research work it is of the utmost importance to know, at an early stage of the investigation, whether a subordinate element stands in a relation of mutual causal influence with all other parts of the system, or whether it is an unchangeable independent structure, influencing the whole by "one-way" causation. Indeed, the mechanist's dogmatic assumption of the latter is far less detrimental to analytical understanding than the procedure of many sociologists who consider exclusively the influence which the whole exerts on its parts and who totally neglect the unchangeable structures existing in the "elements"! One-way causation, acting in the direction from the part to the system is present, at least in some cases. In the opposite direction it is not, and its assumption is a misleading fiction.

The research worker confronted with an organic system is under the methodological obligation to ascertain to what extent and in what regards the object of his investigation is a system of universal interaction and to what extent and in what regards it is a mosaic built up of unchangeable independent structures.

This obligation is particularly stringent for the student of behaviour because there is no other organic system in which universal causal interaction and mosaic-like independent structures alternate and interlock in so utterly incalculable a manner as they do in animal and human behaviour! Jakob von Uexküll, in his drastic way, once said: "When a dog runs, the dog is moving his legs; when a sea urchin runs, the legs are moving the sea urchin". I hold that it is an extremely pertinent question, whether the dog moves the legs or the legs the dog—particularly in social psychology! Where investigation has to deal with universal causal coherence, it must necessarily resort to the slow and painstaking method of correlative analysis. Where the existence of independent, unchangeable structures has been proved, there we may begin with linear causal analysis and with experiments isolating constituent parts. This is exactly why the discovery of an independent structure has, every time, brought our understanding a tremendous step forward. But whether the one or the other procedure is brought into play, is not, or ought not to be, dependent on the question whether the investigator is a "holistic" vitalist or an "atomistic" mechanist, but exclusively *from the nature of the object*! Attributing Gestalt features to a mosaic system of independent structures just as irretrievably falsifies the facts as does the attempt to isolate "elements" in a system of universal interaction. The biologist and particularly the behaviour student must maintain an absolute readiness to use both methods; which of them has to be applied at a given moment is a question that cannot be settled by metaphysical speculation or by the dogmatic misapplication of a slogan, but one that must be answered by patient inductive research, separately for each individual object and at every single step of the investigation.

Among all organic systems hitherto known there is hardly one which conforms to our definition of a whole so completely, as does Gestalt perception. But, though every Gestalt is indubitably a whole, not every whole is a Gestalt. Ehrenfel's criterion of independence of—or interchangeability of—elements is the most essential character of true Gestalt, and it is only to be found in a central nervous process, in which *many* single elementary excitations *converge* into one common effect. This intrinsic function of *integration* is performed by the apparatus which, out of single and interchangeable sensory data, builds up the unmistakable one-ness of perception. It is a process which is possible only on the afferent side of the central nervous system, a statement which almost amounts to a tautology. These are the reasons why I propose not to use the term Gestalt in so wide and loose a sense as Wolfgang Koehler, but only to describe a much narrower concept, i.e. that of Gestalt perception, exactly as Ehrenfels and Wertheimer originally did.

To emphasize the narrowness of the concept of Gestalt as I intend to use it here, I would lay stress on a fact which is usually lightly passed over by Gestalt psychologists: Gestalt perception can only exist in the realm of a sense which is able to render a configuration of stimuli. For this reason Gestalt perception is only possible to a sensory organ receiving data which are either spatially or temporally determined. It is useless, therefore, to look for Gestalt phenomena in the sphere of the olfactory and the gustatory sense.

In accordance with this very restricted conception of Gestalt I shall confine myself, in this paper, to the perceptory side of animal and human behaviour. Whenever, for brevity's sake, I use the word Gestalt, it is used for Gestalt *perception!* I shall try to convey some idea of the very complicated manner in which Gestalt perception interlocks and co-operates with other types of perceptory function which, in the literal sense, bear the character of mosaics or sums. I shall try to show how indispensable both regulative "wholes" and mosaic systems are in the life of a higher organism.

II. The Innate Releasing Mechanism

Whenever, without previous experience, an animal responds to a biologically relevant situation with specific behaviour of indubitable survival value, the observer cannot help feeling that the animal "knows" that situation. Indeed the loose and anthropomorphic description that an animal "knows innately" or "recognises instinctively" its prey, its female, or its young, is often used by good ethologists, even in writing. Yet this expression is distinctly misleading, because all real "knowledge" or "recognition" always implies Gestalt perception. The human observer in whose own life learning and Gestalt perception plays a much more obtrusive rôle than innate responses, is necessarily tempted to assume that an animal which innately reacts as if it "knew" the situation, must possess something like an "inherited memory" that had, in some mysterious way, been previously acquired by the species. C. G. Jung, in his work on the "Archetypus" speaks of "vererbte Erinnerungsbilder" (inherited memory images) and Alverdes, in his paper "Die Wirksamkeit der Archetypen in den Instinkthandlungen der Tiere", expresses the same opinion.

However, a closer experimental study has shown that the perceptory process through which innate responses are released, is very different indeed from Gestalt perception. The effect of acquired responses to Gestalt is always dependent on the perception of a complex quality, into which a great number of sensory data with all their relations and relations between relations are woven to form one unmistakable unit. In striking contrast to this complexity, the perceptory side of innate reaction is invariably dependent on very few and very simple releasing stimuli. The receptory apparatus which, like a lock, keeps innate activities under control until the biologically adequate situation is reached, does not respond to the complex of stimuli characteristic of this situation, but is selectively tuned to respond only to very few among them. Because this central nervous apparatus removes the inhibition under which the higher centres constantly keep instinctive activities, it is called the *Innate Releasing Mechanism* (IRM) by comparative ethologists. Because the few, yet characteristic stimuli to which it responds, represent, metaphorically speaking, a simplified diagram of the adequate situation, I have formerly called it the "Angeborenes auslösendes Schema" (innate releasing diagram), a term which Tinbergen and I later relinquished, because it rather suggests the existence of "innate pictures" in the sense of Jung's "Archetypus". The releasing stimuli, to whose reception an IRM is tuned, have been termed "sign" or "key" stimuli. I prefer the latter term, because the simile of lock and key is really apt for the IRM and the specific stimulation to which it responds.

Wherever the response of an organism is elicited exclusively through an IRM, it invariably is far less selective than any response to acquired Gestalt perception. It is a crude but rather reliable rule that a response which can be elicited by a "dummy", is an innate one, and that one which cannot, is acquired. Yet the selectivity of an IRM must be sufficient to prevent the activity controlled by it from "going off erroneously" in any but the biologically adequate situation, or at least to make this eventuality improbable enough not to impair the survival of the species. This selectivity is attained by an adaptive "choice" of the key stimuli, to which the receptor of the IRM is "tuned". The pike's preying activity responds to the silvery glinting of the minnow's sides, the tick's blood-sucking reaction is released by the stimuli of butyric acid and a temperature of 37° Celsius. Simple though these IRMs are, they suffice to characterise the adequate object unambiguously enough to prevent the responses from ever going astray—unless human subtlety plays tricks on the poor animal.

The selectivity of acquired responses to Gestalt perception on the multitude of sensory data and relations between them is immensely improbable on mere chance. Therefore, Gestalt is practically "unmistakable". However, as the unmistakable total quality is dependent on all integrated parts, a change in one of these will effect a change of the whole. The Gestalt of a well-known face can be rendered by a crude sketch, but if, in this sketch, one detail, for instance the contour of the nose, is slightly altered, the whole portrait does not become quantitatively "less like" the original, but the likeness is totally destroyed. In this dependence on detail there is a very great difference between Gestalt perception and responses elicited by IRMs. If, in an innately releasing stimulus situation, we remove one key stimulus after the other—an experiment which can easily be done with dummies—the response does not break down suddenly, as any acquired reaction to a Gestalt would do, but only gradually diminishes in intensity.

Alfred Seitz, experimenting on the fighting reaction of the Cichlid fish, *Astatotilapia strigigena*, first ascertained the key stimuli to which the IRM in question responded: the shining blue colour, the black marginal stripe of median fins, the black gill membrane, and furthermore the movements of spreading fins and gill membrane, moving parallel to the opponent, beating the tail sideways in a peculiar manner, and, last not least, the tactile stimulus of the adversary's bite, were found to be the key stimuli which a model must send out in order to release the fighting activity with maximum intensity. The removal of any one of these stimuli only causes a corresponding quantitative decrease in the intensity of the response, never a change in its quality. Even when only one of the key stimuli was presented, unmistakable fighting activity was released. Its intensity however varied exceedingly in correlation to the stimulus that was chosen: the properties of colour and form, though indubitably effective, proved to be considerably less effective than those of movement. A flattened, rectangular, colourless piece of hard paraffin, attached to a glass rod and moved so as to stand parallel to the subject would elicit a slightly stronger response than a perfect model with spread fins and gill membrane, but presented without movement. A real male fish, anæsthetised with Urethan and presented in a celluloid holder, would release a still weaker reaction, because, though it showed the nuptual colouring, its fins and gill membrane remained folded. An imitation of the tailbeat would instantly increase the valence of any model by a very considerable amount, the tactile stimulus of biting or ramming proved to be the strongest of all and would, quite by itself. release the strongest intensity of the fighting activity, i.e., instant counter-ramming. Seitz then tried to find models which, though combining quite different sets of key stimuli, were equal to each other in their releasing valence. If, for instance, the releasing value of the perfect model with spread fins and gill membrane was increased by the additional stimulus of moving broadside-on, it was approximately equal to the crude paraffin square, executing tailbeats. Seitz built up a number of such "equations" and compared the releasing values which one and the same key stimulus developed in different combinations wth others. This value proved, for each key stimulus, to be an absolute constant. In other words, the valence of each model was strictly equal to the sum of all key stimuli emanating from it. This rule was called "Reiz-Summen-Regel" by Seitz, a term which was translated into English as "law of heterogeneous summation" by Tinbergen. In regard to the effect of and relation between the several key stimuli, the IRM is the very reverse of a Gestalt, being a *mosaic* and literally the sum of its elements!

III. The Releaser Principle

The selective response of an IRM to a biologically adequate object is obviously the achievement of an evolutionary process which has adapted the perceptory apparatus within the central nervous system to "receive" certain characteristic stimuli emanating from the object. Obviously, it is only the "lock", and not the "key" of the response, which can be adaptively altered in the interest of the species. All that the IRM can accomplish in the way of adaptation is to "develop a more perfect enclosure of the adequate object", as Baerends aptly puts it. The pike, to express it very crudely, is not in a position to attach a little red signal flag at the minnow's tail, the better to release preying responses. But this is quite exactly what can be done when the releasing object is an animal of the same species. The jackdaw can, phyletically speaking, attach a bright yellow pad at each corner of the nestling's mouth in order better to release and to guide the parent bird's feeding responses. When the object which is sending out key stimuli, and the subject upon whose IRM they impinge, are animals of one species, not only the "receiving station", the IRM but also all the structures, colours, and movements which send out key stimuli, come within the scope of all those factors which effect the evolutionary development of the species. There is a multitude of organs and movements whose sole function is the sending out of key-stimuli correlated to IRMS of the respective species. The bright colouring of so many young birds' mouths, the peacock's tail, all the striking movements of threatening and courtship display, the scent glands of so many mammals, practically all the sound utterances of higher animals and innumerable other differentiations, down to the queer, arrow-like stimulating organ of snails, serve this same function. All these stimulus-sending organs and movements are termed releasers in comparative Ethology.

Practically all the social co-ordination of animal behaviour is brought about by the function of releasers and correlated IRMS. Visual releasers in particular often attain a very high level of differentiation. Because of their striking beauty and easy accessibility to the human senses, these stimulus-sending organs and movements have, since the days of Darwin, attracted the naturalist's attention and the greater part of investigations which occupy themselves with IRMS are concerned with those correlated to visual releasers. It is indeed the visual releaser which has taught us the most important physiological facts about the nature of the IRM. All releasers, and particularly the visual ones, are characterised by the simplicity of the key stimuli which they send out. Nevertheless these stimuli are very pregnant and, to a high degree "unmistakable", or, in other words, of a high general improbability. The compromise between simplicity and improbability is reached by that symmetrical regularity which is the mark of all visual releasers.

The differentiation of the sending-apparatus of key-stimuli in itself betrays certain limitations to the differentiation of the "receiving station" of the IRM. Symmetrical and regular forms are forms whose regularity can be expressed in a comparatively simple mathematical relation, and it is these that, for some unknown reason, evidently lend themselves particularly well to the processes of perception. Even human Gestalt perception, although it is able to extricate extremely complex regularities out of a most intricate maze of sensory data, nevertheless has a distinct preference for mathematical simplicity. What is called a most "pregnant" form in Gestalt psychology is objectively that of the mathematically simplest regularity. There cannot be any doubt that *the perceptory side of the IRM is limited to extremely "pregnant" key stimuli*, in other words, to mathematically simple ones. As I shall explain later on, the single key stimulus can be represented by a relational property, but if so, by one of extreme simplicity that can be described in a few words. "Red below" is a key stimulus for the fighting response of the stickleback, "standing broadside on" for that of Cichlid fishes.

Perfect geometric regularity of form and movement, pure notes and unmixed spectral colours, all the typical qualities of releasers, are certainly "easy to remember" and very simple to describe, but they can only be attained by superlatively complicated processes in evolution and ontogenesis. If so many higher animals went to these extremes in the differentiation of their releasers, it was certainly because it is impossible to tune the IRM to respond to less pregnant signals. The very existence and omnipresence of releasers in the realm of higher animals constitutes a very strong argument for our assumption that it is in principle impossible for the IRM to respond selectively to complex Gestalt perceptions. Hitherto, all our experimental and observational evidence tends to reinforce this argument.

If, in a zoological book, one reads the description of the colour patterns of male and female of one of these sexually dimorphous species, one is struck by the fact that the description of the female is several times longer than that of the male. To our Gestalt perception, it is just as easy to differentiate between a female mallard and a female gadwell, as between the males of both species. My daughter knew the difference at the age of four. But it is next to impossible to convey to anyone the faculty of telling these cryptically-coloured, releaser-less birds apart by verbal description. This description would have to go into such minute details of plumage patterns and proportions that even a listener with an extraordinary power of imagination would find it impossible to form a picture of the bird. As Goethe says: "Das Wort bemüht sich nur umsonst, Gestalten schöpferisch aufzubauen". Unlike acquired Gestalt perception, the IRM conveys to the individual an almost unconnected sum of informatory data, in a way curiously similar to that of a verbal description, and as the form of releasers is dictated by this limitation of the IRM, all releasers are surprisingly easy to describe unambiguously in spoken and written words. If one describes the male mallard as the one with the uniformly green head and a white ring round the neck, and the male gadwell as the grey one with the black posterior half of the body, such descriptions are quite unmistakable.

IV. Interaction of Innate Releasing Mechanism and Gestalt Perception

In some animals the response elicited by IRMs so completely supersedes all acquired reactions to Gestalt perception that whenever a conflict between both functions arises the organism seems to be totally blind to Gestalt. A robin redbreast, for instance, is a very intelligent little bird whose faculty for Gestalt perception is highly differentiated: a robin is able to recognise, by their physiognomy, not only other individual robins, but even humans. Yet, by presenting to a male robin a square inch of the russet breast feathers of its species, we can release its fighting activity to the fullest extent, exactly as if the bird were confronted with a real rival. From its actions we have absolutely no right to conclude that the bird perceives any difference between the two situations! If we present the bird with a model complete in every detail, but lacking the red breast feathers, no fighting ensues. Similiarly, in the stickleback all fighting responses and all sexual activities are elicited by IRMS and can be released by the crudest of dummies, although the fish indubitably possesses the faculty to recognise its own kind by Gestalt perception; the common reaction of social "schooling" is evidently not dependent on IRMS, but on conditioned responses to an acquired Gestalt.

This type of relation between IRM and Gestalt perception must not, however, be generalised. Even in some fishes, true Gestalt learning, in the form of personal recognition of an individual, is able to inhibit innate responses. In the Cichlid fishes, the mutual care of both parents for their offspring has led to the evolution of complicated instincts, releasers, and IRMS co-ordinating the activities of the mated pair, in defending their territory against intruders, relieving each other in "incubation", in protecting and guiding the young. Particularly interesting is the personal recognition of the mate, a faculty which was experimentally proved by Noble and Curtiss in the Jewelfish, *Hemichromis bimaculatus*, and by myself in *Herichthys cyanoguttatus*. When both mates attack an intruder, they cannot help seeing each other's threatening display which, if shown by any other fish, would instantly evoke intense fighting activity in any of the two fishes. Particularly if the intruder loses courage and ceases to display and to fly his fighting colours, while both mates continue to do so, it is exceedingly surprising that they do not attack each other—at least to an observer who knows the warp and woof of innate responses! Although the strongest of key stimuli are indubitably impinging on both fishes, their mutual personal recognition succeeds in inhibiting their fighting responses.

There is a rather dastardly experiment which makes it still harder for the fishes' higher brain functions to cope with the fighting drive: a stranger fish, a courageous fighting male for choice, is introduced into the tank of a nesting couple of Jewel-fishes and, when their fighting activities are at their highest, the strange male is suddenly and unobtrusively removed again. In this situation, the "after-discharge" of all fighting activities imperatively urges the fishes to "fight something" and the "temptation" to attack each other becomes overwhelming. And yet the mates refrain from doing so! They may come very near fighting, from unmistakable intentional movements it becomes abundantly clear how strong an urge is driving them to attack, but, at the last moment before they strike, the personal recognition of the partner vanquishes the innate response. This feat of acquired recognition is very remarkable in a fish; if one performs exactly the same experiment with Egyptian Geese (*Alopochen aegyptiacus*) or ruddy sheldrake (*Casarca ferruginea*) a furious marital fight invariably results!

However, the interaction between IRM and learning is not exclusively antagonistic. Every conditioned response is dependent upon an "unconditioned" one, as a basis on which to develop. What Pavlov and his school call an unconditioned reflex is in most cases elicited through the means of a more or less complicated IRM. When a dog learns to react to a little bell as a signal for approaching food, there is hardly any innate connection between the conditioned stimulus and the unconditioned response: the same response could just as well have been conditioned to the lighting of a little red lamp. But when a bee learns that, among different radially symmetric forms, all of which have an innate valence for it, a particular one will yield honey, there is a dual functional relation between the innate response and the specific ability to learn: the IRM directs the learning process to its adequate object, while learning, on its side, complements the IRM by making the response more selective. Thus two physiologically different processes form a distinct functional unit.

This unit plays an important and interesting part in the ontogenetic development of the behaviour of some birds and insects—whether also in that of Man, is still doubtful. There are IRMS connected with conditioning processes, both of a very special type adapted to supplement each other: the IRMS are particularly "wide" or unselective, while the learning processes directed by them make up for their lack of selectivity by being restricted to an extremely short duration of time, within which it is sufficiently improbable that the response can be conditioned to anything but the adequate object. A good example of this kind of co-operation is to be found in the IRMS and conditioning processes of the newly hatched Greylag gosling. In the first few hours of its life, the tiny bird reacts with its "greeting response" rather indiscriminately to any object which (*a*) moves, and (*b*) utters sounds. But, while greeting, the gosling intently scans the releasing object and, after a few repetitions, becomes conditioned to it in a very peculiar way: it is not only the greeting response which is henceforward fixated to the particular object which first released it, but, with it, practically all the other reactions with which a young gosling responds to the parent bird. This kind of conditioning differs in three essential points from all other types of learning: (*a*) It is confined to a fixed and very limited period in the organism's life. (*b*) The stimulus situation which will, later on, elicit certain responses, is determined at a time when these responses have not yet matured. (*c*) Unlike all other types of learning, this process is irreversible. Because of this last mentioned property I termed it "*Imprinting*" (Prägung), when I first described it in 1935. For many years imprinting was only known in birds—with a few doubtful analogies in human psychopathology. It was only a short time ago, that true imprinting was found in insects by Thorpe.

A very curious feature of the Gestalt perceptions which are acquired through imprinting, is their generic character. If in our experiments, we let a young bird become imprinted "erroneously" to another than its own species, we never yet found the subject's responses irreversibly fixated on the individual that had induced the imprinting process, but only on the species of that individual. This is particularly surprising in those cases, in which young birds have been imprinted to the human species whose individuals show such an extreme breadth of variation. It is, however, an inherent faculty of Gestalt perception to "abstract" from the accidental, variable properties of an object, and to respond exclusively to essentials. But it is still a complete riddle, how the Gestalt perception of such a young bird can "know" what is variable and what is invariable and generically essential in the one human being which induces imprinting!

"Pure" processes of response to an IRM, of imprinting, and of true Gestalt learning, as we describe them for the sake of theoretical clarity, are actually rare. Much more frequently, all three functions co-operate in one organic unit, as in the following example. A Mallard duckling will, immediately after hatching, respond to its mother's call note by means of an IRM. This response directs its imprinting towards its mother or, as I proved experimentally, to any other object emitting that call. The imprintable phase is even shorter than in the Greylag and at an age of five or six hours it is no longer possible to induce the duckling to follow a human being. As yet the duckling responds indiscriminately to any mother mallard, but two days later it has learned to know its mother personally and will have nothing to do with another mallard, even if the latter leads young of the same age. Thus, a "wide" IRM is first made more selective by imprinting, and this selectivity is still further increased by true Gestalt learning later on.

V. Gestalt as a "Constancy Effect"

As I have already said, it is a function characteristic of Gestalt perception to "abstract" from the accidental and to extract the prevailing regularity out of the variable sensory data. This performance is, however, by no means confined to true Gestalt perception alone, but is a very general feature of the central nervous organisation which, out of variable sensory data, builds up perceptions. Much attention should be given, in this respect, to the so-called *constancy effects*.

We perceive the colour of any given object as "the same", whether we see it in the blueish morning light, in the more reddish light of the evening, or in the yellowish light of an electric lamp, although, objectively, the object reflects a very different wave-length under these varied conditions. This subjective constancy of colour is the achievement of a very complicated "calculation" done by an unconsciously working apparatus within our central nervous system. This "calculation" is done in the following way: First, the average colour of the light, as it is reflected by all the objects within the visual field, is drawn into consideration. Then, from this colour, the wave-length prevailing in the in-coming light is "deduced". This colour of the illimination is brought into relation with the colour reflected by the object in question, and this relation turns out to be a constant depending on the reflecting properties of the object. Thus, what we perceive as the colour of the object is nothing else than its inherent property of reflecting wave-lengths in preference to others, and not, by any means, the wave-lengths which it actually reflects at a given moment.

All this "calculation" is based on an "assumption": the central nervous apparatus "assumes" that all objects within the visual field do not, on the average, reflect any wave-length in particular preference to others, so that the mixture of wave-lengths reflected by them adds up to what we perceive as "white" light. Of course, this "assumption" is only based on a rather unreliable probability. It is easy to falsify the premises of the "hypothesis" by filling the visual field with objects all equally reflecting one colour more than others, whereby the central nervous apparatus is misled into the "deduction" that this colour—which is really due to the improbable coincidence of the reflecting properties of objects—is the colour of illumination. If we then put in the visual field one object of reflecting properties different from all the others, our apparatus logically but erroneously deduces that this particular object has the property of reflecting a colour which is complementary to the one that is mistaken for the colour of illumination. What is called simultaneous contrast, is nothing other than the result of this particular mistake of our colour constancy "calculus".

The quotation marks, under which all the terms for logical operations have been put, are meant to indicate that all these processes not only take place unconsciously, but are, in principle, inaccessible to our conscious self-observation. Helmholtz, in his studies on binocular perception of distance, was the first to take notice of these processes and has called them "unconscious conclusions". There cannot be any doubt that these operations are performed on a central nervous level very different indeed from that of conscious logical inference and that they are, in very many respects, much more akin to the functions of mechanical calculating machines. Modern cybernetics have taught us what surprising performances can be achieved mechanically. Not even the response to "formed stimuli", bearing all the features of Gestalt, such as transposibility and independence from elements, is beyond the scope of contrivances which astonish the biologist by their comparative simplicity. In the study of the constancy effects, if anywhere in biology, the results of cybernetics are directly applicable! The cyberneticist's concept of a computor includes something which certainly is much more than a mere model of those mechanisms of the central nervous system of which we have just described one. If any part of the living organism is a mosaic system, built up of particulate, independent elements, and if any life process shows, by its very limitations, its dependence on a mechanical substratum, it is these parts of the central nervous system and their function of constant perception of objects. And yet, among all life processes, there is none which more distinctly beards the character of a whole!

Other effects of perceptual constancy are contrived in a very similar manner; that of size constancy may serve as one more example. The size, which we perceive any given object to have, is the result of a computation performed on the principle of re-afference studied by E. von Holst. The motor impulses which are sent out to the muscles performing the accommodation or focussing of the eyes, are partly re-conducted to a computor which relates them to the absolute size of the retinal image. From this relation between two variables the constant size of objects is computed. Falsification of the premises results in illusions very characteristic of this process. If the focussing musculature is paralysed, so that the motor impulse to focus on a point near to the eyes takes no effect, the phenomenon known as "micropsy" sets in. All the objects within the visual field suddenly appear quite near before the subject's eye, simultaneously assuming tiny dimensions. The room in which the subject is standing seems to shrink to a doll's chamber enclosing his head while his chin, like Alice's, threatens to hit the floor. This quaint optical illusion is easily intelligible as a result of a miscalculation of the size constancy computor. From the re-afference of the motor impulse that had been sent out in vain, the computor "believes" that the eyes have been accommodated to a distance of a few inches only, and as the objects of the room, though really yards distant, are still perfectly in focus, the computor logically but erroneously "deduces" that they must be, indeed, at the distance of the intended accommodation, and proceeds to the "conclusion" that they are correspondingly small. A reciprocal illusion can be elicited by poisons which cause a cramp in the accommodating muscles of the eye. If the subject then holds his thumb some inches before his eyes and tries to look into the distance, he perceives a gigantic thumb towering in that distance! Whoever has experienced these illusions himself, has had a very convincing proof of the mechanical character of these functions.

The two mechanisms of colour and size constancy suffice to emphasise some features which these two comparatively simple functions have in common with the much more complicated types of Gestalt perception:

(*a*) The computor invariably integrates many sensory data into one single report.

(*b*) The process of this integration is functionally analogous to a logical conclusion, often even to a mathematical operation, as in the case of the complicated trigonometrical computation performed by binocular perception of distance.

(*c*) The process by which the computor arrives at its conclusions is inaccessible to conscious self-observation and is, for this reason, uncontrollable by higher mental functions and incorrigible by insight. We cannot change our perceptions in the least, even if we are perfectly aware of the deception and all its causes. The computor's report bears the character of evident truth—the German word for perception—"Wahrnehmung"—means, in literal translation, "taking as true"!

(*d*) The constant regularity which the computor generates from the multitude of variable sensory data is always due to a permanent property of the object. The primary survival value of these computors lies in the function of making objects of the organism's environment recognisable irrespective of the conditions under which they are perceived.

What appears as an object in our phenomenal world is the result of these constitutive functions of our perception. All of them are objectivising in the literal sense of the word. Of the true Gestalt perception this is true in even a higher sense than of the more primitive constancy computors of colour and size. In its simplest and, without doubt, phylogenetically most primitive form, Gestalt perception is nothing else than the function of another constancy computor which enables us to perceive the shape of an object as one of its permanent properties. It is as well to remind English-speaking readers that the original, non-scientific meaning of the word "Gestalt" is equivalent to that of "shape" or "form". In ordinary German, one cannot speak of the Gestalt of a melody or a movement, but only of that belonging to an object of constant spatial shape. The original survival value of Gestalt perception indubitably lies in perceiving constant shape as the supremely important property of individual objects.

If I turn the pipe which I am smoking while writing these lines to and fro between my fingers, its image assumes an immense numbers of different contours, yet its shape, as I perceive it, remains perfectly constant. This faculty is so familiar to us that we fail to realise what a tremendous feat it is on the side of the computor to "deduce" the permanent form from the innumerable combinations of sensory data which represent the ever changing contours of the moving pipe as it is depicted on the retina. The process, by which the changes in the retinal image are correctly "understood" or "interpreted" as movements of the whole object in space and not as changes in its shape, must involve computations fully equivalent to complicated operations of projective geometry. Yet the perception of distance evidently does not take an important part in this performance, as we can just as well interpret that movements of a solid body by watching its shadow. It is only the direction of turning movements which, in this case, becomes ambiguous. The extreme exactitude and high sensitivity of this interpretation becomes particularly impressive when we are watching an object which, at the same time, moves in space and changes its shape. Let us suppose, for example, that we are watching a duck swimming on the water, turning this way and that and, simultaneously, ruffling and depressing its plumage. The bird's contours become changed by perspective foreshortening and, in a very similar manner, by the movements of its body and plumage. Yet our perception will never on any account mistake one of these causes for changes in the bird's contours for the other, even if they take effect simultaneously and appear superimposed upon each other.

VI. The "Abstracting" Function in Gestalt Perception, and Intuition

The computor which enables us to perceive the shape of objects as constant, though immeasurably more complicated, is functionally akin to that of colour and of size constancy in that it originally evolved in the service of the same function of recognising individual objects. But, in the course of evolution, any organ may change its function—and a central nervous computor is nothing else than an organ. Organs have a queer knack of suddenly developing unsuspected applicabilities and can be turned to tasks entirely different from those in whose service they originally evolved. Two such changes of function have taken a decisive part in the evolution of Man. One was that of the prehensile hand and of the central representation of space correlated with its function. The other was that of Gestalt perception.

All effects of constancy, including that of Gestalt, are based on the single function of extricating the essential constant factor by abstracting from the inessential variable sensory data. The differentiation of this function attains an amazing development in the service of shape constancy and it needs only to be driven one little step further to make possible an absolutely new operation miraculously analogous to the formation of abstract, generic concepts. Not only small children, but also higher birds and mammals, are able to perceive a supra-individual, generic Gestalt in all the individual objects of the same kind. The same faculties which enable these organisms to recognise one individual dog in all shades of light, at all distances and from all angles, need only carry their abstraction from the inessential one step further to render possible the momentous feat of perceiving one common Gestalt in all dogs of all races, different though they may be. A monkey, a cat, a raven, or a young child is certainly not able consciously to abstract the zoological diagnosis of *Canis familiaris Linnaeus*, indubitably it is the performance of the Gestalt computors which enables them to see "the" dog "in" all the different representatives of the species. Very probably this function of generic recognition achieved by Gestalt perception is not only the phylogenetical precursor of conscious abstraction. We know by much observational and experimental evidence that the human capacity of Gestalt perception by far exceeds that of all animals. In my opinion, the great change of function just described is one of the indispensable conditions which had to be fulfilled in order to make possible conceptual thought and speech.

I hold that Gestalt perception of this type is identical with that mysterious function which is generally called "Intuition", and which indubitably is one of the most important cognitive faculties of Man. When the scientist, confronted with a multitude of irregular and apparently irreconcilable facts, suddenly "sees" the general regularity ruling them all, when the explanation of the hitherto inexplicable all at once "jumps out" at him with the suddenness of a revelation, the experience of this happening is fundamentally similar to that other when the hidden Gestalt in a puzzle-picture surprisingly starts out from the confusing background of irrelevant detail. The German expression: "in die Augen springen", is very descriptive of this process.

Intuition is generally regarded as the prerogative of artists and poets. I would assert that it plays an indispensable rôle in all human recognition, even in the most disciplined forms of inductive research. Though in the latter the important part taken by intuition is very frequently overlooked, no important scientific fact has ever been "proved" that had not previously been simply and immediately seen by intuitive Gestalt perception. Intuition it was when Kepler first perceived, in the complicated epicycles of the planets' apparent movements, the simple regularity of their real orbits, or when Darwin first saw, in the intricate tangle of living and extinct forms of life, the convincingly clear Gestalt of the genealogical tree. Without intuition, the world would present to us nothing but an impenetrable and chaotic tangle of unconnected facts. It would be quite impossible to us to find the laws and regularities prevailing in this apparent chaos, if the mathematical and statistical operations of our conscious mind were all that we had at our disposal. It is here that the unconsciously working computor of our Gestalt perception is distinctly superior to all consciously performed computations.

This superiority is due to the fact that intuition, like other highly differentiated types of Gestalt perception, is able to draw into simultaneous consideration *a far greater number of premises* than any of our conscious conclusions. It is the practically unlimited capacity for taking in relevant details and leaving out the irrelevant ones which makes the computor of this highest form of Gestalt perception so immensely sensitive an organ.

The most important advantage of intuition is that it is "seeing" in the deepest sense of the word. Like other kinds of Gestalt perception and unlike inductive research, it does not only find what is expected, but the totally unexpected as well. Thus intuition is forever guiding inductive research. Though he may be quite unconscious of it, even the most exact and "inartistic" of research workers is invariably guided by intuition in the choice of his object, in the choice of the direction in which to look for important results.

On the other hand, intuition shares all the typical weakness of Gestalt and other perception. True to its character of a "Wahr-Nehmung", intuition is *very easily deceived.* Though its computors work with the utmost logical exactitude, it is easily led astray by its "uncritical" acceptance of false premises, and its correspondingly erroneous "conclusions" are passed on to our consciousness as an utterly convincing "revelation" whose absolute truth is incorrigibly maintained in the face of all better knowledge and indeed very often puts better knowledge in the wrong. This is also why men excellently endowed with faculties of Gestalt perception very often prove the most obstinate fools, once they have succumbed to this type of perceptory delusion. Next to its incorrigibility, the greatest weakness of intuition lies in its incontrollability. Just as all other processes of perception, intuition arrives at its conclusions by a way which is totally inaccessible to our self-observation. The correctness of the result cannot, therefore, be checked by consciously repeating that way step by step. If I said, a short while back, that intuition shows inductive research which way to look for results, I have to add here that it does very little more: it only indicates the gaol, but not the way by which to arrive at it!

I am fully aware that many readers and especially many psychologists will reject my hypothesis that intuition is nothing but the function of a central nervous "computor" which works rather like a blind mechanism and is, at least in principle, explicable on a physiological basis. "Intuition", just like "instinct", still is regarded by many as something miraculously infallible, something which not only cannot, but ought not to be explained in terms of physiology. Yet I dare to assert that its evident affinities to other and simpler perceptory processes, about whose physiological nature no sensible doubt can be raised, justify our explanatory optimism. The inductive research worker does not believe in miracles and this disbelief does not diminish the reverential awe in which he holds all nature. His maxim is that of Rudyard Kipling's Purun Bhagat, of whom the poet says: "Nothing was farther from his mind than miracles. He believed that all things were one big miracle, and once a man has got to know that, he has got something to go upon."

Activity Patterns in the Human Brain

by W. Grey Walter

The most complex organic pattern known is the nervous system of man, containing something of the order of ten thousand million nerve cells. Many of these cells and their processes, the nerve fibres, are arranged in intricate three-dimensional patterns, related to the receptors and effectors of the body, but a proportion of them have little apparent fixed organisation. Around the stem and branches and foliage of the nerve-tree is draped a diffusely-connected network. This fringe of uncertain function is characteristic both of primitive creatures and of those late in the scale of evolution; it is associated with simplicity and also with a high degree of adaptability and plasticity. The diffuse nature of the tissue serves to remind us that to deal with uncertainty is the principal function of the higher centres, which must pilot a vulnerable animal through a changing and hostile world, a world where chaos and cosmos are interlaced and superimposed, where anything may happen, but nothing happens twice.

Until quite recently the study of nervous function has been mainly of its fixed attributes, of anatomy and reflexes, but with increasing technical resources and more powerful theoretical notions, attention is veering toward the subjectively familiar but experimentally bewildering *variety* of patterns which typify animal behaviour. In the familiar accounts of experiments on learning, such as emanate from conditioned reflex laboratories, it is usually the constancy and regularity of acquired responses which are stressed. It should be remembered, however, that great pains are taken to ensure uniformity and freedom from disturbance in such experiments and, moreover, observation is usually limited to one or two variables. Considering the huge number of experiments on learning which have been made during the last few decades, it is astonishing how little attention has been paid to the way in which a new pattern or idea grows in the mind of the subject. How does an animal decide that a new stimulus is worth responding to? How is the orderly form of a repeated "conditioned" stimulus distinguished against the background of uniform disorder and irrelevant signals?

Such problems as these have been illuminated by consideration of the nervous system as a generalised transmission system of unknown properties, a sort of "black box" into which signals are injected and from which other signals emanate. Comparison of the input and output permits certain conclusions to be drawn about the functional elements inside the box, even though the structural details cannot be accurately inferred if the box cannot be opened. This approach is familiar in the field of Information Theory and leads to the concept of the nervous system as a device for collecting and storing information about the world it lives in and conveying information to that world and even manipulating it. The problem of distinguishing or creating an orderly pattern from disorder can then be tackled in the manner of the Transmission engineer who has to deal with "signals" superimposed on "noise". This contrast between signals and noise is fundamental to understanding any system of communication and introduces exactly what has been lacking hitherto in the study of animal behaviour patterns—the *statistical* element. It is well worth considering the recognition of form, the growth of new patterns of behaviour, and the creation of new ideas and devices, as deriving from a formal statistical appraisal of the environment. As a first step we may postulate that within the Black Box of the cranium is some device capable of sampling incoming sensory signals in such a way that their statistical deviation from randomness is assessed and their significance accordingly established. Instead of the telephone-exchange analogy of the last generation we arrive at something more like a totalisator that automatically works out the odds in favour of a given pattern or series of events being worthy of attention.

In a race-course totalisator the odds given are a function only of the sum of money already staked on each contestant; but the wagers laid themselves depend both upon the odds offered and, to a varying degree, also on the "form" of the various mounts and jockeys in relation to the length of the race, the nature of the course, the weather, and so forth. In comparing such a system with the nervous system we must be careful to include these latter factors also for they compare with the individual's inborn reflexes and memory of significant forms. Just as in gambling, an animal has the choice of seeking out a long-odds chance or backing short-odds favourites. The unpopular but adventurous path has danger but by definition freedom from competition; the safer and more crowded way can yield only a small return to each individual. Those animals that have a hot tip for an outsider are the ones which dominate the earth; the faculty of discerning significance where others see only disorder is highly prized and of great survival value. We may now consider in outline some of the mechanisms which endow the nervous system with the ability to beat the book in the natural handicap stakes.

For various reasons it is convenient to divide patterns into two groups—those in which the components are arranged in space, and those in which there is a sequence in time. Clearly, the whole pattern of the perceived world is extended both in space and in time, but there is reason to believe that the methods of perception are different for the two classes. In aesthetics, the appreciation of a painting or statue or building depends upon factors different from those employed in reading or hearing music, poetry, or stories. The obvious radical difference between space-patterns and time-patterns is that the latter are projected upon a uni-directional parameter; time, for us, has an arrow that points to the grave. This may not be comforting, but for purposes of communication it can be convenient.

In man the most important class of spatial pattern is the visual; the proprioceptive appreciation of position of the limbs and body and the tactile perception of form and texture are generally subordinate to the sense of sight. Even when the visual sensation is in error, the senses of touch, pressure, and movement usually condone and compound the perjury. The mechanisms whereby visual patterns are recognised and remembered are still rather mysterious but certain inferences can be drawn from studies of the electrical activity of the brain.

Every living cell maintains an electrical potential difference between its inside and the outside world. In cells specialised for conduction—nerve cells—activity is associated with a dramatic reduction in this potential difference and in the brain the vast congregation of nerve cells generates an enormously complex and continually varying pattern of electrical discharge. These electrical changes are so diminutive that elaborate equipment must be used to detect them from the surface of the head and even more intricate devices are necessary for exact measurement. A record of the electrical changes in the brain is called an electro-encephalogram or EEG. In normal adult humans, the most prominent features of the EEG are usually rhythmic oscillations at about ten per second—these are called *alpha* rhythms. Now the size and regularity of the alpha rhythms vary greatly in different individuals and there is evidence that persons with mainly visual habits of thought exhibit smaller and less persistent alpha activity, while those who think in terms of sounds and movements rather than visual images have large, regular alpha rhythms. Furthermore, in nearly all people who show this alpha activity, the rhythms are augmented when the eyes are shut and the mind is tranquil—they are attenuated by opening the eyes or by mental effort. (Fig. 1. a, b).

Analysis of these effects suggests that the important factor in arresting the alpha activity is the effort or compulsion to see and appreciate pattern. Most people who show large alpha rhythms with the eyes shut do not exhibit the attenuation effect if the eyes are opened to a completely featureless scene; the least trace of pattern—or the effort to find one—usually blocks the alpha activity. Conversely, opening the eyes in the dark may block the rhythms if the subject thinks there may or should be something to see. There has been much discussion about these alpha rhythms; the phenomenon may be a meaningless coincidence produced by the relatively crude method of observation which includes the activities of millions of nerve cells in one record.

There is some evidence, however, that rhythmic oscillation of this type may have a specific essential function in mediating the perception and comparison of visual forms—that of transforming the spatial pattern of things seen into a succession of signals in time. There is a simple experiment which yields subjective evidence that something of this sort is going on in the brain; if one looks through closed eyelids at a bright light flashing on and off at about ten per second one sees more than mere flicker—there is always a sensation of movement. Most people describe a checkered field which pulsates and rotates in a dizzy fashion and may change colour as the flash frequency changes. In this experiment there is no *real* movement and the illusion must be produced by rhythmic waves of excitation spreading across the visual projection areas in the brain.

The transformation from spatial to temporal co-ordinates is known to television engineers as "scanning", and in a transmission system it is used for economy. By scanning a scene to be televised the hundreds of thousands of picture details can be transmitted on a single cable or radio channel instead of on a corresponding number of cables or bands. It can be shown that, in the brain, economy of circuits must be effected by some means if the head is to remain reasonably portable and a scanning process for the dominant sense would be the first device to occur to a competent engineer. Such a system has disadvantages of course—a visual pattern cannot be recognised in less than about one tenth of a second and any change during that period will produce illusions. These limitations are well known to pyschologists; anyone can discover that it is just possible to read about 100 words in ten seconds and that when a light is turned off just before another is turned on it looks as theough there were a movement of one light from the first to the second. In the world of other animals in which we evolved, these drawbacks were of secondary importance, but as the speed of our perception meets the competition of machines which can act with far greater speed, survival may go with faster alpha rhythms.

In mobile terrestrial animals the absolute bulk of the body is an important factor in survival—it is essential to be the right size. For many reasons, the head, containing the distance receptors as well as the brain itself must be both strong and light; extreme economy is therefore needed in the design of the internal mechanisms of perception, and we can perhaps regard the alpha rhythms as examples of the Law of Parsimony applied to organic evolution.

The space-time transformation of visual signals required by the principle of parsimony has consequences beyond mere physiology; the asymmetry of the time dimension provides a simple escape from the tyranny of space where perfect geometrical symmetry can and does exist. Buridan's ass, equipped with a scanning generator, would not die of hunger between his two equal and equidistant bales of hay, nor need Dante's "liber uomo" suffer that fate "intra due cibi, distanti e moventi D'un modo" for the dilemma is automatically solved when the two equal signals are strung on the thread of time where one is forever before the other. This mechanism also permits great delicacy in the recognition of pattern and the abstraction of universals; as McCulloch has pointed out, the perception of Gestalten and the derivation of abstract form may be achieved artificially with great economy by a device which averages all transformations of a group.* A further advantage is that when all incoming sensory signals are projected on to a common time-base, whatever their original modality, they become to a new degree comparable with one another; a form may mean a word and a face a friend. As we have already seen, such processes imply corruptions as well as economy and plasticity—here as always translation has a tinge of treachery.

With such notions in mind we may consider in greater detail the appearance and variety of the alpha rhythms of human brains. In its earliest days the EEG of man was noted for its individuality—no two people, not even uniovular twins, have identical alpha patterns and in any one person the pattern is remarkably constant from year to year once cerebral maturity has been reached at the age of 14 or so. Wide though the variation is, some classification is possible. There are three main groups. First there are those in whom the alpha rhythms, prominent when the eyes are shut and

* A 'group' means here a set of displacements bringing an object into identity with itself, like rotations about an axis of symmetry.

the mind at rest, disappear whenever the eyes are opened or mental activity occurs. Second are those in whom no significant alpha activity can be detected even in conditions of tranquillity with the eyes shut. Third is the smaller group in whom alpha activity persists even when the eyes are open and the mind alert. The first group have been called "R" meaning responsive, the second "M" for minus, the third "P" for persistent. As already mentioned the alpha characteristics correlate with habits of thought and imagination. The M group think mainly in terms of visual imagery, in pictures which are sometimes almost as vivid and detailed as external reality; for them a private cinema show is constantly in progress and their problems are solved on a mental blackboard. When a visual solution is possible and adequate their performance is rapid and precise, but when they are faced with a problem in other modes they become sluggish and confused. At the other extreme, people whose alpha rhythms persist even with the eyes open do not use visual images unless they are compelled to—they think in terms of sound and movement and lose their way when involved in an imaginary maze. The R group are of course intermediate between the other two; while not obsessed by private pictures they can evoke satisfactory visual patterns when necessary and can combine data from the various sense organs more readily than can either the M or P types.

In assessing the significance of these observations, the origin of the differences between the groups will have to be discovered and there has not yet been time to follow a large enough population from birth to maturity to discover how soon and how immutably these internal patterns are established. The evidence available at present, both statistical and experimental, strongly suggests that the alpha characters are inborn and probably hereditary, but whether the degree of responsiveness is a unit character or determined by many factors is not yet certain. The oscillation frequency of the alpha rhythms is distributed more or less normally in the population, so this may be a multifactorial character similar in its genetic determination to stature or intelligence, but the distribution of responsiveness of the rhythms is less straight-forward and may be more like eye-colour in its hereditary relations but complicated by its susceptibility to conditioning. In "identical" twins the resemblance between their alpha rhythms is as great as that between their fingerprints; such differences as exist are in the details of the response to stimulation. It has been shown that, in a person whose alpha rhythms normally respond only to visual stimulation, a conditioned response may be established by repeated association of some other stimulus with light. Such associations—in complex and subtle combinations—are bound to occur in everyone and the details are certain to vary in different individuals so that, within a given alpha group, acquired responses must play some part and endow even the most similar records with clear individuality.

The pattern-abstracting mechanisms represented by the alpha rhythms are of course an important part of the cerebral apparatus which puts together a working model of the world it lives in. It is not surprising therefore that the differences between alpha types are reflected in their attitude to their environment and to one another. Discussion between an alpha-less M and a persistent P is usually fruitless and often acrimonious; worse than not speaking the same language, their mental accents, so to say, are incompatible and neither will give the other credit for clarity, consistency, or good taste. Communication between such a pair is sometimes more agreeable through the intermediary of a less emphatic and more tolerant member of the R group. Both extremes being rare, a clash between them is, fortunately, even more uncommon, but when two people display an illogical and irreconcilable antagonism toward one another, some such discrepancy in their imaginary customs may be worth considering.

If these hypotheses are not too far from the truth, we may legitimately anticipate a re-assessment of personal differences in matters of taste on a literally aesthetic basis. There is, however, one important matter which is still obscure; the extent of the visual field swept by the internal scanning mechanisms. As is well known, the retina is unlike a photographic film in that the coarseness of its grain is not constant over its whole surface. In a patch about 0.3 mm. wide at the centre, more or less on the optical axis of the lens system, the light receptors, the "cones", are very closely packed and each is connected to the brain through a private nerve fibre so that images falling here can be resolved in great detail; toward the periphery, groups of cones and the more sensitive but less discriminating "rods" are connected all together to a single common nerve fibre. The consequence of this is that visual acuity—the power to see detail—is high in the centre of the field and falls off markedly in the periphery. Anyone can test this by gazing fixedly with one eye at a page of print; it will be found that only about one word can be seen clearly at a time, the rest of the page being quite indistinct and unreadable. The solid angle subtended by this circle of high acuity is only about 2°. Therefore in order to view any sort of scene—a face or a landscape—the eyes must scan its surface for detail, and the larger the scene the longer it will take for all parts of the field to be brought under the area of central vision where detail can be recognised. It is not surprising that, in view of the smallness of the region of acute vision, a great part of the brain is concerned entirely with the control of eye movements. Normally, in order to read the simplest word, both eyes must be aimed and focussed together and the diameter of the pupils adjusted, and this must go on ceaselessly as long as clear vision is required. In the field of Art, quite apart from the impressionistic or interpretative function of the painter, any technique which can condense a scene into a smaller compass will tend to give satisfaction to the viewer. A landscape which subtends say, an angle of 45° at the eye can be seen clearly only after a series of several hundred glimpses, requiring thousands of co-ordinated eye movements, to say nothing of the mental effort required to remember and link up the parts of the puzzle and the added dimension of depth. From the physiological standpoint the reproduction of such a scene, reduced in size to subtend an angle of say 10°, flattened and shorn of irrelevant detail, evenly lit and perhaps intensified in colour, represents an economy of a hundredfold in the effort of perception. How much of the value and satisfaction of a painting is attributable to this easement of physiological strain, to the lighter loading of a battery of hard-pressed intra-cranial servo-mechanisms?

There seems a possibility then, that in visual perception, there may be two scanning stages, one involving the eyes themselves and another after the signals have reached the brain. We do not know, however, whether the alpha process covers the whole field as projected on the receiving areas or only the central, or whether there are two separate central scanners, one for central detail and the other for peripheral background. We have some evidence—not at present very strong—that the scanning sweep of the alpha rhythm is a sort of logarithmic spiral, more closely coiled at the centre and wider at the periphery of the visual projection regions. This system contrasts with that used for television which is a true rake or "raster", combing the camera and receiver screen in a series of parallel lines. A spiral sweep, combining economy with elegance in a characteristically biological fashion, would give just that extra resolution in the centre of the field needed to take advantage of the fine grain of the central retina.

An impression of the internal mechanisms at work may be obtained by examining closely the illusory patterns already referred to which are seen when looking at a flickering light. Many experimental subjects say that they see something like a Catherine-wheel which spins at a speed varying with the rate of flicker and reverses its rotation at a critical frequency near ten per second. At the same time the centre of the visual field during flicker is usually described as a spot with finer detail and less relation to the whirling motion than the periphery.

Alpha rhythms are by no means the only pattern of electrical activity seen in the normal brain. In most children up to the age of 10 or 12 there is commonly a rhythmic discharge at about six per second, not in the visual regions, but further forward toward the temples. This we have called *theta rhythm*; it is not markedly responsive to visual pattern but is associated in some delicate fashion with pleasure and pain. In a young child, theta activity can be evoked readily by contriving some degree of frustration, as in snatching away a proferred sweetmeat. In older children the relation is less material; the suggestion or memory of humiliation or anger is more likely to evoke a theta response. In good-tempered adults the theta component of the brain patterns is scarcely visible in ordinary circumstances, but in many people it can be evoked by suddenly interrupting a prolonged pleasant stimulus, such as stroking the head. The provision of a really disagreeable stimulus is adequate too, but is much harder to arrange in laboratory conditions when any attempt at provocation is palpably artificial. The subject must feel himself deeply offended by some personal affront; one's enemies are not likely to yield themselves into one's hands, of strangers one cannot know anything sufficiently telling, and a friend one may not, by definition, offend.

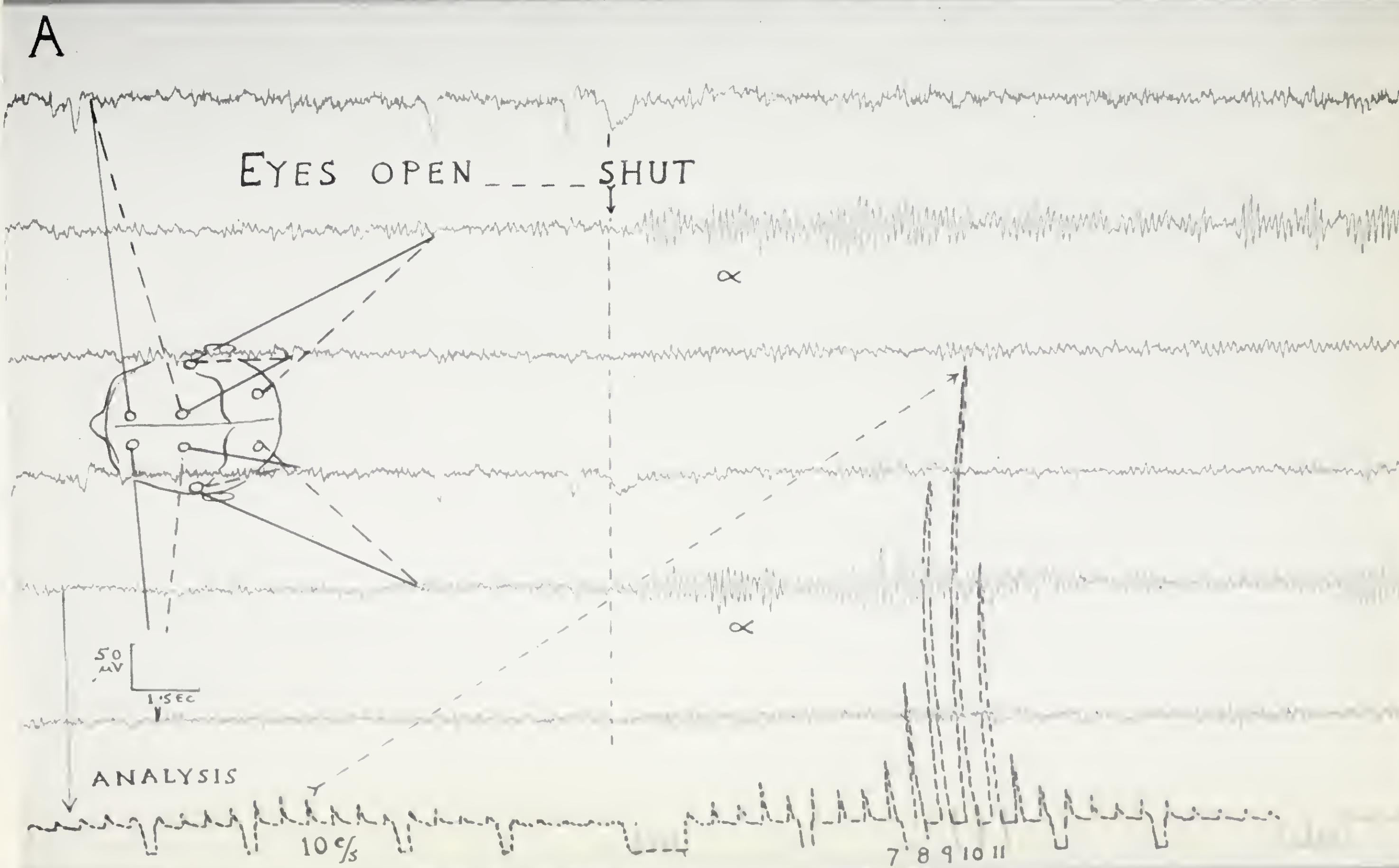
In people with an abnormal tendency to aggressive behaviour, the bad-tempered folk sometimes labelled psychopaths, theta activity is often prominent and may occupy quite a large area of the temporal and parietal lobes of the brain. Their childish intolerance, impatience, suspicion, and selfishness is mirrored in the juvenile appearance of their brain patterns. If the theta rhythms scan for pleasure as the alpha rhythms scan for pattern one may say that such people are constitutionally blind to the possibility of an agreeable situation.

This correlation of profound subjective impressions and attitudes with an apparently simple electrical discharge may well seem facile and superficial, but there is experimental evidence that the mental and electrical phenomena are in fact closely related. Using flickering light stimuli of high intensity we have shown that visual stimulation at the frequency of a theta rhythm may evoke, even in a normal subject, a feeling of annoyance and frustration even when no stimulus with emotional content is present (Fig. 2). Furthermore, when emotional aggravation is added to the theta flicker, the two effects summate, both electrically and psychologically, producing in a normal equable subject a transient resemblance to an aggressive psychopath. Contrariwise, if the subject is encouraged to control and suppress the feelings aroused by the flicker, the evoked electrical disturbance is quenched.

Here there is evidence not only of an intimate relation between the pattern of thought and the form of living processes, but also between the visual receiving area of the brain and some other regions less easily specified, for the flicker stimuli set up sympathetic oscillations far from the zone of their reception (Fig. 3). Sometimes stimulation at a higher frequency, say 18 per second, produces in the temporal or frontal regions a response at a factor of the stimulus rate—at 9, 6, or even 3 per second. When one of these factors is in the theta range the characteristic sensations appear. In epileptics such effects frequently develop into seizure patterns; the whole brain receives a barrage of harmonically related signals, which, blending with the spontaneous rhythms, create the conditions in which consciousness and control are lost—but that is another story.

The evocation of complex electrical patterns and their related states of mind by simple rhythmic stimuli seems a most undesirable and dangerous propensity, for these patterns are irrelevant to the situation—there is no apparent advantage in recalling an ancient hatred just because one is gazing at a flickering light. We must hark back to our opening generalisation—to deal with uncertainty is the principal function of the higher centres. The primate brain, as a statistical predictor, makes few assumptions about what can and what cannot happen; from its first experience of birth it provides for the implication of almost any phenomenon by almost any other. This we know simply by the vast capacity for learning which we possess; a man may learn by experience to associate two series of events between which any connection seemed at first wildly improbable. For such associations to be possible, provision must be made for every signal entering the nervous system to be relayed to every part, not merely to the specialised receiving zone. Thus from the knot of an event is generated a web of speculation; when two series of events are perceived together they form the warp and woof of a shimmering fabric into which is woven the pattern of the probability that the two events are significantly related. The repetition, in time, of this pattern permits the construction of a hypothesis of correlation; the idea that one series of events implies the other. In a time-pattern, repetition plays the part of symmetry in space patterns.

With the capacity to imagine pattern where there is confusion goes the tendency to create cosmos where there was chaos. We have remarked that a pattern seen, however vivid and pleasing—or disagreeable—may be a fortuitous illusion. We should not feel surprise or revulsion therefore when we find that some



G. 1a

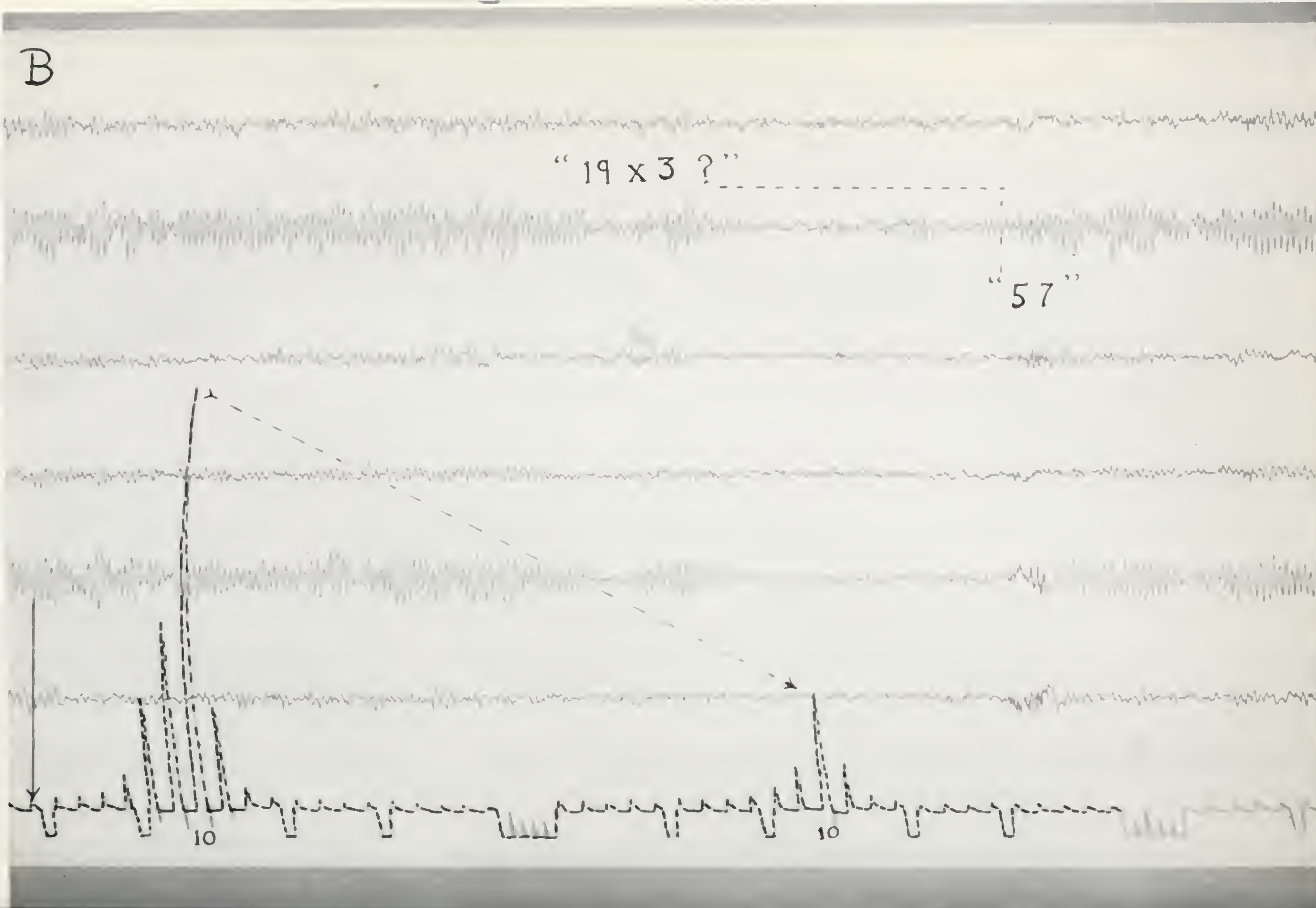
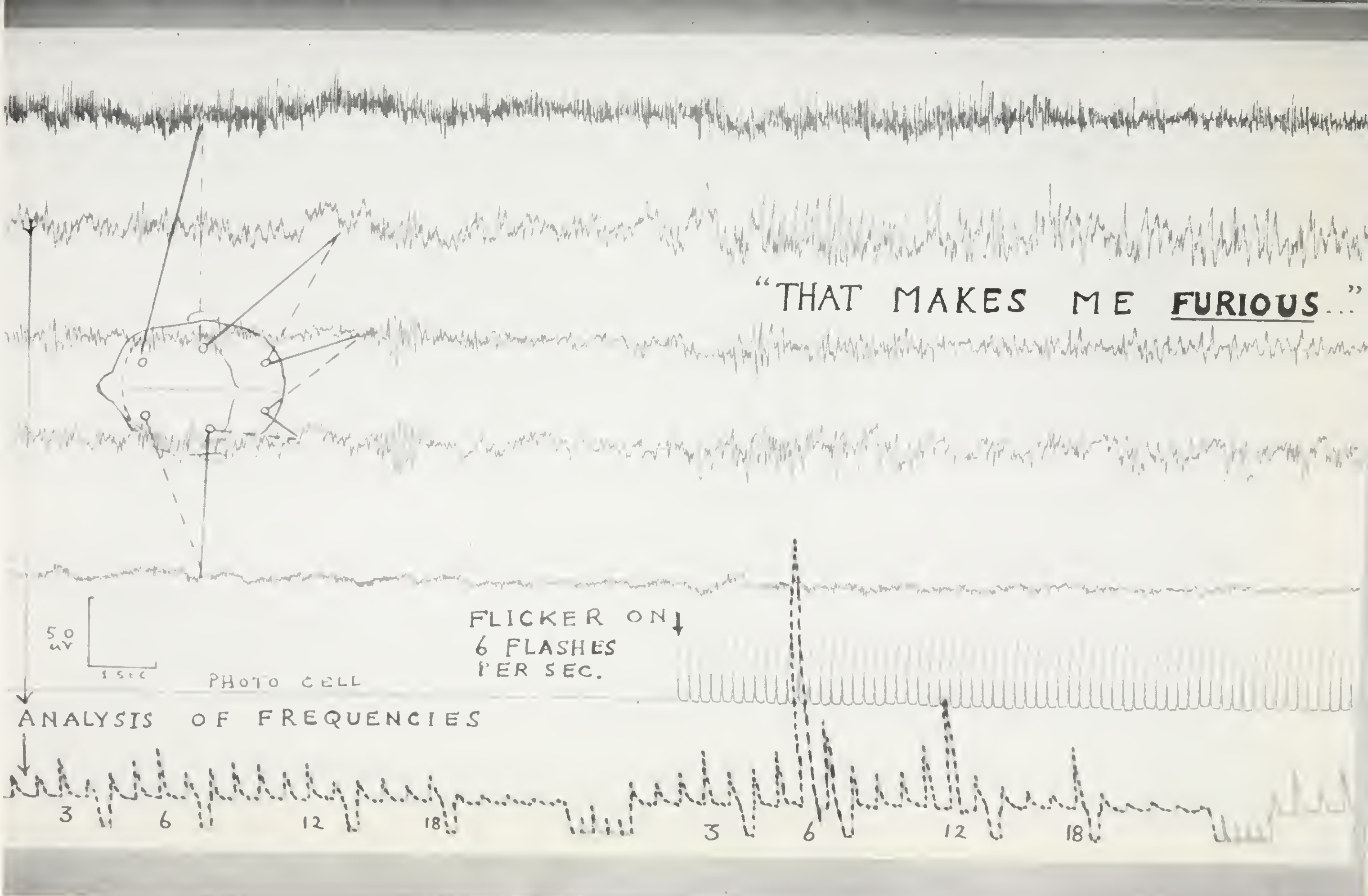


FIG. 1b

FIG. 2



"THAT MAKES ME FURIOUS..."
50 µV
1 SEC
PHOTO CELL
FLICKER ON
6 FLASHES PER SEC.
ANALYSIS OF FREQUENCIES
3
6
12
18
3
6
12
18

FIG. 3

artificial designs have as tenuous a relation to reality as the fantasies evoked by flicker. Even a donkey's tail may generate a cynosure.

Illustrations: *explanatory notes*

FIG. I. EEG of a normal responsive subject showing:

(*a*) The great augmentation of the occipital alpha rhythms on closing the eyes.

(*b*) Their attenuation while solving a simple problem. The position of the electrodes on the head, the time-scale and the voltage-scale are indicated in (a). In both records the change in the alpha rhythms is indicated quantitatively by the spectrum analysis (shown dotted).

FIG. 2. Evocation, in a normal subject, of 6 c/s theta activity and emotional disturbance by flicker at 6 flashes per second. Note the activity also at 3, 12 and 18 c/s.

FIG. 3. Photographic records of activity evoked by flicker at 12 flashes per second during two exposures, each of 0.5 secs. The records were obtained with a new type of display system known as a Toposcope, in which the spatial distribution, frequency, and geometry of the brain activity are emphasized. There are 22 separate channels driving cathode-ray oscilloscopes arranged in a pattern corresponding to a view of the head from above. Activity in any area is shown as a brightening of the corresponding oscilloscope. In this case the flicker evokes a small response in the occipital region 'O' and a much larger one in the right temporal lobe 'T', together with a multiple harmonic response in the frontal regions, 'F'. The frequency, phase, and time-relations of each component can be obtained by multiplying the number of petals in each pattern by the reading (here at 4 c/s) of the frequency-meter on the right of the illustration. The variety and disperson of such patterns are correlated with changes in the subjective sensations produced by the stimulation.

Gestalt Psychology and Artistic Form

by Rudolf Arnheim

THE FRENCH SPEAK of Gestalt psychology as *la psychologie de la forme*. This translation is meant to indicate that the Gestalt principle is only indirectly concerned with the "subject-matter" of natural things. To call a football team or a painting or an electric circuit a Gestalt is to describe a property of their organisation. Gestalten function as wholes, which determine their parts. Four musicians who form a string quartet will create a unified style of performance. This style is a delicate crystallisation of affinities and conflicts of temper. It is the balance of convergent and divergent social forces and, in turn, modifies the behaviour of each player. Change the arm of the left boy in the Laocoon group, and the entire piece of sculpture assumes a different composition. Such internal play of influences obeys rules that are largely independent of the particular medium in which they are observed. In a sense, they refer to "formal" properties.

If, however, we mean by "form" the outer appearance of things—as we do when speaking of the arts—it is necessary to see that the Gestalt theory deals with form only as the manifestation of forces, which are the true object of its interest. Physical and psychical forces can be studied only by their perceivable effects. Thus the overall direction of energy in a given system may appear as a visible axis in the observed pattern. The degree of balance in the distribution of forces may be reflected in the degree of observable symmetry. The direction and strength of water power shows in the "form" of the flow. In the star shape of a flower we recognise the even spread of undisturbed growth. The flaws of a crippled tree or a hunched back tell of interferences with lawful development. Anxiety may express itself in the muscle tension of the body or the broken curve of a gesture.

In all these cases, form is strongly determined by forces inherent in the object itself. This is not always so. It is hardly true at all for the work of art. In the visual arts, except for the effect of such inherent qualities of the medium as the weight of stone, the grain of wood, or the viscosity of oil paint, form is imposed on matter by external force. Neither can a work of art be grown, nor does the artist often use highly organised materials such as crystals or plants. Dancers and actors, who use their own bodies, and to some extent photography, which uses the direct registration of physical objects, are the outstanding exceptions; but it is precisely for this reason that they are suspected of being hybrids of art and nature. The artist prefers the submissiveness of amorphous matter.

Physically, then, the work of art is a "weak Gestalt", an object of low organisation. It makes little difference to the marble of the Laocoon group that an arm is broken off, nor does the paint of a landscape revolt when a busy restorer adds a glaring blue to its faded sky. But, as Benedetto Croce would point out to us, we are now not speaking of art at all. Art cannot be a physical fact because "physical facts have no reality, whereas art, to which so many devote their entire lives and which fills everybody with divine joy, is eminently real". This means that art exists only as a psychological experience; and the forces which generate such experience are the proper object of our attention.

The work of art defined as an experience turns out to be a Gestalt of the highest degree. In fact, from the beginning, Gestalt theorists looked to art for the most convincing examples of sensitively organised wholes. Christian von Ehrenfels, whose essay "Ueber Gestaltqualitäten" gave the theory its name, speaks of a melody as being different from the sum of the tones which constitute it. And we discover with delight such testimony as Cézanne's answer to Vollard, who had pointed out to him two tiny spots of uncovered canvas in his portrait: "You understand, Monsieur Vollard, if I should put there something haphazard, I should be compelled to do my whole picture over, starting from that place!"

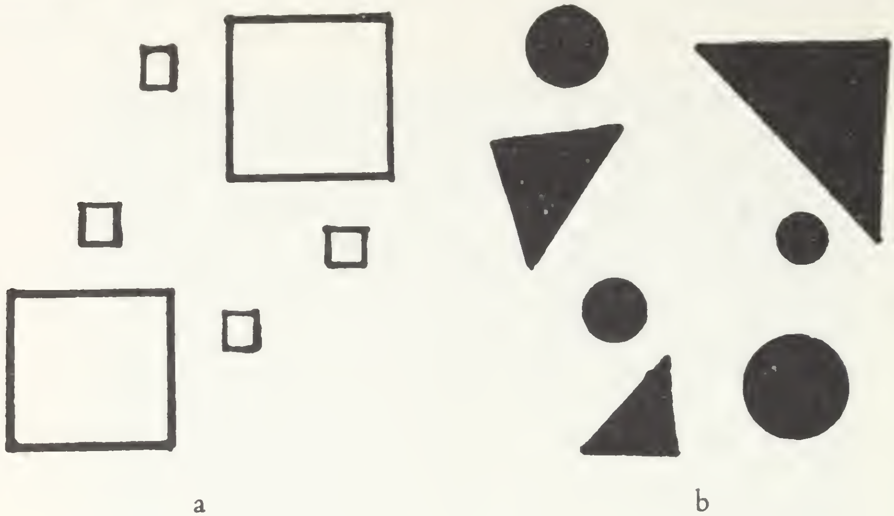
The psychological forces that determine artistic form operate essentially in the perceptual process of vision and in the area of motivation and "personality". For the purpose of analysis these factors can be discussed separately. Actually, they interact all the time. Also a more complete presentation would require consideration of further psychological levels, notably thinking and memory.

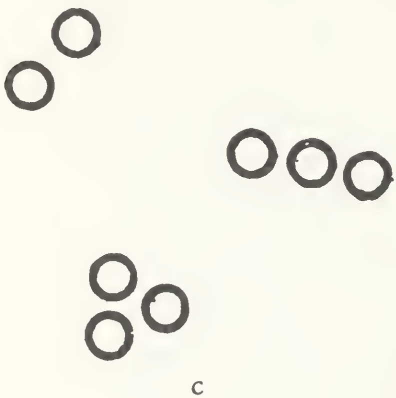
Vision cannot be explained merely by the properties of the observed object but is dependent on what goes on in the brain. Think of a red triangle in the centre of a rectangular grey ground. "Objectively" we have nothing but two areas of different colour, situated in the same plane, independent of each other, and at perfect rest. If we scrutinise the observer's experience and consider at the same time what is going on in the neural mechanism of vision, we realise first of all that we are dealing with a highly dynamic process. The triangle has broken up the unity of the grey and is constantly defending itself against the tendency of the plane to regain its homogeneity and to expel the invader. This is successful to the extent that the triangle appears suspended in front of the grey plane thus permitting the ground to continue "behind" the triangle and to maintain its wholeness. The triangle also is far from static. It is dense, compared with the looser texture of the ground. Its pointed corners stab outward in directed, centrifugal movement. Also the red, being a more active colour than grey, shows the property of long wave-length hues to appear closer to the observer. It attacks him. Were it blue, it would withdraw from him. Red is warm and radiates across the ground. Were it blue, it would be cold and contract toward its centre. Furthermore, the triangle is held in balance by its central location. If it were placed eccentrically, we could actually experience the pushes and pulls that would tend to displace it—for instance, by drawing it toward the centre of the ground. Even in its central position our triangle is no more "at rest" than a rope that does not move because two men of equal strength are pulling it in opposite directions. The antagonistic forces happen to balance each other. Nevertheless, their power remains perceivable to the sensitive eye.

This is not all. Shape and size of the two units constantly define each other. The smallness of the triangle determines the largeness of the ground. The stable verticals and horizontals of the rectangle are enhanced and challenged by the obliqueness of the triangle, and vice versa. The brightness and colour values also interact. The lightness of the ground darkens the triangle. The red evokes in the grey the complementary green.

A simple example has been analysed with some detail in order to show that any description of form in the static terms of sheer geometry, quantity, or location will fatally impoverish the facts. Only if one realises that all visual form is constantly endowed with striving and yielding, contraction and expansion, contrast and adaptation, attack and retreat, can one understand the elementary impact of a painting, statue, or building and its capacity to symbolise the action of life by means of physically motionless objects.

Since visual dynamics is not inherent in the physical object—where are the forces which constitute it? Gestalt psychologists refuse to describe them as an effect of empathy, that is, as a mere projection of previously acquired knowledge upon the percept. They assume that the sensations of push and pull are the conscious counterpart of the physiological processes which organise the percept in the neural field of the optical sector, that is, the cerebral cortex, the optic nerve, and possibly the retinæ of the eyes. According to this theory, visual dynamics is not a secondary attachment of the stimulus, due to accidental, subjective associations, but rather precedes the "geometric" pattern of shape and colour in that this pattern is the result of the organising forces, of whose activity the observer is partially aware. The theory would seem to explain why in actual experience the dynamic, or expressive, aspects are the most powerful and immediate qualities of the percept. In comparison, the static attributes of shape, size, line, or location, on which scientists have concentrated their attention, would seem to be relatively indirect and late products of vision. The detached, measuring gaze of the investigator in the laboratory preserves little of the spontaneous excitement which the child, the primitive, the artist find in the world of sight.





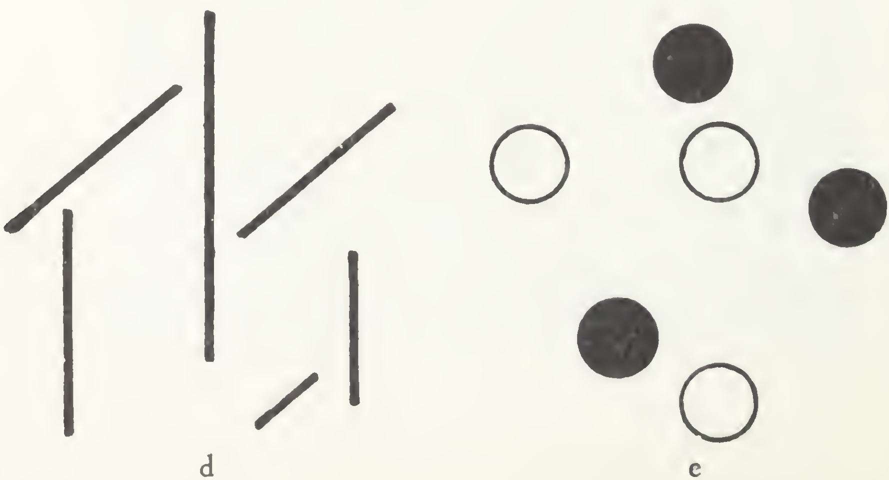


FIG. 1 Visual grouping results from similarity of
a size
b shape
c location
d direction
e brightness and color

Once this point is strongly made, one may turn to the principles of articulation, to which Gestalt psychologists have devoted most of their investigations of visual form. What makes the visual field split up into segregated objects—trees, houses, cars, people? What makes the "abstract" painter confident that all observers will see roughly the same units of form in his composition? Experiments have shown that articulation is controlled essentially by the nature of the stimulus configuration itself. Thirty years ago, Max Wertheimer established some "rules of visual grouping". It seems now probable that these rules can be reduced to one, namely, the principle of similarity. The relative degree of similarity in a given perceptual pattern makes for a corresponding degree of connection or fusion. Units which resemble each other in shape, size, direction, colour, brightness, or location will be seen together.

The principle of similarity organises stimulus elements in time as well as in space. The form pattern of a painting, which impinges upon the observer's mind, is not his first visual experience. It is the most recent phase of a prolonged process, within which memory traces interact according to the principle of similarity. The relative strength of the factors which make up the temporal and the spatial contexts will determine what the observer sees at any given moment. Owing to its high degree of unity and precision, good artistic form is capable of imposing its own articulation upon different observers in spite of the different "visual history" which each individual brings to the present experience.

It is possible and necessary to interpret the principle of similarity as a special case of a more general law, according to which the forces which constitute a psychological or physiological field tend toward the simplest, most regular, most symmetrical distribution available under the given conditions. This means that of the many possible groupings of elements in a visual pattern the one which makes for the simplest organisation of the whole context will spontaneously occur to the observer.

Described in this way, the organisational processes, which take place in the creation of visual form, are shown to obey a law which governs the functioning of the mind as a whole. In addition, we thus discover a similarity between the behaviour of

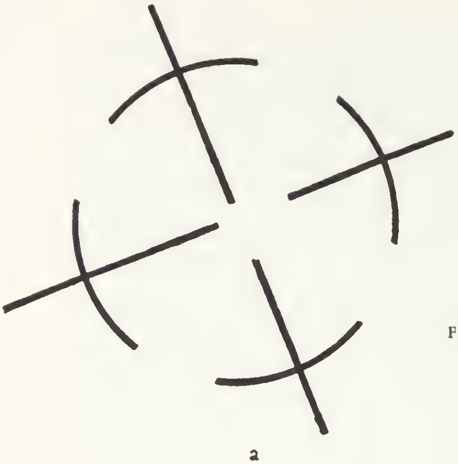


FIG. 2 The principle of simple form.
a. Circle and cross are seen instead of four independent patterns.
b. Complex figure breaks up into triangle and rectangle.

psychological and physical processes. In fact, in 1920, Wolfgang Koehler in his book on "Die physischen Gestalten" pointed to the second law of thermodynamics as a manifestation of the basic Gestalt principle. Physicists assume that the world tends to pass from less probable to more probable configurations or states. There is no reason why the physiological forces in the nervous system should make an exception to this rule. In other words, the mental processes which create visual form can be understood as a reflection of the tendency to simplest structure assumed to exist in the corresponding brain field.

Psychologists and physicists have arrived at similar conclusions independently of each other. As a curiosity it may be mentioned that while Gestalt theorists recognise a tendency to "good form" or "well organised structure", the physicists see a development from order to disorder. Presumably the contradiction is partly terminological; but the necessary unification of these views is likely to lead to considerations that will be of interest to both parties.

If the human mind in general and the mechanism of vision in particular are governed by a tendency to simplest structure, we may ask why we see any objects at all. Obviously, the simplest possible field of sight would be totally homogeneous like a white-washed wall—inarticulate, plain, motionless, a foretaste of the dismal state in which, according to the physicists, the chilled universe will find itself at the end of time. Our eyes are saved from such boredom by the fact that the organism is not a "closed system". The influx of external energy constantly upsets and delays the striving toward final rest. In vision, the disturber of the peace is light energy, which, through the action of the eye-lenses, comes to us in the form of information about objects. Now information, according to Norbert Wiener, is negative entropy; that is, it imports order or form. For our purposes, "objects" can be defined as processes that have been temporarily arrested on their way to final equilibrium. The images of all objects show the partial success of that process, namely, some regularity, some symmetry, some simplicity of form. But they also show the marks of striving and growing, of segregation and independence. Thus the form of objects allows us symbolically to envisage the nature of life in its restless striving towards rest.

Far from being a passive mechanism of registration like the photographic camera, our visual apparatus copes with the incoming images in active struggle. It is upset by the intrusion and animated by the stimulation. It seizes upon the regularities of form, which allow comprehension, and tries to subject the bewilderingly accidental agglomeration of objects in space to whatever order is obtainable. Every-day vision initiates and anticipates the duel of the artist with the image.

So far we have singled out the activity of the eye, as though it were a self-contained organism, minding its own business and forming pictures for the pictures' sake. This makes for a short-sighted psychology of perception. If applied to aesthetics, it leads to a narrow conception of art as a purely formal manipulation of images. But vision, in daily life as well as in art, functions as a part of the total mind. As such it is an instrument of observation at the service of vital needs. It also reflects symbolically the entire state of mental affairs which constitute "personality". Consequently, pictorial form can be expected to be determined essentially by four factors: (1) the structure of the images of external objects projected on the eyes; (2) the formative powers of the visual apparatus; (3) the need of the organism for observing, selecting, and understanding; (4) attitudes, mood, temperament, tensions, inner conflicts, etc.

The first factor would bear on the realistic truthfulness of pictorial representation. The second accounts for the exploration of shape, for "composition" as a pleasing arrangement of balanced form, for decorative ornament. The third and fourth require more detailed discussion.

The function of artistic form remains incomprehensible as long as one fails to remember that vision does not primarily serve to satisfy detached curiosity and enjoyment. By means of the eyes the organism scans the environment beyond the limits of its own body in order to discover useful or dangerous things. Needs make for perceptual selection. For instance, any movement in the environment automatically attracts attention because movement means a change of conditions, which may call for a reaction. Uninteresting things cast their images on the retina, but as a rule are not perceived.

This selective factor manifests itself in pictorial representation. It determines subject-matter and form. It tells what the artist—or his patron—considers important or safe. The psychologist notices that some historical periods or individual artists concentrate on the human figure, others on objects connected with utility and consumption, others again on nature. He finds that under certain conditions art withdraws from subject matter altogether. Form is influenced by concern with, or neglect of, detail. Needs and mores make for distortion. Pictures of the human figure may show large breasts but no genitals. In children's drawings much more space may be devoted to the face than to the body. Arms or clothes may be left out entirely. The dependence of form factors such as size, proportion, location, shape, shading, direction, on the inner needs of the draftsman, are being studied in a recently developed psychological test, which requires patients to draw the picture of a man and a woman. In a more passive way, an observer's interpretation of the perceptual qualities of inkblots (whole vs. part, shape vs. colour, shading, movement, etc.) is found to be significant in the Rorschach test. With certain precautions, it may be possible to apply these findings fruitfully to the analysis of artistic form.

Visual form must also be considered as a basic means of understanding the environment. Man's notions of what things are, how they act, and how they are related to each other, rely greatly on appearance. Particularly the young mind of children and primitives derives most of its judgments from the direct interpretation of perceptual form. Thus a latch-key may look lazy or aggressive, or magic power may be attributed to an object of disturbing shape. In a more general sense the child by gradually conquering the basic geometric forms and applying them to trees, houses, people, or animals grasps something of the nature of these objects. The towering size of a father, the generous spreading of a tree, the flimsiness of smoke are captured by means of comprehensible form and thus acquired for the child's conception of the world.

The child conquers form by observing the objects around him, but also by freely exploring the products of his pencil and crayon on paper. There is no reason to assume that the early drawings and paintings of children are all representations of the environment and that the basic geometric forms evolve from copying the shape of objects. A Gestalt psychologist would expect that the tendency to simple structure would increasingly direct the child's first scribbles. The clear, balanced, comprehensible shape of a circle, a straight line, or a rectangular relationship will be a source of great pleasure. In fact, unless parental pressure hampers free development, non-representational forms—which look like "abstractions" to an art critic but are eminently concrete to the child—will be created for their own sake. Increasingly often, they will also be related to objects of the environment. There is constant interplay between the growing complexity of the forms that can be mastered and the subtler observation of reality, to which richer forms can do better justice.

The clarification of visual forms and their organization in integrated patterns as well as the attribution of such forms to suitable objects is one of the most effective training grounds of the young mind. Educators and psychologists are beginning to see that intelligence does not only operate in verbal abstractions. Visual thinking manifests and develops general intelligence, and the stepwise progress of visual order reflects the development of the person as a whole.

Visual order as a tool of insight has been stressed by the late

Gustaf Britsch and his disciples, Kornmann and Schaefer-Simmern. Their findings in the field of art education are in striking agreement with Gestalt principles. It is true that these educators have concentrated on the "formal" aspects of art, but they have also stressed the fact that mechanical copying or imitation leads to the neglect of visual organisation, that is, to ugliness. An image can only be valid if it transmits the artist's conception of his subject by means of the spontaneous symbolism of orderly form. Beauty can be defined as the correspondence of meaning and perceptual symbolism. In the true work of art, the deepest meaning is conveyed by the elementary properties of size, shape, distance, location, or colour. The power of this visual language lies in its spontaneous evidence, its almost childlike simplicity. Darkness means darkness, things that belong together are shown together, and what is great and high appears in large size and in high location.

Beauty is lost when meaning and form are split asunder. This results, on the one hand, in playing with formal relationships or pure "composition", which carries no message or contradicts meaning. On the other hand, it leads to the misnamed "literary" approach, which limits meaning to what the observer knows about the subject-matter and therefore offers chaotic, visually incomprehensible form. The tragic consequence of this split in our time has been that so many people have become blind to the meaning of form and that they believe they "see" when they absorb meaning without form.

Point Four of our programme remains to be considered. The symbolism of form is not only a means of interpreting the environment visually, it also reflects the person of its creator. A human body means one thing to Lucas Cranach and another thing to Giorgione, because two different people are looking. Systematic attempts to understand pictorial representations as "projections" of the human personality are being made by therapeutically oriented psychologists. They deal with visual symbolism in two ways.

One of them is used by the psycho-analysts. Whereas Freud himself had cautioned his students that for a correct analysis of symbols one must rely on the comments of the individual who produced them; other analysts, in their discussions of art, do not hesitate to use easy standard interpretations of the dream-book type. This makes for an embarrassingly shallow approach to art. Visual form becomes a code language used by the artist to refer, with monotonous insistence, to the basic physiology of sex. The suspicion that most analyses of this kind are arbitrary is not only based on their disappointing results but also on their method. They use what we may term metaphoric symbolism. One concrete thing is said to stand for another concrete thing, a mandolin for a woman, a man for the artist's father, a bird or a cave for the male or the female genitals. Now interpretations of this kind are safe when metaphors have become institutionalised, that is, when they have been consciously established by cultural convention. For instance, in Christian art the dove stands for the holy ghost and the lily for virginity. But it is in the nature of the psycho-analytic symbols that much of the time their meaning is not permitted to reach consciousness. Only the avowed practice of some surrealists, who have institutionalised Freud, permits us to be sure that they do what the analyst says they are doing. In other cases no such proof exists, unless a reliable depth analysis of the particular artist is available.

Art can also be interpreted psychologically by means of what may be called isomorphic symbolism. This method does not depend on alleged associations of one object with another object but on perceptual qualities inherent in visual form itself. As an example the investigation of Rose H. Alschuler and La Berta Weiss Hattwick, "Painting and Personality", may be cited. These authors analysed a large number of "designs" done by nursery school children and compared them statistically with what was known about the children themselves. They assert, for example, that children who prefer warm colours show "warmer" relationships to other people while cold colours go with more controlled behaviour. The practice of overlaying one colour with another is found in highly "repressed" children. Children who use heavy strokes and squares, rectangles, or verticals are more assertive than the self-centred children, who like circles in their pictures.

In order to interpret these results one must assume that structural characteristics of visual form are spontaneously related to similar characteristics in human behaviour. We have called this type of symbolism "isomorphic" because this is the term used by gestalt psychologists to describe identity of structure in different media. For instance, a person's mood may be structurally identical with the bodily behaviour which accompanies that mood. This isomorphic correspondence has been used to explain the fact that the "expression" of physical behaviour seems to be directly comprehensible to the onlooker. The gesture of a dancer, but also the motions of a towel on the clothes-line or the shape of a cloud, contain structural features whose kinship with similarly structured mental features is immediately felt. If it is true that structural similarities transcend the difference between body and mind and make for unified total behaviour and experience, then we should expect the child to choose, for the pictures he makes, forms that match his own attitudes. Thus here again the findings of Gestalt theory and work in the arts seem to confirm each other.

The four determinants of visual form which we have discussed have been variously considered in the theory and practice of the arts, often in a one-sided way. There are those who hold that art is merely a faithful recording of whatever percept, memory, image, or phantasy besets the artist's mind. Others, on the contrary, concentrate on the organising powers of the eye without considering that all creation of form involves a coping with the world of experience. Again, the gradual progress of visual order is studied with little reference to the manifestations of the total personality in every stroke or shape. Or the picture is viewed as nothing but a kind of clinical map without sufficient awareness of the developmental steps in visual and motor organisation.

If we wish to understand the relationship between visual form and the total organism, we must consider the complex interaction of the many forces that make up a person.

Meditations on a Hobby Horse or the Roots of Artistic Form *by E. H. Gombrich*

THE SUBJECT OF THIS ARTICLE is a very ordinary hobby horse. It is neither metaphorical nor purely imaginary, at least not more so than the broomstick on which Swift wrote his meditations. It is usually content with its place in the corner of the nursery and it has no aesthetic ambitions. Indeed it abhors frills. It is satisfied with its broomstick body and its crudely carved head which just indicates the upper end and serves as a holder for the reins. How should we address it? Should we describe it as an "image of a horse?" The compilers of the Oxford Pocket Dictionary would hardly have agreed. They defined *image* as "*imitation of object's external form*" and the "external form" of a horse is surely not "imitated" here. So much the worse, we might say, for the "external form", that elusive remnant of the Greek philosophical tradition which has dominated our aesthetic language for so long. Luckily there is another word in the Dictionary which might prove more accommodating: *representation.* To *represent*, we read, can be used in the sense of "*call up by description or portrayal or imagination, figure, place likeness of before mind or senses, serve or be meant as likeness of . . . stand for, be specimen of, fill place of, be substitute for*". A portrayal of a horse? Evidently not. A substitute for a horse? Yes. That it is. Perhaps there is more in this formula than meets the eye.

I.

Let us first ride our wooden steed into battle against a number of ghosts which still haunt the language of art criticism. One of them we even found entrenched in the Oxford Dictionary. The implication of its definition of an image is that the artist "imitates" the "external form" of the object in front of him, and the beholder, in his turn, recognises the "subject" of the work of art by its "form". This is what might be called the traditional view of representation. Its corollary is that a work of art will either be a faithful copy, in fact a complete replica, of the object represented or that it constitutes a degree of "abstraction". The artist, we read, abstracts the "form" from the object he sees. The sculptor usually abstracts the three-dimensional form and abstracts *from* colour, the painter abstracts contours and colours, and *from* the third dimension. In this context one hears it said that the draughtsman's line is a "tremendous feat of abstraction" because it does not "occur in nature". A modern sculptor of Brancusi's persuasion may be praised or blamed for "carrying abstraction to its logical extreme". Finally the label of "abstract art" for the creation of pure forms carries with it the same implications. Yet we need only look at our hobby horse to see that the very idea of abstraction as a complicated mental act lands us in curious absurdities. There is an old music hall joke describing a drunkard who politely lifts his hat to every lamp-post he passes. Should we say that the liquor has so increased his power of abstraction that he is now able to isolate the formal quality of uprightness from both lamp-post and the human figure? Our mind, of course, works by differentiation rather than by generalisation, and the child will for long call all four-footers of a certain size "gee-gee" before it learns to distinguish breeds and "forms"![1]

II.

Then there is that age-old problem of universals as applied to art. It has received its classical formulation in the Platonising theories of the Academicians. "A history-painter", says Reynolds, "paints man in general; a portrait-painter a particular man, and therefore a defective model"[2]. This, of course, is the theory of abstraction applied to one specific problem. The implications are that the portrait, being an exact copy of a man's "external form" with all "blemishes" and "accidents", refers to the individual person exactly as does the proper name. The painter, however, who wants to "elevate his style" disregards the particular and "generalises the forms". Such a picture will no longer represent a particular man but rather the class or concept "man". There is a deceptive simplicity in this argument but it makes at least one unwarranted assumption: that every image of this kind necessarily refers to something outside itself—be it individual or class. But no such reference need be implied if we point to an image and say "this is a man". Strictly speaking that statement may be interpreted to mean that the image itself is a member of the class "man". Nor is that interpretation as far fetched as it may sound. In fact our hobby horse would submit to no other interpretation. By the logic of Reynold's reasoning it would have to represent the most generalised idea of horseness. But if the child calls a stick a horse it obviously means nothing of the kind. It does not think in terms of reference at all. The stick is neither a sign signifying the concept horse nor is it a portrait of an individual horse. By its capacity of serving as a "substitute" the stick becomes a horse in its own right, it may graduate into the class of "gee-gees" and even receive a proper name of its own.

When Pygmalion blocked out a figure from his marble he did not at first represent a "generalised" human form, and then gradually a particular woman. For as he chipped away and made it more lifelike the block was not turned into a portrait—not even in the unlikely case that he used a live model. So when his prayers were heard and the statue came to life she was Galatea and no one else—and that regardless of whether she had been fashioned in an archaic, idealistic, or naturalistic style. The question of reference, in fact, is totally independent of the degree of differentiation. The witch who made a "generalised" wax dummy of an enemy may have meant it to refer to someone in particular. She would then pronounce the right spell to establish this link—much as we may write a caption under a generalised picture to do the same. But even those proverbial replicas of nature, Madam Tussaud's effigies, need the same treatment. Those in the galleries which are labelled are "portraits of the great". The figure on the staircase made to hoax the visitor simply represents "an" attendant, a class. It stands there as a "substitute" for the expected guard—but it is not more "generalised" in Reynold's sense.

III.

The idea that art is "creation" rather than "imitation" is sufficiently familiar. It has been proclaimed in various forms from the time of Leonardo, who insisted that the painter is "Lord of all Things"[3], to Klee, who wanted to create as Nature does.[4] But the more solemn overtones of metaphysical power disappear when we leave art for toys. The child "makes" a train either of a few blocks or with pencil on paper. Surrounded as we are by posters and newspapers carrying illustrations of commodities or events we find it difficult to rid ourselves of the prejudice that all images should be "read" as referring to some imaginary or actual reality. Only the historian knows how hard it is to look at Pygmalion's work without comparing it with nature. But recently have we been made aware how thoroughly we misunderstand primitive or Egyptian art whenever we make the assumption that the artist "distorts" his motif or that he even wants us to see in his work the record of any concrete experience.[5] In many cases these images "represent" in the sense of "substitution". The clay horse or servant buried in the tomb of the mighty takes the place of the living. The idol takes the place of the God. The question whether it represents the "external form" of the particular divinity or, for that matter, of a class of demons does not come in at all. The idol serves as the substitute of the God in worship and ritual—it is a man-made God in precisely the sense that the hobby horse is a man-made horse; to question it further means to court deception.[6]

There is another misunderstanding to be guarded against. We often try instinctively to save our idea of "representation" by shifting it to another plane. Where we cannot refer the image to a motif in the outer world we take it to be a portrayal of a motif in the artist's inner world. Much critical (and uncritical) writing on both primitive and modern art betrays this assumption. But to apply the naturalistic idea of portrayal to dreams and visions—let alone to unconscious images—begs a whole number of questions.[7] The hobby horse does not portray our idea of a horse. The fearsome monster or funny face we may doodle on our blotting pad is not projected out of our mind as paint is "ex-pressed" out of a paint-tube. Of course any image will be in some way symptomatic of its maker, but to think of it as of a photograph of a pre-existing reality is to misunderstand the whole process of image-making.

IV.

Can our substitute take us further? Perhaps, if we consider how it could become a substitute. The "first" hobby horse (to use 18th century language) was probably no image at all. Just a stick which qualified as a horse because one could ride on it. (Fig. 1). The *tertium comparationis*, the common factor, was function rather than form. Or, more precisely, that formal aspect which fulfilled the minimum requirement for the performance of the function—for any "rideable" object could serve as a horse. If that is true we may be enabled to cross a boundary which is usually regarded as closed and sealed. For in this sense "substitutes" reach deep into biological layers that are common to man and animal. The cat runs after the ball as if it were a mouse. The baby sucks its thumb as if it were the breast. In a sense the ball "represents" a mouse to the cat, the thumb a breast to the baby. But here too "representation" does not depend on formal, that is geometrical, qualities beyond the minimum requirements of function. The ball has nothing in common with the mouse except that it is chasable. The thumb nothing with the breast except that it is suckable. As "substitutes" they fulfil certain demands of the organism. They are keys which happen to fit into biological or psychological locks, or counterfeit coins which make the machine work when dropped into the slot. In the language of the nursery the psychological function of "representation" is still recognised. The child will reject a perfectly naturalistic doll in favour of some monstrously "abstract" dummy which is "cuddly". It may even dispose of the element of "form" altogether and take to a blanket or an eiderdown as its favourite "comforter"—a substitute on which to bestow its love. Later in life, as the psycho-analysts tell us, it may bestow this same love on a worthy or unworthy living substitute. A teacher may "take the place" of the mother, a dictator or even an enemy may come to "represent" the father. Once more the common denominator between the symbol and the thing symbolised is not the "external form" but the function; the mother symbol should be loveable, the father-imago fearable, or whatever the case may be.

Now this psychological concept of symbolisation seems to lead enormously far away from the more precise meaning which the word "representation" has acquired in the figurative arts. Can there be any gain in throwing all these meanings together? Possibly there is. For anything seems worth trying to get the function of symbolisation out of its isolation. The "origin of art" has ceased to be a popular topic. But the origin of the hobby horse may be a permitted subject for speculation. Let us assume that the owner of the stick on which he proudly rode through the land decided in a playful or magic mood—and who could always distinguish between the two?—to fix "real" reins and that finally he was even tempted to "give" it two eyes near the top end. Some grass could have passed for a mane. Thus our arch-artist "had a horse". He had made one. Now there are two things about this fictitious event which have some bearing on the idea of the figurative arts. One is that, contrary to what is sometimes said, communication need not come into this process at all. He may not have wanted to show his horse to anyone. It just served as a focus for his fantasies as he galloped along—though more likely than not it fulfilled this same function to a tribe to which it "represented" some horse-demon of fertility and power.[8] We may sum up the moral of this "Just So Story" by saying that substitution may precede portrayal, and creation communication. It remains to be seen how such a general theory can be tested. If it can, it may really throw light on some concrete questions. Even the origin of language, that notorious problem of speculative history,[9] might be investigated from this angle. For what if the "pow-wow" theory, which sees the root of language in imitation, and the "pooh-pooh" theory which sees it in emotive interjection, were to be joined by yet another? We might term it the "niam-niam" theory postulating the primitive hunter lying awake in hungry winter nights and making the sound of eating, not for communication but as a substitute for eating—being joined, perhaps, by a ritualistic chorus trying to conjure up the phantasm of food.

V.

There is one sphere in which the investigation of "representational" functions of forms has made considerable progress of late, that of animal psychology. Pliny, and innumerable writers after him, have regarded it as the greatest triumph of naturalistic art for a painter to have deceived sparrows or horses. The implication of these anecdotes is that a human beholder easily recognises a bunch of grapes in a painting because for him recognition is an intellectual act. But for the birds to fly at the painting is a sign of a complete "objective" illusion. It is a plausible idea, but a wrong one. The merest outline of a cow seems sufficient for a Tsetse trap, for somehow it sets the apparatus of attraction in motion and "deceives" the fly. To the fly, we might say, the crude trap has the "significant" form—biologically significant, that is. It appears that visual stimuli of this kind play an important part in the animal world. By varying the shapes of "dummies" to which animals were seen to respond, the "minimum image" that still sufficed to release a specific reaction has been ascertained.[10] Thus little birds will open their beak when they see the feeding parent approaching the nest but they will also do so when they are shown two darkish roundels of different size "representing" the silhouette of the head and body of the bird in its most "generalised" form. Certain young fishes can even be deceived by two simple dots arranged horizontally, which they take to be the eyes of the mother fish in whose mouth they are accustomed to shelter against danger. The fame of Zeuxis will have to rest on other achievements than his deception of birds.

An "image" in this biological sense, then, is not an imitation of an object's external form but an imitation of certain privileged or relevant aspects. It is here that a wide field of investigation would seem to open. For man is not exempt from this type of reaction.[11] The artist who goes out to represent the visible form is not simply faced with a neutral medley of forms he seeks to "imitate". Ours is a structured universe whose main lines of force are still bent and fashioned by our biological and psychological needs, however much they may be overlaid by cultural influences.

We know that there are certain privileged motifs in our world to which we respond almost too easily. The human face may be outstanding among them. Whether by instinct or by very early training, we certainly are ever disposed to single out the expressive features of a face from the chaos of sensations that surrounds it and to respond to its slightest variations with fear or joy. Our whole perceptive apparatus is somehow hypersensitised in this direction of physiognomic vision[12] and the merest hint suffices for us to create an expressive physiognomy that "looks" at us with surprising intensity. In a heightened state of emotion, in the dark, or in a feverish spell the looseness of this trigger may assume pathological forms. We may see faces in the pattern of a wallpaper, and three apples arranged on a plate may stare at us like two eyes and a clownish nose. What wonder that it is so easy to "make" a face with two dots and a stroke even though their geometrical constellation may be greatly at variance with the "external form" of a real head? The well-known graphic joke of the "reversible face" might well be taken as a model for experiments which could still be made in this direction (Fig. 2). It shows to what extent the group of shapes that can be read as a physiognomy has priority over all other readings. It turns the side which is the right way up into a convincing face and disintegrates the one that is upside down into a mere jumble of forms which is accepted as a strange headgear.[13] In good pictures of this kind it needs a real effort to see both faces at the same time. Our automatic response is stronger than our intellectual awareness.

Seen in the light of the biological examples discussed above there is nothing surprising in this observation. We may venture the guess that this type of automatic recognition is dependent on the two factors of resemblance and biological relevance and that the two may stand in some kind of inverse ratio. The greater the biological relevance an object has to us the more will we be attuned to its recognition—and the more tolerant will therefore be our standards of formal correspondence. In an erotically charged atmosphere the merest hint of formal similarity with sexual functions creates the desired response and the same is true of the dream symbols investigated by Freud. The hungry man will be similarly attuned to the discovery of food—he will scan the world for sensations likely to satisfy his urge. The starving may even project food into all sorts of dissimilar objects—as Chaplin does in "Goldrush" when his huge companion suddenly appears to him as a chicken. Can it have been some such experience which stimulated our "niam-niam" chanting hunters to see their longed-for prey in the patches and irregular shapes on the dark cave walls? Could they perhaps gradually have sought this experience in the deep mysterious recesses of the rocks, much as Leonardo sought out crumbling walls to aid his visual fantasies? Could they finally have been prompted to fill in such "readable" outlines with coloured earth—to have at least something "spearable" at hand which might "represent" the eatable in some magic fashion? There is no way of testing such a theory, but if it is true that cave artists often "exploited" the natural formations of the rocks,[14] this, together with the "eidetic" character of their works,[15] would at least not contradict our fantasy. The great naturalism of cave paintings may after all be a very late flower. It may correspond to our late, derivative, and naturalistic hobby horse.

VI.

It needed two conditions, then, to turn a stick into our hobby horse: first, that its form made it just possible to ride on it; secondly—and perhaps decisively—that riding mattered. Fortunately it still needs no great effort of the imagination to understand how the horse could become such a focus of desires and aspirations, for our language still carries the metaphors moulded by a feudal past when to be chival-rous was to be horsy. The same stick that had to represent a horse in such a setting would have become the substitute of something else in another. It might have become a sword, sceptre, or—in the context of ancestor worship—a fetish representing a dead chieftain. Seen from the point of view of "abstraction", such a convergence of meanings onto one shape offers considerable difficulties, but from that of psychological "projection" of meanings it becomes more easily intelligible. After all a whole diagnostic technique has been built up on the assumption that the meanings read into identical forms by different people tell us more about the readers than about the forms. In the sphere of art it has been shown that the same triangular shape which is the favourite pattern of many adjoining American Indian tribes is given different meanings reflecting the main pre-occupations of the peoples concerned.[16] To the student of styles this discovery that one basic form can be made to represent a variety of objects may still become significant. For while the idea of realistic pictures being deliberately "stylised" seems hard to swallow, the opposite idea of a limited vocabulary of simple shapes being used for the building and making of different representations would fit much better into what we know of primitive art.

VII.

Once we get used to the idea of "representation" as a two-way affair rooted in psychological dispositions we may be able to refine a tool which has proved quite indispensable to the historian of art and which is nevertheless rather unsatisfactory: the notion of the "conceptual image". By this we mean the mode of representation which is more or less common to children's drawings and to various forms of primitive and primitivist art. The remoteness of this type of imagery from any visual experience has often been described.[17] The explanation of this fact which is most usually advanced is that the child (and the primitive) do not draw what they "see" but what they "know". According to this idea the typical children's drawing of a mannikin is really a graphic enumeration of those human features the child remembered.[18] It represents the content of the childish "concept" of man. But to speak of "knowledge" or "intellectual realism" (as the French do)[19] brings us dangerously near to the fallacy of "abstraction". So back to our hobby horse. Is it quite correct to say that it consists of features which make up the "concept" of a horse or that it reflects the memory image of horses seen? No—because this formulation omits one factor: the stick. If we keep in mind that representation is originally the creation of substitutes out of given material we may reach safer ground. The greater the wish to ride, the fewer may be the features that will do for a horse. But at a certain stage it must have eyes—for how else could it see? At the most primitive layer, then, the conceptual image might be identified with what we have called the minimum image—that minimum, that is, which will make it fit into a psychological lock. The form of the key depends on the material out of which it is fashioned, and on the lock. It would be a dangerous mistake, however, to equate the "conceptual image" as we find it used in the historical styles with this psychologically grounded minimum image. On the contrary. One has the impression that the presence of these schemata is always felt but that they are as much avoided as exploited.[20] We must reckon with the possibility of a "style" being a set of conventions born out of complex tensions. The man-made image must be complete. The servant for the grave must have two hands and two feet. But he must not become a double under the artist's hands. Image-making is beset with dangers. One false stroke and the rigid mask of the face may assume an evil leer. Strict adherence to conventions alone can guard against such dangers. And thus primitive art seems often to keep on that narrow ledge that lies between the lifeless and the uncanny. If the hobby horse became too lifelike it might gallop away on its own.[21]

VIII.

The contrast between primitive art and "naturalistic" or "illusionist" art can easily be overdrawn.[22] All art is "image-making" and all image making is rooted in the creation of substitutes. Even the artist of an "illusionist" persuasion must make the man-made, the "conceptual" image of convention his starting point. Strange as it may seem he cannot simply "imitate an object's external form" without having first learned how to construct such a form. If it were otherwise there would be no need for the innumerable books on "how to draw the human figure" or "how to draw ships". Wölfflin once remarked that all pictures owe more to other pictures than they do to nature.[23] It is a point which is familiar to the student of pictorial traditions but which is still insufficiently understood in its psychological implications. Perhaps the reason is that contrary to the hopeful belief of many artists the "innocent eye" which should see the world afresh would not see it at all. It would smart under the painful impact of a chaotic medley of forms and colours.[24] In this sense the conventional vocabulary of basic forms is still indispensable to the artist as a starting point, as a focus of organisation.

How, then, should we interpret that great divide which runs through the history of art and sets off the few islands of illusionist styles, of Greece, of China, and of the Renaissance, from the vast ocean of "conceptual" art?

One difference, undoubtedly, lies in a change of function. In a way the change is implicit in the emergence of the idea of the image as a "representation" in our modern sense of the word. As soon as it is generally understood that an image need not exist in its own right, that it refers to something outside itself and is therefore the record of a visual experience rather than the creation of a substitute, the basic rules of primitive art can be transgressed with impunity. No longer is there any need for that completeness of essentials which belongs to the conceptual style, no longer is there the fear of the casual which dominates the archaic conception of art. The picture of a man on a Greek vase no longer needs a hand or a foot in full view (Figs. 3 and 4). We know it is meant as a shadow, a mere record of what the artist saw and we are quite ready to join in the game and to supplement in our imagination what the real motif undoubtedly possessed. Once this idea of the picture as a sign referring to something outside itself is accepted in all its implications—and this certainly did not happen overnight—we are indeed forced to let our imagination play around it. We endow it with "space" around the figure, which is only another way of saying that we understand that the reality to which it referred was three-dimensional, that the man could move and that even the aspect momentarily hidden "was there".[25] When mediaeval art broke away from that narrative conceptual symbolism into which the formulae of classical art had been frozen, Giotto made particular use of the figure seen from behind which stimulates our "tactile" imagination by forcing us to imagine it in the round. (Fig. 5).

Thus the idea of the picture as a representation of a reality outside itself leads to an interesting paradox. On the one hand it compels us to refer every figure and every object shown to that imaginary reality which is "meant". This mental operation can only be completed if the picture allows us to infer not only the "external form" of every object represented but also its relative size and position. It leads thus to that "rationalisation of space" we call scientific perspective by which the picture plane becomes a window pane through which we look into the imaginary world the artist creates there for us. In theory, at least, painting becomes synonymous with geometrical projection.[26]

The paradox of the situation is that once the whole picture is conceived as the representation of a slice of reality a new context is created in which the conceptual image plays a different part. For the first consequence of the "window" idea is that we cannot conceive of any spot on the panel which is not "significant", which does not represent something. The empty patch thus comes easily to signify light, air, and atmosphere, and the vague form is interpreted as enveloped by air. It is this confidence in the representational context which is given by the very convention of the frame which makes the development of impressionist methods possible. The artists who tried to rid themselves of their conceptual knowledge, who conscientiously became beholders of their own work and never ceased matching their created images against their impressions by stepping back and comparing the two—these artists could only achieve their aim by shifting something of the load of creation on to the beholder. For what else does it mean if we are enjoined to step back in turn and watch the coloured patches of an impressionist landscape "spring to life"? It means that the painter relies on our readiness to take hints, to read contexts, and to call up our conceptual image under his guidance. The blob in the painting by Manet which stands for a horse is no more an imitation of its external form than is our hobby horse. (Fig. 6). But he has so cleverly contrived it that it evokes the image in us—provided, of course, we collaborate.

Here there may be another field for independent investigation. For those "privileged" objects which play their part in the earliest layers of image-making recur—as was to be expected—in that of image reading. The more vital the feature that is indicated by the context and yet omitted, the more intense seems to be the process that is started off. On its lowest level this method of "suggestive veiling" is familiar to erotic art. Not, of course, to its Pygmalion phase, but to its illusionist applications. What is here a crude exploitation of an obvious biological stimulus may have its parallel, for instance, in the representation of the human face. Leonardo achieved his greatest triumphs of life-like expression by blurring precisely the features in which expression resides, thus compelling us to complete the act of creation. Rembrandt could dare to leave the eyes of his most moving portraits in the shade because we are thus stimulated to supplement them.[27] (Fig. 7). The "evocative" image, like its "conceptual" counterpart, should be studied against a wider psychological background.

IX.

My hobby horse is not art. At best it can claim the attention of Iconology, that emerging branch of study which is to art criticism what linguistics is to the criticism of literature. But has not modern art experimented with the primitive image, with the "creation" of forms, and the exploitation of deep-rooted psychological forces? It has. But whatever the nostalgic wish of their makers the meaning of these forms can never be the same as that of their primitive models. For that strange precinct we call "art" is like a hall of mirrors or a whispering gallery. Each form conjures up a thousand memories and after-images. No sooner is an image presented as art than, by this very act, a new frame of reference is created which it cannot escape. It becomes part of an institution as surely as does the toy in the nursery. If—as might be conceivable—a Picasso would turn from pottery to hobby horses and send the products of this whim to an exhibition we might read them as demonstrations, as satirical symbols, as a declaration of faith in humble things or as self-irony—but one thing would be denied even to the greatest of contemporary artists: he could not make the hobby horse mean to us what it meant to its first creator. This way is barred by the angel with a flaming sword.

Footnotes: *explanatory notes*

1. In the sphere of art this process of differentiation rather than abstraction is wittily described by Oliver Wendell Holmes in the essay "Cacoethes Scribendi" from *Over the Teacups*, London, 1890: "It's just my plan . . . for teaching drawing. . . A man at a certain distance appears as a dark spot—nothing more. Good. Anybody . . . can make a dot. . . Lesson No. 1. Make a dot; that is, draw your man, a mile off. . . . Now make him come a little nearer . . . The dot is an oblong figure now. Good. Let your scholar draw an oblong figure. It is as easy as to make a note of admiration. . . . So by degrees the man who serves as a model approaches. A bright pupil will learn to get the outline of a human figure in ten lessons, the model coming five hundred feet nearer every time . . ."

2. *Fourth Discourse* (Everyman Edition, p. 55). I have discussed the historical setting of this idea in "Icones Symbolicae", *Journal of the Warburg and Courtauld Institutes*, XI. 1948, p. 187 and some of its more technical aspects in a review of Charles Morris, *Signs, Language and Behavior* (New York, 1946) in *The Art Bulletin*, March 1949. In Morris's terminology these present meditations are concerned with the status and origin of the 'iconic sign'.

3. Leonardo da Vinci, *Paragone*, edited by I. A. Richter, London, 1949, p. 51.

4. Paul Klee, *On Modern Art*, London, 1948. For the history of the idea of *deus artifex* cf. E. Kris and O. Kurz, *Die Legende vom Künstler*, Vienna, 1934.

5. H. A. Groenewegen-Frankfort, *Arrest and Movement, An Essay on Space and Time in the Representational Art of the Ancient Near East*. London, 1951.

6. Perhaps it is only in a setting of realistic art that the problem I have discussed in *Icones Symbolicae, loc. cit.*, becomes urgent: Only then the idea can gain ground that the allegorical image of, say, Justice, must be a portrait of Justice as she dwells in heaven.

7. For the history of this misinterpretation and its consequences cf. my article on "Art and Imagery in the Romantic Period", *The Burlington Magazine*, June, 1949.

8. This, at least, would be the opinion of Lewis Spence, *Myth and Ritual in Dance, Game, and Rhyme*, London, 1947. And also of Ben Jonson's Busy, the Puritan: "Thy Hobby-horse is an Idoll, a feirce and rancke Idoll: And thou, the *Nabuchadnezzar* . . of the *Faire*, that set'st it up, for children to fall downe to, and worship." (Batholomew Fair, Act. III. Scene VI).

9. cf. Géza Révész, *Ursprung und Vorgeschichte der Sprache*, Berne, 1946.

10. cf. Konrad Lorenz, "Die angeborenen Formen möglicher Erfahrung", *Zeitschrift für Tierpsychologie* V. 1943 and the discussion of these experiments in E. Grassi and Th. von Uexküll, *Vom Ursprung und von den Grenzen der Geisteswissenschaften und Naturwissenschaften*, Bern, 1950.

11. K. Lorenz, *loc. cit.* The citation of this article does not imply support of the author's moral conclusions. On these more general issues see K. R. Popper, *The Open Society and its Enemies*, esp. I. pp 59 ff and p. 268.

12. F. Sander, "Experimentelle Ergebnisse der Gestaltpsychologie", *Berichte über den 10. Kongress für Experimentelle Psychologie*, Jena, 1928, p. 47, has shown that the distance of two dots is much harder to estimate in its variations when these dots are isolated then when they are made to represent eyes in a schematic face and thus attain physiognomic significance.

13. For a large collection of such faces cf. Laurence Whistler, *Oho! The Drawings of Rex Whistler*, London, 1946. Our seventeenth century example is reproduced from F. Malaguzzi-Valeri, *Arte Gaia*, Bologna, 1928, p. 29.

14. G. H. Luquet, *The Art and Religion of Fossil Man*, London, 1930, pp. 141 f.

15. G. A. S. Snijder, *Kretische Kunst*, Berlin, 1936, pp. 68 f.

16. Franz Boas, *Primitive Art*, Oslo, 1927, pp. 118-128.

17. e.g. E. Löwy, *The Rendering of Nature in Early Greek Art*, London, 1907, H. Schaefer, *Von aegyptischer Kunst*, Leipzig, 1930, M. Verworn, *Ideoplastische Kunst*, Jena 1914.

18. Karl Buehler, *The Mental Development of the Child*, London, 1930, p. 113-117, where the connection with the linguistic faculty is stressed. A criticism of this idea was advanced by R. Arnheim, "Perceptual Abstraction and Art", *Psychological Review*, 54, 1947.

19. G. H. Luquet, *L'Art Primitif*, Paris, 1930.

20. The idea of avoidance (of sexual symbols) is stressed by A. Ehrenzweig, "Unconscious Form-Creation in Art", *The British Journal of Medical Psychology*, XXI. 1948 and XXII, 1949.

21. E. Kris and O. Kurz, *loc. cit.*, have collected a number of legends reflecting this age-old fear: Thus a famous Chinese master was said never to have put the light into the eyes of his painted dragons lest they would fly away.

22. It was the intellectual fashion in German art history to work with contrasting pairs of concepts such as haptic-optic (Riegl), paratactic-hypotactic (Coellen), abstraction-empathy (Worringer), idealism-naturalism (Dvorak), physioplastic-ideoplastic (Verworn), Multiplicity-Unity (Wölfflin), all of which could probably be expressed in terms of "conceptual" and "less conceptual" art. While the heuristic value of this method of antithesis is not in doubt it often tends to introduce a false dichotomy. In my book *The Story of Art*, London, 1950, I have attempted to stress the continuity of tradition and the persistent rôle of the conceptual image (cf. index *S.V.* "Egyptian Methods").

23. H. Wölfflin, *Principles of Art History*, New York, 1932.

24. cf. the Reith Lecture by J. Z. Young, *Doubt and Certainty in Science*, reprinted in *The Listener*, 23rd November 1950. The fallacy of a passive idea of perception is also discussed in detail by E. Brunswik, *Wahrnehmung und Gegenstandswelt*, Vienna, 1934. In its application to art the writings of K. Fiedler contain many valuable hints, cf. also A. Ehrenzweig, *loc., cit.* for an extreme and challenging presentation of this problem.

25. This may be meant in the rather engimatic passage on the painter Parrhasios in Pliny's *Natural History*, XXXV. 67, where it is said that "the highest subtlety attainable in painting is to find an outline . . . which should appear to fold back and to enclose the object so as to give assurance of the parts behind, thus clearly suggesting even what it conceals".

26. cf. E. Panofsky, "The Codex Huygens and Leonardo da Vinci's Art Theory", *Studies of the Warburg Institute*, vol. 13, London, 1940, pp. 90 f.

27. cf. J. v. Schlosser, "Gespräch von der Bildniskunst", *Präludien*, Vienna, 1927. where, incidentally, the hobby horse also makes its appearance.

FIG. 1 *The Hobby Horse:* Engraving by Israel van Meckenem (about 1500)

FIG. 2 *Reversible Face:* Drawing by G. M. Mitelli (1634–1718)

FIG. 3 *Portrait of Hesire:* Egyptian Relief (about 2700 B.C.)

FIG. 4 *An Athlete:* Greek Vase Painting (5th Century B.C.)

FIG. 7. *Portrait of a Man:* Painting by Rembrandt (1666)

FIG. 5 *The Annunciation to the Shepherds:* Detail of a Fresco by Giotto (about 1306)

FIG. 6 *The Races at Longchamp:* Painting by Manet (about 1872)

Chronological Survey on Form

by Lancelot Law Whyte

The following survey covers some of the more important stages in the development of (*a*) different conceptions of "form", and (*b*) knowledge of natural and cultural forms, in the West. The dates are approximate, and frequently indicate the mid-point of an individual's life. English usages are taken from the Oxford English Dictionary.

The word *form* has some twenty distinguishable meanings, but these mainly derive from the Latin *forma*, and hence from the Greek εἶδος (idea, intelligible structure, species) and μορφη (sensible shape).

Contrasted usages are brought together in order to indicate the changing emphasis of the Western intellect in its effort to come to grips with "form" in all its manifestations. Eastern ideas are excluded, because their different setting prevents summarisation. Caution is necessary in using this survey as all ideas have earlier roots.

B.C. 25000	Estimated date of earliest known cave drawings.
Before 4000	The regular motions of the sun, moon, and stars, and the changing shape of the moon give rise to the idea of a Supreme Power of the calendar controlling all existence.
About 3000	The Mesopotamians build monumental temples, and the Egyptians use the principle of mathematical form in a decimal system. Hieroglyphic scripts.
2800	Egyptian step pyramids.

2000 Mesopotamian and Egyptian mensuration and calculations on simple geometrical solids.

582 THALES founds abstract geometry.

580 ANAXIMANDROS constructs a map of the known world and speculates on organic evolution. A Babylonian document predicts relative positions of sun, moon, and planets.

550 The school of PYTHAGORAS studies number, geometry, and music. Numbers are the essence of things. The conception of form as the characteristic principle of a thing begins to appear, correlative to the conception of matter. The limit gives form to the unlimited. The five regular solids are probably known.

415 DEMOCRITUS speculates on atoms, treating form as a secondary consequence of atomic arrangements, and the variety of forms as due to different arrangements of the same atoms.

385 PLATO regards ideas as pure forms, and the world as forms in process of being realised. Analogy between natural and artistic production. In Plato's later years his conception of form may have evolved towards number. Discovers conic sections. Introduces definitions.

335 ARISTOTLE distinguishes form from matter, and recognises a formative principle by which the potentialities of stuff are realised. Everything strives towards form, which is the qualitative essence of things, though related to quantity. Formal causes. Organic form is the result of function. Studies the comparative morphology of political states.

320 EUCLID creates the first deductive theory of geometry and thus establishes the conception of formal reasoning. Light travels in straight lines.

250 ARCHIMEDES studies geometrical forms, such as spiral, sphere, cylinder, cone, etc.

225 APPOLONIOS develops the synthetic mathematics of form using geometrical, non-algebraic, methods, e.g. all conics as sections of one cone.

125 HIPPARCHUS proposes the use of geometry to describe the planetary motions.

A.D. 130 PTOLEMY develops trigonometry, astronomy, and geography, and studies refraction of light.

237 PLOTINUS considers that the ideas of pure intelligence, when embodied in material, suffer loss in value and significance.

280 PAPPUS consolidates Greek mathematics, gives the theory of seven simple machines, and considers bees to possess geometrical fore-thought.

400/700 Hindu arithmetic, algebra, trigonometry. Use of zero.

830 AL-KHWARIZMI, of Bagdad, surveys Hindu mathematics, and extends algebra, trigonometry, and astronomy.

1205 LEONARDO of Pisa surveys Hindu and Moslem mathematics, and carries them further.
Early Scholastics develop the conception of formal proof as the result of translation of Greek texts, mainly Aristotle and Euclid.

1214 GROSSETESTE defines form as that by which a thing is what it is. The Oxford School of logicians, from Grosseteste to OCCAM, seek to define the form of any selected phenomenon, i.e. the conditions which are necessary and sufficient to produce it.

1243 ALBERTUS MAGNUS discusses the hierarchy of organic forms, following Aristotle.

1250 THOMAS AQUINAS uses Aristotelian ideas and develops the Scholastic doctrine of form as the essential creative quality or determinant principle of a thing, and the root principle of activity. Eduction, the emergence of form from the potentiality of stuff. The world as a hierarchy of forms. Essential form is either bound up with matter, or exists immaterially in pure intelligence, the primary forms being in the mind of God. Hylo-morphism: the Scholastic theory of matter and form.

1254 ROGER BACON regards mathematics as the alphabet of philosophy. Form is latent in matter.

1300 *fourme*, or *form* used for the character, nature, or structure of a thing; for its visible aspect or shape; for its image, representation, or likeness; for the manner or procedure of doing anything; and soon after for model, type, pattern, or example. Also for beauty, comeliness, and in general the appearance of a living thing or person.

1304 THEODORIC of Freiberg and AL-FARASI of Persia independently give correct non-quantitative theory of the rainbow.

1411 BRUNELLESCHI discovers the mathematical laws of perspective.

1486 LEONARDO DA VINCI displays a comprehensive interest in all natural forms, in a manner which in the following centuries becomes differentiated and separated into the aesthetic, scientific, and practical activities of specialised individuals. Compares the forms of woman's hair and falling water, etc.

Form used for arrangement or order of parts in a whole, in literature and music. Also for logical arrangement, orderly arrangement, regularity.

1593 FRANCIS BACON defines form as the objective conditions on which a sensible body or quality depends for its existence and the knowledge of which enables it to be fully reproduced. The law and manner of arrangement and constitution. "The Form of a thing is its very essence." "The Form of Heat . . . , therefore, means no more than the Law of Heat". The latent process towards form.

1593 VESALIUS' anatomical drawings.

1600 KEPLER identifies the planetary ellipses, and studies the symmetry of honey-combs.

1603 GALILEO recognises that the form of many mechanical phenomena is independent of their size (dynamical similarity). Uses the telescope to see Saturn's rings.

1623 DESCARTES' idea of a universal mathematics. Under his influence the mathematical analysis of quantities begins to displace the earlier interest in spatial forms.

1640/70 *Formal* is used for the first time as meaning "*merely* a matter of form", e.g. a mere *formality* (1647), thus implying the Democritan-Cartesian view that the effective agencies or basic principles are not matters of form. From roughly this time form is regarded less as a primary active principle, as in Aristotelian thought, and more as the static, passive, and relatively trivial configuration of a number of parts, as in atomic theory.
But other usages continue: "The form by which a thing is what it is" (MILTON). "The plastik or formative tendency from matter apparently homogeneous and of a similar substance exciteth bones, membranes, veynes, and arteries". The figure of a crystal arises "from a seminal root and formative principle of its own". "The formative operator . . . will endeavour the formation of the whole" (THOMAS BROWNE). Also *form* as feminine style.

1664/75 The microscope is used by HOOKE, and by LEEUWENHOEK who sees spermatozoa.

1666 LEIBNIZ initiates the search for a universal formal system of reasoning.

1684 NEWTON's "Principia", etc. "The particles cohere in regular figures". " . . . it is not to be conceived that mere mechanical causes could give birth to so many regular motions", i.e. the planetary motions which are nearly planar and in the same direction. Newton recognised that the history of specific forms lay outside the scope of his natural philosophy.

1693 SHAFTESBURY develops the idea of inward form, or inner process by which form is realised.

1720/50 *Organism* and *organisation* come into use, connoting harmonious arrangement of parts.

1725 VICO in "Scienzia Nuova" emphasises the morphological approach to the study of cultures and history.

1750/90 BUFFON, ERASMUS DARWIN, LAMARK, and others arrange organic species in sequences in accordance with their morphology.

1764 KANT views space and time as *a priori* subjective forms. Form as the principle which holds together the several elements of a thing.

1750-1800 Mathematics becomes explicitly concerned with numerical and algebraic forms.

1771 Nebulae discovered.

1790 GOETHE studies form in many natural and human processes; uses the terms *Morphologie*, *Gestalt*, *Bildung* (development of form, but after Goethe mainly cultural self-development). "The formative process is the supreme process, indeed the only one, alike in nature and art". "If nature in her non-living foundation were not so basically stereometric, how could she finally attain the incalculable variety of life". Goethe, like Leonardo, displays the comprehensive interest in form which today is differentiated into specialised activities.

1794 WEDGWOOD produces first photograph, using camera.

1796 BLUMENBACH'S *Bildungstrieb* (*nisus formativus*), or general formative principle which develops, sustains, restores, and reproduces organic forms.

1800 HEGEL regards form as the active determining principle which becomes content in the course of the historical process.
(These conceptions of a formative process remain infertile for exact science, through their neglect of specific structural factors. The Teutonic romantic sense of "werden" (becoming) leads to impatience with the specific stabilised forms of the Latin peoples).

1800 CUVIER'S classical studies in comparative anatomy.

1807 YOUNG'S wave theory of light.

1811 MECKEL draws parallel between phylogenetic and ontogenetic development.

1815 SCHELLING recognises a single formative energy as the inner aspect of nature transcending mechanism and teleology.

1822 FOURIER's analysis of mathematical and spatial forms into harmonic wave components.

1830 HESSEL shows that crystals fall into 32 symmetry classes.

1842 VON BAER recognises that more general characters appear before more special ones in the course of embryonic development. PASTEUR discovers left and right-handed molecules.

1851 *form* used for the abstract aspect of the plastic arts and soon after for grammatical form, and for formal logic.

1852 HUXLEY recognises the importance of the temporal aspect of organic form: "The individual animal is the sum of the phenomena presented by a single life:—it is all those forms which proceed from a single egg taken together".

1859 DARWIN's "Origin of Species" gives the first systematic theory of the evolution of organic forms.

1873 FECHNER suggests that the widespread tendency towards regularity is related to the tendency towards stability. (FREUD, 1920, treats the Pleasure Principle as a special case of Fechner's principle.)

1874 DE MORGAN's "Formal Logic".

1877/8 *form* used for the plastic energy of the imagination; also for crystallographic form. *formative* now used less for an active property or principle, and more for the period of time in which formation occurs, e.g. the formative years of adolescence.

1890 VON EHRENFELS discusses Gestalt-qualities.

1890/94 FEDEROV, SCHONFLIES, and BARLOW independently establish the mathematical theory of the 230 crystal types, based on regular Cartesian arrays.

1893 ROUX studies the mechanics of animal development.

1893 CURIE examines symmetry in physics. "C'est la dissymétrie qui crée le phénomène".

The developments of the latest period are conveniently grouped into various trends:—

1893 *Psychology.* FREUD initiates the new systematic study of the morphology of personality, in sense of non-spatial structure.

1897 *Particle physics.* THOMSON confirms the discovery of the electron, and the atomic theory of matter is confirmed by countless subsequent experiments, including the direct observation of the tracks of fundamental particles. Here atomism tends to drive form into the background.

1899 *Mathematics.* HILBERT's "Foundation of Geometry", RUSSELL's "Principles of Mathematics" (1902), and RUSSELL and WHITEHEAD's "Principia Mathematica" (1911–13) heighten the nineteenth century interest in abstract mathematical and logical form, i.e. in the morphology of mathematical structures.

1907 *Speculative Philosophy.* BERGSON, in "Creative Evolution", suggests that the qualities of "duration" escape exact science.

1912 *Crystal structure.* LAUE proposes the use of X-rays to reveal the internal structure of crystals, and the BRAGGS open up this new field.

1912 *Gestalt theory of perception.* During the period from 1912 onwards (mainly 1920–35) the work of WERTHEIMER, KOEHLER, KOFFKA, and others emphasises the rôle of the Gestalt (configuration) in the processes of perception, etc.

1917 *Organic Form.* D'ARCY THOMPSON's "Growth and Form" calls attention to the mathematical study of the forms of organisms.

1917 *The Universe.* EINSTEIN proposes the first mathematical model of the physical universe, and initiates study of the grand morphology of the cosmos.

1918 *Sociology.* DURKHEIM, MALINOWSKI, and RADCLIFFE-BROWN in their anthropological studies and SPENGLER in "Decline of the West" develop the morphological approach to individual cultures and to history. BENEDICT's "Patterns of Culture" (1934).

1921 *Human Constitution.* KRETSCHMER's "Physique and Character", and later SHELDON's "Varieties of Human Physique" (1940) attempt to correlate physique and temperament i.e. the forms of body and of character.

1923 *Symbolic forms in human culture.* CASSIRER's "Philosophy of Symbolic Forms" and LANGER's "Philosophy in a New Key" (1942) examine the symbolising activity of the human mind in all aspects of culture, of which ritual, art, psychological symbols (FREUD, JUNG), language, and mathematical symbolism are special examples.

1925 *Patterns in fundamental physics.* SCHRÖDINGER's wave mechanics, following on DE BROGLIE's suggestions, emphasises the presence of regular patterns in atomic processes, though these later partly fade out in an abstract statistical theory.

1924 *Biological Organisation.* CHILD's "Physiological Foundations of Behaviour" exploits the "pattern" concept in describing the organisation of physiological processes and of animal behaviour.

This illustrates a tendency in biological theory (BERTALANFFY, WOODGER, etc.) to overcome the mechanism-vitalism conflict by studying the changing pattern or structural organisation of living systems. Recent experiments, (e.g. on the rapid exchange of individual atoms and chemical groups, which continually slip out of position and are continually replaced) suggest that the special properties of organisms, such as the stability of organic structure and form, are pattern rather than atomic properties.
From 1925 onwards it becomes clear that the characteristic forms and properties of adult organisms are partly the expression of the structural properties of individual minute units of protein (genes, enzymes, etc.) of characteristic pattern. Experiments on embryological development also demonstrate the importance of dominant organising tissues, organ forming substances (organisers), and enzymes probably derived from genes, all of which express pattern properties.

1928 *Brain Rhythms.* BERGER records the electrical rhythms due to patterns of synchronous nervous activity in the human brain, and thus opens up the study of brain activity patterns, a new field of incalculable importance.

1929 *New Aim of a Synthesis of Quantitative Physics.* EDDINGTON's speculations on the numerical constants of atomic and cosmological physics establish a new aim in basic physics: a comprehensive morphology of the realm of measured quantity, from the atomic nucleus to the cosmos, providing a rational synthesis of all physical constants.

1936 *Crisis in Particle Physics.* The discovery of "unstable elementary particles" (e.g. the meson), the steady accumulation of new types of "elementary particles" (1932–50), and the growing difficulties of nuclear theory, suggest that the classical concept of the elementary material particle is inappropriate, and an abstract statistics is used in its place, pending further clarification.

The above are recognised steps in the history of the exploration of form. During the last fifteen years other similar advances have doubtless been made, though not yet recognised. One example may be suggested:

1942 *Spherical Point Patterns.* FEJES initiates the study of the regular, and most nearly regular, arrangements of a small number of points on a sphere. This may be the first sign of greater attention to *spherical* arrangements (to complement the developed studies of *linear* or Cartesian forms), and to asymmetrical or nearly regular forms (as against the perfect symmetry of the Platonic solids, crystal arrangements, etc.).

19?? A space is left for the reader to fill in items which have been omitted, or further steps made in the coming years:

It is clear that there has been increasing awareness of the morphological character of many of the sciences, which are now seen to be concerned with *complex* structures or forms of particular kinds. It appears that the attention paid hitherto in exact science to increasing precision of analysis into smaller and smaller parts needs now to be supplemented by a method capable of representing the processes of complex systems composed of many parts. But there is no sign as yet of a simple and comprehensive method of describing the changing form or structure of a complex of relationships.

Selected Bibliography on Form *by Lancelot Law Whyte*

This somewhat arbitrary selection of books from an immense field may serve as an introduction to some of the more important aspects of form. The scope has here been extended beyond the visual forms of science and art, to cover mathematical, logical, and symbolic forms. Linguistic and musical form have been omitted. Popular works and specialist treatises will be found side by side, but a brief description is given of each book. The date of the most recent edition and city of publication are given.

A few books have been included which bear indirectly on the problem of form, or contain a few suggestive pages.

The 160 titles have been grouped very roughly under the following heads:

1. GENERAL
2. MATHEMATICS, LOGIC
3. PHYSICS, ASTRONOMY, ETC.
4. BIOLOGY
5. MAN, THE HUMAN FORM, GESTURE, ETC
6. THE HUMAN BRAIN, PSYCHOLOGY, GESTALT
7. SYMBOLIC FORMS
8. ART

1. *General*

CASSIRER, E. Idee und Gestalt. Berlin 1921.
Contains valuable essay on Goethe and mathematical physics, dealing with the problem of form.

COOK, T. The Curves of Life. London 1914.
Spirals in nature and art, based on manuscripts of Leonardo da Vinci.

DUHEM, P. Le Système du Monde. Paris 1913-17.
Histoire des doctrine cosmologiques de Platon a Copernic. 5 vols.
Comprehensive study of cosmological ideas, including those of Plato, Aristotle, Aquinas, etc. on form.

FRIEDMANN, H. Welt der Formen. Munich 1930.
Survey of form, from point of view of philosopher, scientist, and mathematician.

GOETHE, J. W.
All Goethe's writings are permeated with a sense of form, e.g. his writings on geology, mineralogy, optics, colour, plants, and animals.

GHYKA, M. C. Le Nombre d'Or. Paris 1931.
Pythagorean rites and rhythms in Western civilisation.

JAEGER, F. M. Lectures on the Principle of Symmetry and its Application in all Natural Sciences. London 1920.
This classic work remains the best general survey of its subject in any language.

KUKELHAUS, H. Urzahl und Gebärde. Berlin 1934.
Mediaeval mysticism of number and form in crystals, symbols, human body, art, architecture, etc.

LEONARDO DA VINCI.
Drawings of natural forms, human anatomy, water, geometry, etc. Notebooks.

MOHOLY-NAGY, L. Vision in Motion. Chicago 1947.
Extensively illustrated, forms in movement, etc.

NICOLLE, J. La symetrie et ses applications. Paris 1950.
A fairly easy up-to-date survey of symmetry in physics and biology, less comprehensive than Jaeger.

RUYER, R. Esquisse d'une philosophie de la structure. Paris 1930.
Interesting attempt at a general philosophy of forms in space and time, both physical and mental.

STEINER, R. Goethes Naturwissenschaftliche Schriften. Dornach 1926.
A study of Goethe's scientific writings, emphasising his interest in "Gestaltung"; to be read with caution.

WATSON, D. L. Scientists are Human. London 1938.
Contains interesting ideas on Gestalt, similarity of forms, symbols, etc.

WIENER, N. Cybernetics. New York 1948.
Famous study of control and communication in the animal and the machine, with chapter on "Gestalt and Universals".

WEYL, H. Philosophy of Mathematics and Natural Science. Princeton 1949.
Masterly survey; translation of 1926 article, supplemented by new Appendices, including one on Morphe and Evolution.

WHYTE, L. L. The Next Development in Man. London 1944.
Chapter 2 outlines a philosophy of formative process.

WHYTE, L. L. The Unitary Principle in Physics and Biology. London 1949.
A scientific philosophy of formative process.

2 *Mathematics and Logic*

COURANT, R. and ROBBINS, H. What is Mathematics? Oxford 1941.
An elementary approach to the philosophy of mathematical form.

HILBERT, D. and COHN-VOSSEN, S. Anschauliche Geometrie. Berlin 1932.
Deals with curves, point-lattics, differential geometry, topology, etc.

KLEIN, C. F. Elementarmathematik vom höheren Standpunkte aus. Vol II: Geometrie. Berlin 1925.
The fundamental philosophy of geometry. Difficult.

LAUTMANN, A. Symétrie et dissymétrie en mathematique et en physique. Paris 1946.
Two essays by a young French mathematician killed by the Occupation Forces, 1944.

RADEMACHER, H. and TOEPLITZ, O. Von Zahlen und Figuren. Berlin 1933.
Interesting study of problems in geometry and number theory.

RUSSELL, B. Introduction to Mathematical Philosophy. London 1924.
Brilliant introduction to contemporary ideas of mathematical structure, order, etc.

SPEISER, A. Die Theorie der Gruppen von endlicher Ordnung. New York 1945.
This treatise on group theory contains useful pages on the history of symmetry, ornament, etc.

TARSKI, A. Introduction to Logic and the Methodology of the Deductive Sciences. Oxford 1942.
Brilliant elementary introduction to mathematical logic.

WHITEHEAD, A. N. Introduction to Mathematics. London 1948.
Masterly and simple.

3. *Physics, Astronomy, etc.*

ASTBURY, W. T. Fundamentals of Fibre Structure. Oxford 1933.
Molecular structure of fibres.

BAGNOLD, R. A. The Physics of Blown Sand and Desert. London 1941.
Forms of sand dunes, etc.

CAVE, C. J. P. Clouds and Weather Phenomena. Oxford 1943.
Attractive little book, with 42 illustrations.

CORNISH, V. Waves of the Sea and other Water Waves. London 1910.
Non-technical, 50 illustrations.

CORNISH, V. Waves of Sand and Snow, and the Eddies which make them. London 1914.
Non-technical, 80 illustrations

CORNISH, V. Ocean Waves and kindred Geophysical Phenomena. Cambridge 1934.
Waves in water, sand, and snow; illustrated, with notes by H. Jeffreys on the mathematical theory of waves.

COTTON, C. A. Geomorphology, and Introduction to the Study of Landforms. Christchurch, Auckland 1942.
Best up-to-date survey.

CURIE, P. Oeuvres. Paris 1908.
Includes classic papers on symmetry in physics.

GRODZINSKI, P. A Practical Theory of Mechanisms. Manchester 1947.
Classification of mechanisms in machines and instruments.

KÖHLER, W. Die physischen Gestalten in Ruhe und im stationären Zustand. Braunschweig 1920.
Important but inconclusive study of form in physical systems. Decreasing asymmetry. Tendency towards "Prägnanz".

NIGGLI, P. Grundlagen der Stereochemie. Basel 1945.
Basic work on the symmetry properties of finite point configurations, molecular structures, etc.

OLLIVIER, H. Physique générale. Paris 1921.
Vol. 1 contains an introduction to the theory of symmetry in physics.

PHILLIPS, F. C. Introduction to Crystallography. London 1946.
Good introduction to the mathematical theory of crystal structure.

RENAUD, P. Analogies entre les principes de Carnot, Mayer, et Curie. Paris 1937.
Attempt to extend Curie's work on symmetry, linking tendency and symmetry.

SMART, W. M. The Sun, the Stars, and the Universe. London 1928.
Introduction to astronomical forms.

TUTTON, A. E. H. Crystallography. London 1922.
General survey of properties of crystals.

WELLS, A. F. Structural Inorganic Chemistry. Oxford 1945.
Inorganic chemistry reviewed in terms of three-dimensional structural arrangements.

WORTHINGTON, A. M. A Study of Splashes. London 1908.
200 photographs of splashes.

4. *Biology*

ARBER, AGNES. The Natural Philosophy of Plant Form. Oxford 1950.
An important study of plant morphology, neglecting physiology.

BERTALANFFY, L. V. Das Biologische Weltbild. Vol. I. Bern 1949.
This first volume covers the place of life in nature and science, dealing extensively with the "ganzheit" of organic phenomena.

BERTALANFFY, L. V. Theoretische Biologie. Vol. I. Berlin 1932.
A comprehensive work on the problems of theoretical biology.

CALKINS, G. N. The Smallest Living Things. London 1935.
Bacteria, Protophyta, Protozoa, etc. as revealed by the microscope.

CHALLENGER, VOYAGE. Reports. 50 vols. London 1880–91.
Special volumes contain plates of marine organisms.

CHILD, C. M. Physiological Foundations of Behaviour. New York 1924.
Classic work on physiological and behavioural patterns. One of the earliest works to emphasise organic "pattern".

COLD SPRING HARBOUR. "Aspects of Growth". Symposia on Experimental Biology. Vol. II. Cold Spring Harbour U.S.A. 1934.

COTT, H. B. Adaptive Colouration in Animals. London 1940.
Classic study of mimicry, etc.

DALCQ, A. M. Form and Causality in Early Development. Camb. 1938.
Survey of experimental embryology and author's own work.

DALCQ, A. M. La pensée moderne devant le probleme de la forme. Hermann Paris No. 1068, 1949.
Forming part of "L'Unité formelle et physiologique du Vivant".
Interesting survey of some contemporary ideas on embryology.

DE BEER, G. R. Embryos and Ancestors. Oxford 1940.
Haeckel's theory of recapitulation replaced by a detailed analysis of the relations of ontogeny and phylogeny.

FRITSCH, F. E. AND SALISBURY, E. J. Plant Form and Function. London 1938.
General descriptive introduction.

GOEBEL, K. Organography of Plants. 2 vols. London 1900.
Trans. by I. B. Balfour.
Comprehensive treatise on the formation of organs in plants.

HENDERSON, L. J. The Order of Nature. Harvard 1917.
A profound study of mechanism and teleology.

HERRICK, C. J. Neurological Foundations of Animal Behaviour. New York 1924.
Companion volume to Child's "Physiological Foundations", from protozoa to man, emphasising integration of behaviour.

HUXLEY, J. S. Problems of Relative Growth. London 1932.
Basic work on quantitative aspects of the growth of animals.

LAPORTE, L. J. Panorame du micromonde. Paris 1940.
Photographs of small organisms.

LE GROS CLARK, W. E. and MEDAWAR, P. B. Essays on Growth and Form, presented to D'Arcy Wentworth Thompson. Oxford 1945.
Twelve essays on aspects of biological form by leading specialists, some developing Thompson's ideas.

LEWIS, F. T.
Dr. Lewis of Harvard has published important papers on the shapes of cells, e.g. Proc. Am. Acad. Arts and Sciences, Vol. 77, March 1949. Other references in D'Arcy Thompson.

NEEDHAM, J. Biochemistry and Morphogenesis. Cambridge 1950.
Most up-to-date survey in English of morphogenesis from chemical point of view. Extensive bibliography.

NEEDHAM, J. Order and Life. Cambridge 1936.
Important essay on the nature and deployment of biological order.

PARPART, A. K. Editor of "The Chemistry and Physiology of Growth". Princeton, 1949.
Valuable symposium of 10 essays.

PRZIBRAM, H. Die anorganischen Grenzgebiete der Biologie. Berlin 1926.
Study of physical properties bordering on those of organisms, e.g. crystal-organism analogy.

PRZIBRAM, H. Form und Formel im Tierreich. Leipzig 1922.
Interesting but rather rare.

RASCHEWSKY, N. Mathematical Biophysics. Chicago 1948.
Valuable attempt to provide physical description of biological properties.

RINNE, F. Grenzfragen des Lebens. Leipzig 1931.
Survey of the borderland between non-living and living, crystals and organisms.

ROYAL SOCIETY. A discussion on the Measurement of Growth and Form. Under leadership of S. Zuckerman, F.R.S. London 1950.
Thirteen contributions. The most up-to-date survey, sold as "off-print" by Royal Society.

RUSSELL, E. S. Form and Function, A Contribution to the History of Animal Morphology. London 1916.
A comprehensive historical study.

SCHRÖDINGER, E. What is Life? Cambridge 1945.
Brilliant popular essay presenting ideas, many of which have been published previously.

SIMPSON, G. G. Meaning of Evolution. New Haven 1949.
Excellent up-to-date survey for general reader.

SMUTS, J. C. Holism and Evolution. London 1926.
Famous statement of Smuts' philosophy of developing "wholes".

SOCIETY FOR THE STUDY OF DEVELOPMENT AND GROWTH. Quarterly Journal: Growth. U.S.A.
Supplements on Annual Conferences.

SOCIETY FOR EXPERIMENTAL BIOLOGY. Growth in relation to Differentiation and Morphogenesis (S.E.B. Symposium No. 2). Camb. 1948.
Nineteen contributions on various aspects of growth in plants and animals.

THOMPSON, D'ARCY, W. On Growth and Form. Cambridge 1942.
Unique work on mathematical description of organic forms. The further development of Thompson's ideas can be traced in "Essays on Growth and Form", 1945, see under Le Gros Clark; and in Royal Society Symposium, 1950.

WATSON-BAKER, W. World beneath the Microscope. London 1935.
80 superb micro-photographs of organisms.

WADDINGTON, C. H. How Animals Develop. London 1935.
Excellent short survey of development of form and pattern in animals.

WADDINGTON, C. H. Organisers and Genes. Cambridge 1940.
An attempt to combine contemporary ideas in embryology and genetics.

WEISS, P. Principles of Development. New York 1939.
A good exposition of the problems connected with the development of animals.

WILSON, E. B. The Cell in Development and Heredity. New York 1925.
Classic study of the morphology and processes of cells.

WOODGER, J. H. Biological Principles. London 1929.
Not explicitly concerned with form, but masterly on clear thinking about biological themes.

5. *Man, the Human Form, Gesture, etc.* (*see also* 6 *and* 7).

BÜHLER, K. Ausdruckstheorie. Jena 1933.
A survey of various theories of expression.

BATESON, G. and MEAD, M. Balinese Character. A photographic analysis. New York 1942.
Classic anthropological study based on many hundred photographs of family and social life in Bali.

CARUS, C. G. Symbolik der menschlichen Gestalt. Ein Handbuch zur Menschenkenntnis. Edited and extended by Th. Lessing. Celle 1925.
Philosophical essay on symbolism of the human figure by anatomist of mid-nineteenth century.

BARNETT, A. The Human Species. London 1950.
Biology of man, fully illustrated.

BENKARD, E. Das ewige Antlitz. Berlin 1927.
112 death masks.

BROPHY, J. Body and Soul. London 1948.
Non-scientific study of relations of the human figure and the human spirit; illustrated.

BROPHY, J. The Human Face. London 1945.
With 23 illustrations.

DE KLEEN, T. Mudras, the Ritual Hand Poses of the Buddha Priests and Shiva Priests of Bali. London 1924.
With 60 drawings of hand-gesture language.

GESELL, A. The Embryology of Behaviour. London 1945.
Human foetal and infant behaviour, illustrated.

HARRISON, R. J. The Child Unborn. London 1951.
Survey of development of human embryo, with 60 illustrations.

JACOBY, H. J. Analysis of Handwriting. London 1939.
Good introduction to graphology.

KRETSCHMER, E. Physique and Character. London 1936.
Classic study of relation of physical type to temperament.

MEADER, C. L. and MUYSKENS, J. H. The Structure and Processes of Expression, with General Introduction to Biolinguistics. (Part I, Section A of Handbook of Biolinguistics). Toledo, U.S.A. 1950.
The biological and physiological basis of the organs and processes of speech.

NANDIKESVARA. The Mirror of Gesture. Cambridge, U.S.A. 1917. Trans. by Coomaraswamy and Duggirala.
On the Indian gesture language of the dance drama. Illustrated.

SHELDON, W. H. The Varieties of Human Physique. New York 1940.
An introduction to constitutional psychology.

WOLFF, CHARLOTTE. The Human Hand. London 1944.
An interesting study, with a method of hand interpretation; illustrated.

WOLFF, CHARLOTTE. Psychology of Gesture. Methuen 1945.
A scientific study of gesture; illustrated.

WOLFF, W. The Expression of Personality. Experimental Depth Psychology. New York London 1943.
Expression of personality in bodily form and behaviour, gait, voice, handwriting, etc. Illustrated. Bibliography.

6. *The Brain, Psychology, Gestalt*

ADRIAN, E. D. Physical Background of Perception. Oxford 1947.
The action of the central nervous system in the processes of perception.

ADRIAN, E. D. The Basis of Sensation. The Action of the Senses. London 1928.
The nervous processes underlying sensation.

ELLIS, W. D. Source Book of Gestalt Psychology. London 1950.
Valuable summaries of 35 publications in Germany, 1915–39, on Gestalt psychology.

FULTON, J. F. Physiology of the Nervous System. Oxford 1949.
Introduction to the functional forms of the nervous system.

GUILLAUME, P. Psychologie de la forme. Paris 1937.
Valuable survey of Gestalt psychology.

HARTMANN. Gestalt Psychology. 1935.
Probably the most recent general work on Gestalt theory.

HEBB, D. O. The Organisation of Behaviour. London 1949. A Neuropsychological Theory.
Up-to-date study of perception, learning and motivation, including valuable critique of Gestalt ideas. Bibliography.

HILGARD, E. R. Theories of Learning. London 1948.
Surveys applications of Gestalt theory to learning, giving references.

HILL and PARR. Electro-encephalography. London 1950.
Specialist volume on the forms of electrical rhythms in the brain.

KATZ, D. Gestaltpsychologie. Basel 1944.
Survey of Gestalt psychology by leading figure in this school.

KATZ, D. The World of Colour. London 1935.
The psychology of colour perception.

KOEHLER, W. Gestalt Psychology. London 1930.
Authoritative survey, with bibliography. See also under Physics.

KÖHLER, W. The Place of Value in a World of Facts. London 1939.
Interesting speculations on Gestalt.

KOEHLER, W. Mentality of Apes. London 1927.
Classic work on studies made 1913-17.

KOEHLER, W. Dynamics in Psychology. London 1942.
Three essays, on "The Ways of Psychology", "The Field of a Percept", and "Retention and Recall".

KOFFKA, C. Principles of Gestalt Psychology. London 1935.
General survey.

LASHLEY, K. S. Brain Mechanisms and Intelligence. Chicago 1929.
A Quantitative Study of Injuries to the Brain.
Experiments on brain lesions leading towards a theory of the dynamic patterns involved in brain processes.

LASLETT, P. Editor of The Physical Basis of Mind (Broadcast Talks). Oxford 1950.
Suggestions about the forms of brain activity by leading specialists.

PETERMANN, B. The Gestalt Theory and the Problem of Configuration. London 1932.
A critical appraisal of Gestalt psychology, no longer up-to-date.

RICHTER, D. Perspectives in Neuropsychiatry. London 1950.
Essays presented to Prof. F. L. Golla, edited by D. Richter.
Up-to-date symposium containing several contributions on relation of the brain activity patterns to mind and behaviour.

WHEELER, R. H. The Laws of Human Nature. London 1931.
Speculative. Gestalt ideas applied to man.

7. *Symbolic Forms*

CASSIRIER, E. Philosophie der Symbolischen Formen (4 vols.). Berlin 1923-31.
Extensive survey of symbolic forms in general, with particular reference to speech, mythical thought, and cognition.

JOHNSON, M. Art and Scientific Thought. London 1944.
Historical studies in structure and symbolism.

JUNG, C. J. The Secret of the Golden Flower. London 1931.
A Chinese Book of Life (Lu Yen), translated from Chinese, with European Commententary by C. G. Jung.
Includes classic essay by Jung on the psychological interpretation of the Chinese text and of mandala (circular)symbols. Illustrated.

KLOPFER and KELLEY, D. MC.G. The Rorschach Technique. New York 1942.
Comprehensive survey of the Rorschach test for diagnosing personality from interpretation of ink blots.

LANGER, S. Philosophy in a New Key. A study in the Symbolism of Reason, Rite and Art. New York 1948. (Cheap edition).
Brilliant sketch of a philosophy of culture as expression of a symbolising activity of the mind. Theory of symbolic forms in ritual, art, language and science.

MORRIS, C. Signs, Language and Behaviour. New York 1946.
A general theory of signs in relation to behaviour.

PANOFKSY, E. Studies in Iconology, Humanistic Themes in the Art of the Renaissance. New York 1939.
Renaissance symbolism, and the problem of form and content in art.

SCHLESINGER, M. Geschichte des Symbols. Berlin 1912.
A study of cultural and psychological symbolism.

WHITEHEAD, A. N. Symbolism, Its Meaning and Effect. Cambridge 1928.
Short essay.

8. *Art*

Artists on Art. (Edited Goldwater and Treves). London 1947.
An anthology with scholarly bibliography.

BERENSON, B. Aesthetics and History. London 1950.
The aesthetic creed of a leading art expert.

BIEDERMANN, C. Art as the Evolution of Visual Knowledge. Minneapolis 1948.
Study in the language of form in art through the ages. Copiously illustrated.

BIRKHOFF, G. D. Aesthetic Measure. Harvard 1933.
Attempt by a mathematician to establish an algebraic measure of aesthetic value.

BLOSSFELDT. K. Urformen der Kunst. Berlin
120 *large photographs of plants.*

BOAS, F. Primitive Art. Oslo 1927.
A standard work by a leading ethnologist. Illustrated.

BRINKMANN, A. Plastik und Raum als Grundformen künstlerischer Gestaltung. Munich 1922.
An attempt to derive the types of artistic creation from abstract principles.

CANNON, N. I. Pattern and Design. London 1948.
An elementary introduction to the principles of design, with illustrations by children.

DURER, ALBERT. Les quatres livres d'Albert Durer de la proportion des partes et pourtraicts des corps humains. Arnheim 1613.

EVANS, J. Taste and Temperament. A brief study of psychological types in their relation to the visual arts. London 1939.
An attempt to open up a new field of enquiry.

FECHNER, G. TH. Vorschule der Aesthetik. Leipzig 1898.
Experimental investigation of human responses to simple forms.

FOCILLON, H. Vie des formes. Paris 1947.
The Life of Forms in Art. New York 1948.
Thoughts on aesthetic forms in space, in matter, in the mind, and in time by a leading French art historian.

GHYKA, M. C. The Geometry of Art and Life. New York 1946.
Proportion, the Golden Section, the Pythagorean tradition, and geometrical forms in art and life.

GHYKA, M. C. Esthetique des proportions dans le nature et dans les arts, etc. Paris 1927.
A study of the relations of mathematical and aesthetic form.

GIEDION, S. Space, Time and Architecture. Harvard 1944.
Survey of the history of architectural and aesthetic forms, with emphasis on recent styles. Illustrated.

HAMBIDGE, J. Practical Applications of Dynamic Symmetry. New Haven 1932.
Lectures on "Static and Dynamic Symmetry" in geometry, plants, decoration, art and architecture.

HILDEBRAND, A. Das Problem der Form in der bildenden Kunst. Strasburg 1913.
A sculptor seeks to derive aesthetic norms from the investigation of basic perceptual attitudes.

IVINS, W. M. Art and Geometry. A study in space intuitions. Cambridge, U.S.A. 1946.
Attempts to correlate the development of geometry and of space representation in art.

JONES, O. The Grammar of Ornament. London 1868.
Interesting survey of different types of ornament.

KLAGES, L. Vom Wesen des Rhythmus. Kampen auf Sylt 1934.
Contrasts the mathematical regularity of machine movements with rhythm of organisms.

LIPPS, T. Ueber einfachste Formen der Raumkunst, Munich 1909.
Psychological study of the aesthetic sense.

MEURER, M. Vergleichende Formenlehre des Ornaments und der Pflanze. Dresden 1909.
Plant forms in relation to development of architectural and art forms.

MÖSSEL, E. Die Proportion in Antike und Mittelalter (2 vols.) 1926–31.
Spatial forms as basis for aesthetic form.

MÜNTZ, L. Plastische Arbeiten Blinder. Brünn 1934.
With 100 illustrations of work of blind students; touch without sight.

PETRIE, FLINDERS. Decorative Patterns of the Ancient World. London 1930.
Authoritative collection of material. Extensive illustrations.

RIEGL, A. Stilfragen. Berlin 1923.
A study of continuity in the historical evolution of ornament.

WOELFFLIN, H. Kunstgeschichtliche Grundbegriffe. Das Problem der Stilentwicklung in der neueren Kunst. Munich 1943.
An attempt to classify artistic forms.

WORRINGER, W. Abstraktion und Einfühlung. Munich 1911.
Abstraction—geometry and empathy—representation treated as dual aspects of European art, in relation to cultural and psychological factors.

Supplement to the Bibliography

A sample of the many relevant works that have appeared in the period since 1951, or were not previously included (London publishers unless otherwise indicated).

Science

ASHBY, W. R. Design for a Brain (Chapman, 1952).

BEADLE, G. and M. The Language of Life (Gollancz, 1966 and Anchor, N.Y., 1967).

BERNAL, J. D. The Origins of Life (Weidenfeld, 1967).

BERTALANFFY, L. V. Problems of Life (Watts, 1952).

BONNER, J. T. Morphogenesis (Princeton, 1952).

(BUCKMINSTER FULLER, R.) The Dymaxion World of Buckminster Fuller, by R. W. Marks (Reinhold, N.Y., 1960).

CALVIN, M. (Ed.) The Scientific Endeavour (Rockefeller, N.Y., 1965).

FEININGER, A. Form in Nature and Art (Thames and Hudson, 1966).

GARDNER, M. The Ambidextrous Universe (Basic, N.Y., 1964).

HERRICK, C. J. The Evolution of Human Nature (Harper and Row, N.Y., 1956).

JONES R. G. (Ed.) Unity and Diversity in Systems (Braziller, N.Y., 1968).
KEPES, G. Structure in Art and in Science. Vol.I of Vision and Value Series (Braziller, N.Y., and Studio Vista, 1965).
LERNER, D. (Ed.) Parts and Wholes (Macmillan, N.Y., 1962).
LORENZ, K. King Solomon's Ring (Methuen, 1952).
NERVI, P. L. New Structures (Architectural Press, 1963).
PORTMAN, A. Animal Forms and Patterns (Faber, 1952).
SHAPIRO, A. H. Shape and Flow (Heinemann, 1964).
THOMPSON, D'ARCY W. On Growth and Form (Edition abridged by J. T. Bonner, Cambridge, 1961).
WATSON, J. D. Molecular Biology of the Gene (Benjamin, N.Y., 1965).
WEYL, H. Symmetry (Princeton, 1952).
WHYTE, L. L. Accent on Form (Routledge, 1955).
WHYTE, L. L. Internal Factors in Evolution (Tavistock, 1965).

The Arts

ALEXANDER, C. Notes on the Synthesis of Form (Harvard, 1964).
ARNHEIM, R. Art and Visual Perception (Faber, 1956).
BOAS, F. Primitive Art (Dover, N.Y. and Constable, 1955).
BOULEAU, C. The Painter's Secret Geometry (Thames & Hudson, 1963).
FEININGER, A. The Image of Woman (Thames & Hudson, 1961).
GOMBRICH, E. H. Norm and Form (Phaidon, 1966).
KEPES, G. The New Landscape in Art and Science (Theobald, Chicago, 1956). (see also under Science)
MACGILLAVRY, C. H. Symmetry Aspects of M. C. Esher's Periodic Drawings (Uitgeversmaatschappij, Utrecht, 1965).
PHILIPSON, M. (Ed.) Aesthetics Today (Meridian, N.Y., 1961).
PECKHAM, M. Man's Rage for Chaos (Chilton, N.Y., 1965).
READ, H. Origin of Forms in Art (Thames & Hudson, 1965).
WILKINSON, E. M. Goethe's Conception of Form (British Academy, Oxford, 1951).
WITTKOWER, R. Architectural Principles in the Age of Humanism (Tiranti, 1952).

Index

T

U

V

W

X

Y

[illegible]