THE GORDON WILSON LECTURE

REPRESENTATIONS AND THE CONSTRUCTION OF REALITY*

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INTRODUCTION

An ancient problem in the history of natural philosophy is how man comes to know the world around him. A dominant theme since the time of Democritus (1) is that events and physical structures in the world are imaged within our brains in continually updated and readily accessible forms, called representations. Central to this question is whether and if so to what degree representations are isomorphic reflections of the physical world. We now interpret John Locke's metaphor of the *tabula rasa* (2) as a way of saying that the microstructure of the brain is relatively unspecified at birth, and is modified and shaped during post-natal life by experience; i.e., by sensory stimuli and the primary afferent input they evoke. Thus, for Locke, individual brains might differ to a degree determined by differences in life experience. Contrarily, Leibniz (3) and his intellectual descendants maintained that our images are reconstructions, abstractions determined in large part by brain structures and mechanisms innate and unlearned, genetically determined, and to that degree individual and unique among persons, independently of life experience.

These differences between the ideas of the Scottish empiricists and the Continental rationalists persisted from the early 18th century almost to the present day. The weight of evidence shifted to and fro from time to time, perhaps more heavily towards the rationalists, particularly in what is known as the Kantian synthesis (4).

Studies of the last decades have yielded some tentative solutions for these problems. They suggest that to a certain extent both views are correct, for our central neural representations of the physical world are determined both by the microstructure of brain systems, and by the dynamic patterns of neuronal activity within them. The word "microstructure" designates in this context the spatial relations between the terminal branches of axons entering a small region (1 mm or less) of a

also from the effects of brain lesions and from the pattern of anatomical connections, etc.

5. Each was aimed, in the long run, at study of "higher functions": at levels of the nervous system at which we can expect to see abstracted and constructed images of the sensory world, and the operation of the processes of perception.

Further, I contend that when the sensory performances of man and monkey are identical some legitimacy attaches to the proposition that the relevant neural patterns observed in the monkey brain must occur also in the human brain working under identical behavioral conditions and with similar test performances.

THE SENSE OF FLUTTER-VIBRATION

Flutter-vibration is a dual mechanoreceptive sense, for the subjective experience differs with frequency. Low-frequency sinusoids (5-50 Hz) delivered to the glabrous skin of the hand evoke a fluttering sensation localized to the site of stimulation. Sinusoids of higher frequency (50-400 Hz) evoke the widely spreading and poorly localized hum we call vibration. Frequencies above 5-600 Hz are perceived as stationary. It is noteworthy that monkeys and humans possess virtually identical capacities to detect the presence of mechanical sinusoids (8, 9), as well as to discriminate between mechanical sinusoids of different frequencies, or of different amplitudes of the same frequency (10). The identity relations for detection are shown by the averaged psychometric functions at 30 Hz shown in Figure 1-A and by the averaged frequency-threshold functions of Figure 1-B. We therefore pursued studies of the neural events evoked in the peripheral nerve fibers and cortical somatic sensory areas of monkeys with some confidence that the neural events observed *at these levels* in the monkeys would resemble those evoked in the brains of humans, under identical stimulus and behavioral circumstances. We discovered that in the range of the frequency detection capacity of monkeys the stimulus frequency is encoded in a nearly perfectly periodic sequence of nerve impulses in the relevant sets of first order nerve fibers: in the Meissner afferents for the range of flutter (see Figure 2), and in the Pacinian afferents in the range of vibration (8, 10). The relation of the tuning points at different frequencies is shown for these two populations of first order fibers in Figure 3, where they blanket the monkey frequency-detection function. Thus the duality of the subjective experience depends in the first instance upon the duality of the peripheral signalling apparatus. Moreover, the amplitudes of the mechanical sinusoids required to evoke perfectly periodic entrainment in the first-order fibers matched nicely the human and monkey perceptual thresholds. Thus for this sensory mode the peripheral neural apparatus delivers to

brain structure, and the postsynaptic neurons upon which those axon branches impinge. These microstructural relations are determined by genetic and epigenetic factors thought to be selective and degenerate in nature; their connections are dynamic and can be modified by experience. They are determined by processes in principle like those that provide selective advantage in evolution (5, 6).

It is a major theme of my lecture that the central representations of objects and events in the external world can be studied directly in non-human primates. Evidence obtained in studies of this kind has led to one of the central dogmas of Neuroscience: that there are brain representations of material reality, that these representations are instantiated in patterns of activity within the brain, and that they lie at the very heart of the mechanisms of mind. The power and rapidity of cognitive operations are in all likelihood related to the structure of these representations.

My working hypothesis for laboratory research is that reconstructions of sensory events at the level of perceptual operations are achieved by successive and multiple central transformations. These representations are constructed at different levels of what are initially hierarchial and then widely distributed and re-entrant systems. The assumption is that we may infer their dynamic structure by studying sensory representations at different levels of central processing. This general problem of construction has been treated from the theoretical and philosophical points of view in a recent monograph (7).

DATA BASE AND METHODS OF STUDY

I shall now describe the results of three studies of neural representations. Two are taken from my own work, and the third from that of my colleagues in the Philip Bard Laboratories in Baltimore. The three are arranged in sequence to illustrate a transition from relatively isomorphic images of physical reality, to those that are clearly neural reconstructions.

The three experiments have some things in common:
1. In two, detailed studies were first made of the input to the nervous system in primary afferent fibers, input evoked by sensory stimuli.
2. All three include experiments made on the neocortex in waking monkeys as they executed behavioral tasks for rewards. Thus each dealt with the dynamic, time-dependent aspects of brain activity, recorded in behaving brains.
3. Recordings were made simultaneously of behavioral performance and of the activity of single neurons in areas of the neocortex known on other grounds to be essential for correct execution of the task behavior.
4. In each of the studies, correlations were sought between neural and behavioral events, not only on grounds of simultaneity, but
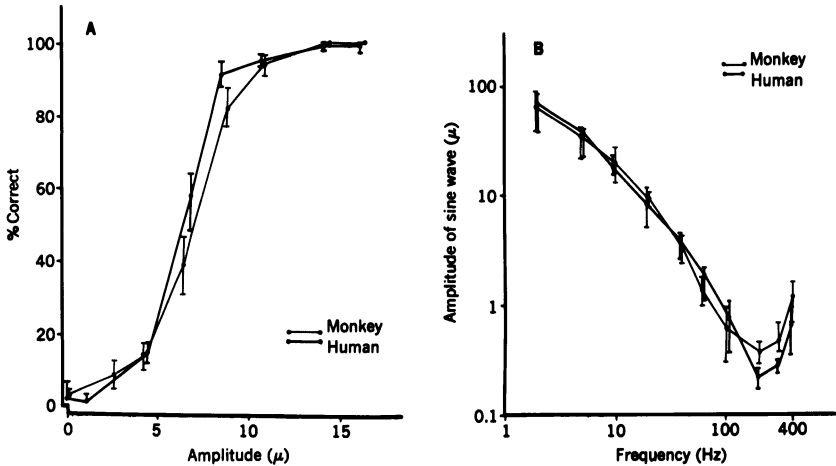
Fig. 1. A: Averaged psychometric functions for groups of human and monkey subjects required to detect a 40 Hz mechanical sinusoid delivered to the glabrous skin of a finger tip. B: Frequency-threshold functions for groups of human and monkey subjects who repeated the experiment of Figure 1-A at a number of different frequencies. Vertical lines = ± 2x SEM. From Mountcastle (11).
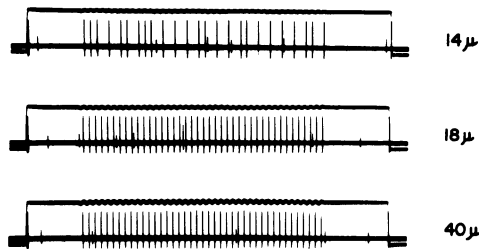

Fig. 2. Recordings of nerve impulses from a single Meissner afferent axon innervating the glabrous skin of the hand of a monkey, isolated by micro-dissection of the median nerve. For each set of records the upper trace is the electrical analogue signal of the position and movement of a 2 mm diameter probe tip; the lower trace is a recording of the electrical signs of impulses in the dissected axon. For each set the probe indents the skin for 550 μm; a 40 Hz sine wave is then superimposed upon the indentations, at peak-to-peak amplitudes of 14, 18 and 44 μm, for the records from above downward. The axon is entrained in a periodic pattern at 18 μm stimulus amplitude, the tuning point. A further increase in amplitude to 44 μm did not affect the pattern of discharge. Adapted from Talbot, et al (8).

the central nervous system a virtually isomorphic image of the temporal order of the frequency of the sensory stimulus.

It is now well known that the classes of large mechanoreceptive afferent fibers innervating the glabrous skin of the hand project over the dorsal column—medial lemniscal pathway to the somatic sensory cortex of the postcentral gyrus. They do so without cross-convergence between these
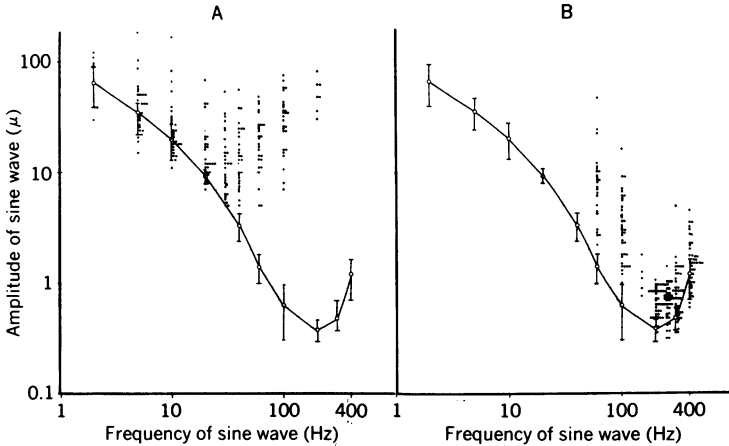
Fig. 3. The solid line is the frequency-detection function for monkeys of Figure 1-B. The filled circles on the graph to the left are the tuning points for a number of Meissner quickly adapting afferents innervating the glabrous skin of the hands of monkeys, studied at different frequencies. Those on the graph to the right are, similarly, tuning points for a number of Pacinian afferent fibers, studied at several frequencies. The full frequency-detection function can be accounted for only in terms of the sensitivities of both sets of fibers. Flutter-vibration is a dual sense, and the monkey thresholds coincide with the tuning thresholds of the most sensitive fibers in the two sets of mechanoreceptive afferents. Adapted from Mountcastle, et al (9).

"sub-modalities" of mechanoreceptive sensibility (for review, see ref 11). There are columns of neurons in the somatic sensory cortex activated exclusively by impulses in the Meissner peripheral afferent fibers— themselves essential for the low frequency end of the frequency detection function; i.e., for the sense of flutter. This fact allowed us to examine the form of the cortical "representation" of the frequency of a certain class of peripheral stimuli; i.e., of their dynamic, time-dependent properties. We were able to do this experiment in the monkey cerebral cortex; and, to do so as the animal executed detection tasks yielding psychometric functions like those of Figure 1-A. I leave aside all the technical details of how such experiments are carried out (see ref 12), and ask you to accept that one can record the electrical signs of the impulse discharges of single cortical neurons under these circumstances. Typical results and the forms of analysis used are shown in Figure 4. Here, for clarity, a 10 Hz stimulus of supra-threshold intensity was used. The salient feature of the cortical transformation is evident here, and is illustrated for another neuron by the impulse replicas of Figure 5 and the analyses of Figure 6. That is, that at no stimulus amplitude was the discharge of the cortical neurons entrained to near-perfect periodicity with the stimulus frequency, as is the case for the relevant set of peripheral nerve fibers.
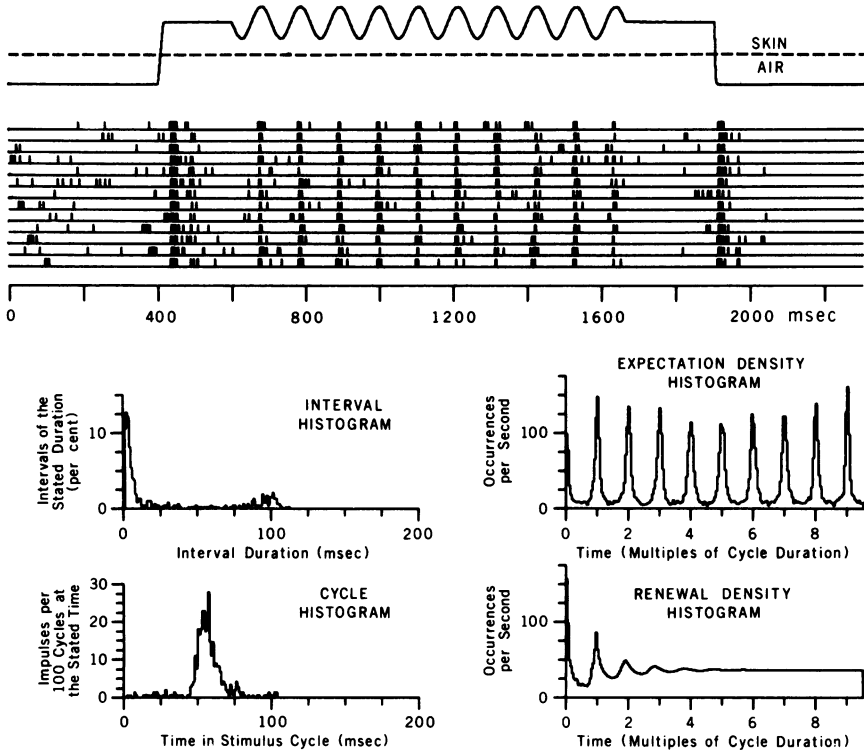
Fig. 4. The records above show the stimulus pattern at 10 Hz and replicas of the impulse discharges evoked by that stimulus in a postcentral neuron of a monkey, in the manner of Figure 2. The nerve impulse replicas (each short upstroke indicates 1 impulse) show sharp on and off discharges when the mechanical probe indents and leaves the skin, and a frequency modulated discharge evoked by the mechanical oscillation. Interval and cycle histograms are shown to lower left; the latter illustrates the strong linkage of impulse discharge to a particular phase of the stimulus cycle. This entrainement is shown in greater detail by the expectation density histogram (the auto-correlation function) to the right. Random shuffling of the temporal sequence in which impulses occur destroys the frequency modulation, as shown by the renewal density histogram, lower right. From Mountcastle, et al (13).

That perfect periodicity at the periphery has been transformed at the cortical level to a code of frequency modulation (13). The analyses of Figures 4 and 6 show that when the sequential temporal order in which the cortical neuronal impulses occur is destroyed by a random shuffle, in the renewal density analysis; the "representation" of stimulus frequency is lost. Such a shuffle of course has no effect upon the periodic signal in peripheral nerve fibers.

It may seem strange to you that I have chosen to describe first a peripheral encoding and central transform of the temporal dynamics of a stimulus set, and to call them representations. I have done so because
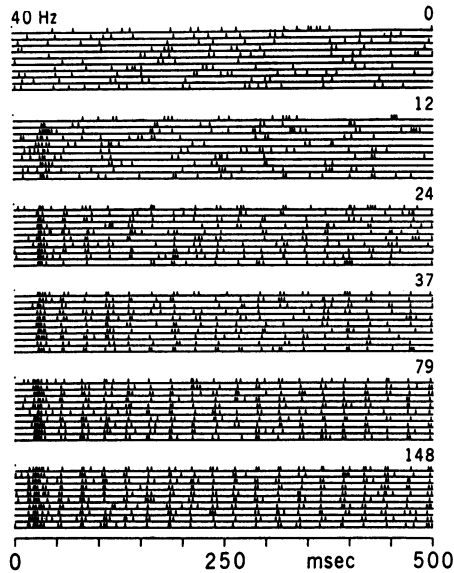
Fig. 5. Impulse replicas like those of Figure 4, for a postcentral neuron activated by 40 Hz mechanical sinusids delivered to the contralateral finger, at several different amplitudes of the sine waves, shown in μm to the right. The response of the cell is modulated with increasing strength by more intense stimuli, but is never entrained periodically as is the first-order fiber of Figure 2. From Mountcastle, et al (13).
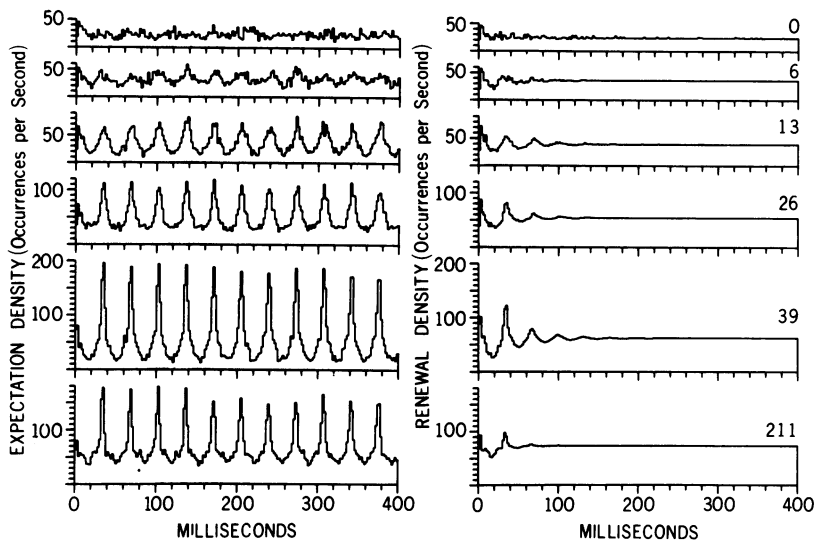

Fig. 6. Analysis of the responses of a postcentral neuron studied in a manner similar to that of Figure 5, but at 30 Hz. The expectation density histograms to the left show that cyclic entrainement is first discernible at 6 μm stimulus amplitude, about the monkey threshold at this frequency. The power of the entrainement grows with more intense stimulation, but is destroyed by random shuffling of impulse interval sequences, as shown by the renewal density histograms to the right. Numerals to the right indicate stimulus peak-to-peak amplitudes in μm. From Mountcastle, et al (13).

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I wish to emphasize this property of brain circuits: they operate in rapid tempo, and must do so to accomplish the precise timing of neural events essential for normal brain operations. The task now, for this mode of mechanoreception, is to track the sequential transformations that occur at even "higher" levels of the brain, so that we may eventually discover the representation of temporal dynamics at the levels of perceptual operations and memory storage.

THE SENSING OF SPATIAL PATTERN

The hand possesses the most acute sensory capacity of any part of the somatic afferent system, If, for example, the different densities of peripheral receptors are taken into account, the capacity for spatial discrimination is virtually identical for the glabrous skin of the fingers and the foveal portion of the retina (14). Perhaps the most elegant demonstration of the human capacity for tactile spatial perception is given by the blind in reading braille. The blind have no unusual innate capacity for touch, but with training a skilled braillist reads the spatially embossed code of braille type at 600 letters/min. This astounding rate of information transmission (60 bits/sec) is of course reduced by the serial dependencies and redundancies of language. Nevertheless, this performance is the most remarkable of which I know in the area of human tactual spatial perception.

K. O. Johnson, J. R. Phillips and S. S. Hsiao in the Bard Laboratories in Baltimore have now carried out a brilliant series of experiments, the results of which contribute significantly to our understanding of tactual spatial perception (15). Their aim was to specify the way in which such stimuli as embossed letters are represented in the first-order afferent inflow to the nervous system, and how that representation is replicated/transformed at the early stages of neuronal processing in the somatic sensory areas of the postcentral gyrus. Their method was to sweep embossed letters of the alphabet across the receptive field of, e.g., a first order nerve fiber innervating the glabrous skin; then, to shift the line of passage of the stimulus by 100 μm, and sweep again. They repeated this stimulation until the entire receptive field had been traversed. Careful time measurement allowed them to re-construct the pattern of afferent input in the total population of afferents of the median nerve engaged by a single passage of the moving stimulus. That is, upon successive, translocated, passages of the stimulus the single nerve fiber (or a single cortical neuron) under study was made to occupy different spatial locations in the total neural population activated by the stimulus during a single passage. The results obtained with this method are shown in Figure 7. The panel to the left shows the results for only four passages of the stimulus, the letter "K", to illustrate the method; the horizontal

lines trace the stimulus movement, and each upstroke is the instant in time at which the fiber under study discharged an impulse. The total reconstruction for the letter "K" in the peripheral fibers of the monkey's median nerve is given in the middle panel of Figure 7, and reconstructions for a number of letters for this fiber in the upper row of Figure 8. These are remarkably isomorphic representations of the stimulus.

The results of a study of a neuron of area 3b of the somatic sensory

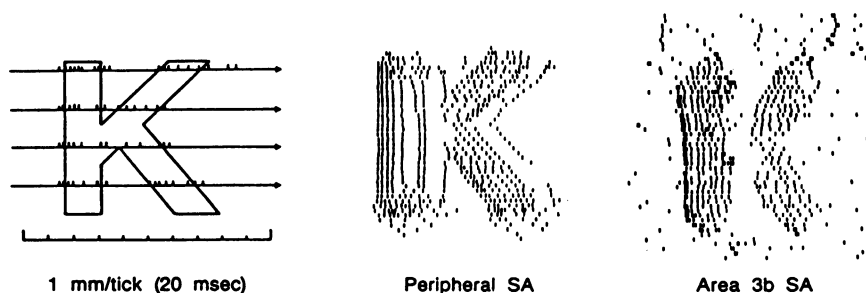1 mm/tick (20 msec)   Peripheral SA   Area 3b SA

Fig. 7. Left: Each horizontal line shows the direction of movement of an embossed letter K across the peripheral receptive field of a slowly adapting mechanoreceptive afferent axon innervating the glabrous skin of a monkey's finger. Each upstroke indicates the instant in time at which a nerve impulse was evoked. Only four traverses are shown, to illustrate the method of study described in the text. *Middle*: The same stimulus is moved across the receptive field many times, and indexed in the second dimension by 100 μm between each sweep. Each dot indicates the occurence of a nerve impulse in the fiber under study. By the reciprocal interpretation described in the text, this figure illustrates the pattern of discharge in the population of median nerve fibers activated during a single stimulus presentation. *Right*: Results of a similar experiment made on a neuron of the postcentral gyrus of a monkey. This cell was linked to slowly adapting afferents innervating the hand. From unpublished experiments of K. O. Johnson, J. R. Phillips and S. S. Hsiao.
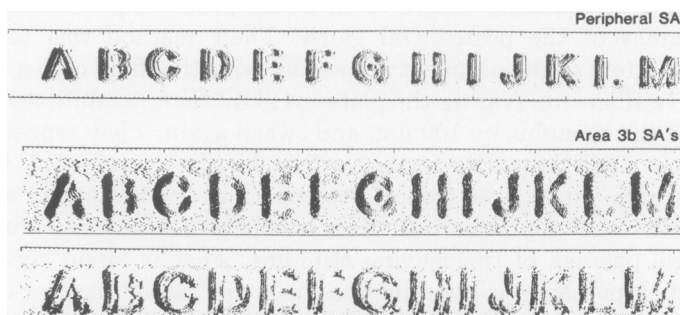

Fig. 8. Results of a study of a peripheral slowly adapting afferent, in the manner of Figure 7 middle, now for a number of letters, shown in the upper row of reconstructions. Those of the lower two rows are for two neurons of the postcentral gyrus, studied in the manner of Figure 7 right. From unpublished experiments of K. O. Johnson, J. R. Phillips, and S. S. Hsiao.

cortex, activated by impulses in slowly adapting (Merkel's) primary afferents, are given for the letter "K" to the right in Figure 7, and for a number of letters for two other neurons of area 3b in the lower two rows of Figure 8. Two important points can be made. Firstly, the representations are discernible only in the time relations between the activity in large populations of neural elements; no signal of a letter appears in the discharge of any single afferent fiber or cortical neuron. Secondly, the quasi-isomorphic representation is a bit fuzzier at the level of the cerebral cortex than for the peripheral nerve fibers. Further studies have shown that these representations are still less isomorphic at the next higher level of cortical processing, in area 1 of the postcentral gyrus. The implication is that what has been seen are the first steps in a chain of transformations that leads to non-isomorphic and more efficient representations at the levels of perceptual processing, the flow through to motor action, and storage in memory—but those are subjects for future research.

THE SENSE OF SURROUNDING SPACE

The two representations I have described are of relatively simple sensory attributes, temporal cadence and two dimensional pattern in tactual sensibility. The initial transduction and representational encoding of these sensory qualities at the level of peripheral nerve fibers innervating the hand are readily discernible in their representations in the primary sensory cortex, even though important transformations occur in the transit from periphery to center. There is reason to believe that these primary cortical representations are radically transformed in further neural processing at still higher levels of brain operations.

The final example of representations I wish to describe is quite different, for it is a central reconstruction that, while it depends in the first instance upon primary afferent input, finds no representational counterpart whatsoever at either peripheral input or primary sensory cortical levels. I refer to the central neural mechanisms of the visual perception of objects and events in surrounding space.

It is at this level of study of the higher functions of the brain that the experimentalist takes his lead from studies by clinical neurologists of the defects in perception and the behavioral abnormalities produced in humans by lesions or disease of the brain, particularly those of the cerebral neocortex.

The Parietal Lobe Syndrome. The florid signs and symptoms of the parietal lobe syndrome are of course familiar to all of you. Lesions of the posterior parietal association cortex are followed by defects in spatial perception and in the visual localization of objects, errors in projection movements of hand and arm, and in map reading, etc. The most striking

of these defects is contralateral neglect. Such a patient neglects the contralateral side of surrounding space, and of his own body; he may fail to dress his contralateral side, or to shave that side of this face; he may even deny that his contralateral arm belongs to him. Two remarkable case reports are illustrative.

Jung described a German artist who at the age of 60 sustained a vascular lesion of the right parietal lobe (16). The artist had commonly produced a continuous flow of dramatic and colorful self-portraits, and he continued to do so after his cerebral lesion. His post-lesion portraits were as artistically sophisticated as ever as regards form and color, but in the portraits made in the early post-lesion months the artist neglected to paint the side of his face contralateral to his cerebral lesion, seen in mirror image. Gradually over the following months more and more of the contralateral face appeared in the portraits, but they were never complete.

Bisiach of Milan has described the results of a series of experiments upon patients with parietal lobe lesions (17). His patients were all native Milanese, and all were familiar with the buildings in the central square of Milan. When Bisiach asked these patients to imagine themselves standing at one end of the square, facing the cathedral, they were unable to name the buildings on the left side of the square, those opposite their right parietal lesions. Contrarily, these same patients when asked to imagine themselves standing at the door of the cathedral, facing the opposite way, readily identified those structures, now to their right, which they had previously professed not to know, and vice versa. The results of this simple experiment have a profound implication. That is, that the representation in memory of surrounding space is not localized to the parietal cortex, per se, but that the parietal lobe and its widely connected system are necessary for ready access to those memory stores.

Study of the Parietal Lobe System in Non-human Primates

My colleagues and I took our cues from clinical studies like these, and planned a series of experiments on the parietal lobe system in monkeys (12, 18). We chose this system as an especially appropriate one for study of the higher functions of the brain directly, for it was clear that the defects in humans characteristic of the parietal lobe system may occur without defects in the primary aspects of sensation or in the control of movement. We first studied a number of monkeys in whom we produced lesions of the posterior parietal cortex. We found, as had others before us, that such lesions produce a syndrome similar to that in human subjects, if less dramatic in our non-speaking subjects. The animals showed a profound contralateral neglect, defects in the visual localization of objects, and errors in reaching into immediate extrapersonal space. We then trained monkeys in a series of behavioral tasks designed to

depend in a critical way upon the behavioral capacities deficient after parietal lesions. We engaged in a long and continuing series of experiments in which we have recorded the activity of neurons in the parietal cortex as the animals performed the tasks; for the initial results and a description of methods, see refs 12 and 18. The general result can be summarized briefly: the functional properties of parietal cortical neurons appear as positive images of the defects of the partial lobe syndrome. Here I wish to describe only a small part of the results obtained, those dealing with certain aspects of visual perception, for they provide a striking example of a central re-construction.

Spatial Perception and the Visual Flow Fields. Anatomical studies of the last decade have yielded a mass of new information concerning the cortical components of the visual system. A summary is shown in Figure 9 (19, 20). The cortical visual system consists of a number of areas sequentially and reciprocally linked by stepwise, transcortical projections. Crossed connections between areas at different levels create a system that is distributed and parallel as well as hierarchical in arrangement. A salient feature of this organization is shown in Figure 9, that there are two major and partially divergent trans-cortical components of the system. The first projects into the temporal lobe, with its target as area TE in Figure 9; this component is known to be essential for the perception of the color and shape of visual objects (21). The second projects into the
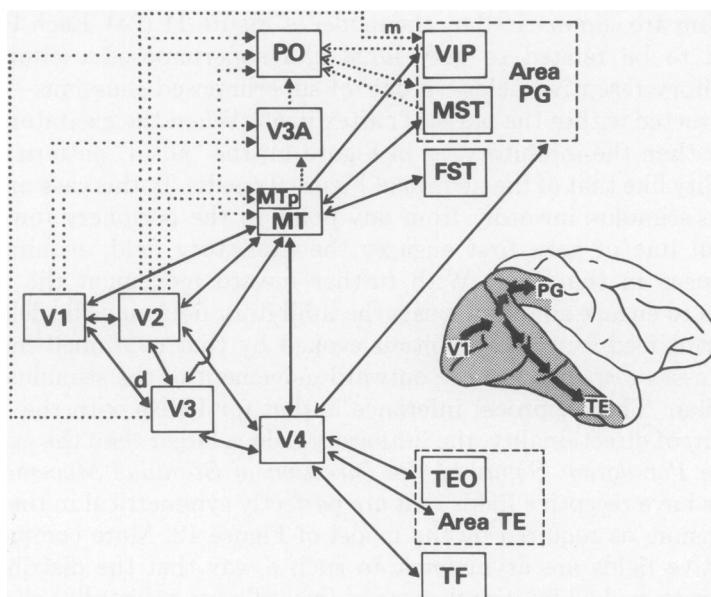

Fig. 9. Schematic diagram outlining the transcortical projections of the visual system of the monkey described in the text. From Fig. 15 of Ungerleider and Desimone (19).

parietal lobe, with its target as cortical area PG of Figure 9; it is essential for the perception of visual object location and movement, and spatial relations in the surrounding environment. The dotted lines in Figure 9 indicate that there is a disproportionate emphasis of the periphery of the visual fields in the parietal component of the system.

We found in our very first experiments that many neurons of the inferior parietal lobule (area PG) respond to visual stimuli (12). Parietal visual neurons (PVNs) have unique functional properties. Their receptive fields are large and bilateral, and in the limit a PVN may respond to a stimulus anywhere in the visual field, though often the peri-foveal zone is spared (22). Figure 10 illustrates the extraordinary directional sensitivity of a PVN; in this case the cell responds to any stimulus that moves into the visual field from the periphery towards the central line of gaze (23). A second class of PVNs is sensitive to stimulus movements in the opposite direction, away from the center towards the peripheral edges of the visual fields. There is no sign of these unusual properties at the input level of the visual system, the axons of the optic nerves. A representation of these aspects of the visual world is constructed within the parietal lobe system; its bilateral nature of course requires interhemispheric intergration across the corpus callosum.

These unusual properties of directional sensitivity aroused great interest from the standpoint of the relevant neural mechanisms. The results of a long series of experiments (I spare you the details) aimed at this problem are summarized by the model of Figure 11 (24). Each PVN was found to be related to very large and superimposed excitatory and inhibitory receptive fields—a pair of superimposed gaussians—that are constructed within the parietal cortex itself. When the excitatory field is larger than the inhibitory, as in Figure 11, the "all-in" pattern of directionality like that of the neuron of Figure 9 results. In this case movement of the stimulus inwardly from any point in the periphery towards the central line of gaze first engages the excitatory field, evoking strong responses in the PVN. With further inward movement the stimulus begins to engage simultaneously the inhibitory field, and the delayed but powerful feed-forward inhibition evoked by that continued movement suppresses responses on the outward movement of the stimulus along a meridian. The reciprocal inference is that for PVNs with the "all-out" pattern of directionality, the inhibitory field is larger than the excitatory.

The Population Signal of the Direction of Stimulus Movement. Few PVNs have receptive fields that are perfectly symmetrical in the circular dimension, as required by the model of Figure 12. More commonly the receptive fields are asymmetric in such a way that the distribution of responses evoked by stimuli moving inwardly (or outwardly) at different angles from the periphery of the visual field towards or away from its

center is adequately described by a circular sinusoidal function. An example is given in Figure 12 for a neuron with a strong inward directionality. This raised the question of whether such PVNs could signal the direction of stimulus motion with much accuracy, even though the
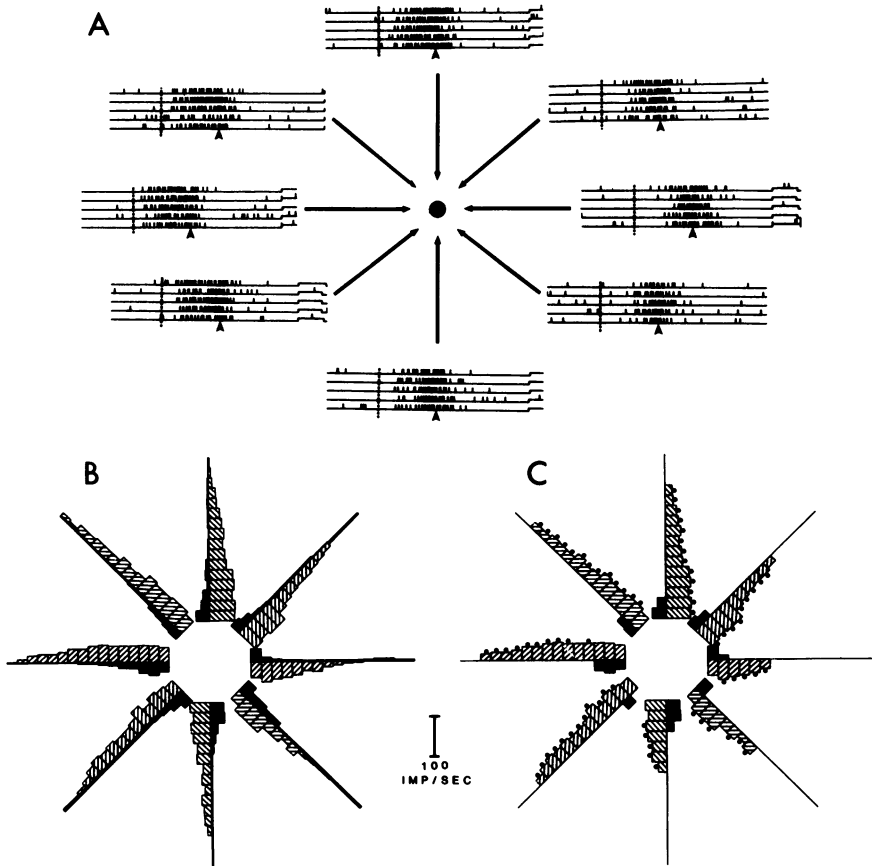

Fig. 10. Impulse replicas (A) and raw and statistically significant data histograms (B & C) for the responses of a parietal visual neuron activated by moving visual stimuli. The receptive field of the cell extended at least to include a 50° radius about the fixation point, the large black dot in A. The impulse replicas in A, five trials for each stimulus direction, show responses during trials of a visual stimulus moving for 100° at 60°/sec in each of 8 directions along the four meridians tested. Vertical dashed lines, stimulus onset; arrowheads, time the radially oriented spatial stimulus passed the point of fixation. The radially oriented spatial histograms in B and C are separated by 20° in the center for clarity. Discharge frequencies during inward halves of stimulus movement shown by hatching, outward by solid shading. Histograms to the right include bins in which discharge was significantly above background; those with significant directionality are indicated by solid dots. This neuron responded intensely to stimuli moving toward the point of fixation, at which the directional preference of the cell suddenly reversed. From Motter, et al (24).
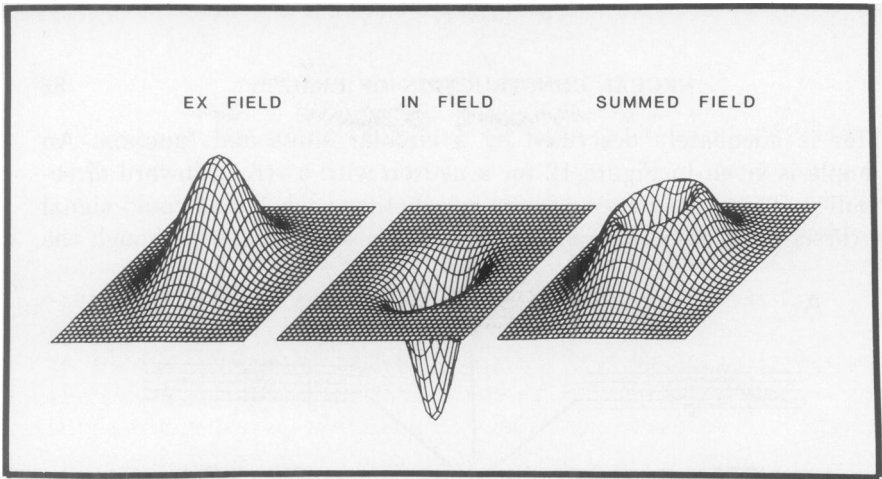
Fig. 11. Three-dimensional, double gaussian model representing the responses of a parietal visual neuron sensitive to inward stimulus motion. The horizontal and vertical dimensions of the visual field are represented on the x- and y-axes, respectively, and response amplitudes on the z-axis. Left, the excitatory receptive field; center, the inhibitory receptive field; right, a summation of the inhibitory and excitatory influences produces strong responses only on the inward limbs of stimulus motion. From Motter, et al (24).
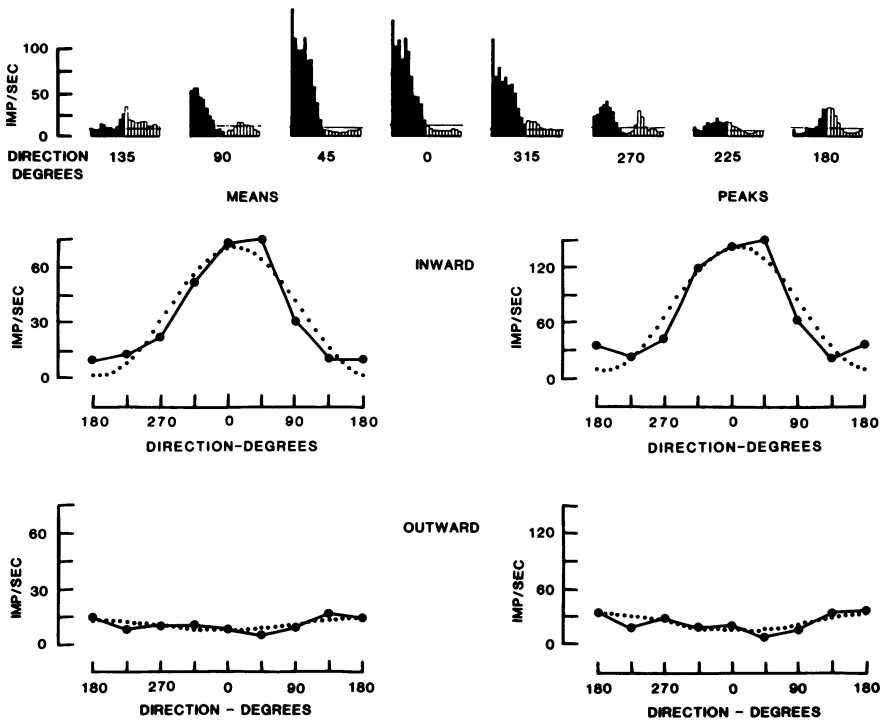

Fig. 12. Sinusoidal variation in the amplitudes of responses of a parietal visual neuron to moving stimuli. The histograms at the top show the time courses for the inward (dark shading) and outward (unshaded) 100° stimulus movements in each of the 8 directions indicated. The mean (left) and peak (right) responses are plotted as functions of the direction of stimulus movements for both the inward (middle) and outward (bottom) halves of stimulus movements. Solid lines connect data points; dotted lines show sine waves fitted to the data by periodic regression. From Steinmetz, et al (23).

sinusoidal fit allows one to specify a best direction for each neuron. The indeterminate signal of stimulus direction provided by each individual PVN constrasts with the remarkable accuracy of primates in perceiving the direction of movement of such stimuli, and reacting to them. This raised the possibility that a more accurate signal of stimulus direction might be embedded, i.e., constructed, in the activity of the total population of PVNs driven by the movement of a stimulus in a single direction.

We applied to this problem a simple analysis and model, that of linear vector summation. There are three assumptions: 1) that when a PVN discharges in response to any visual stimulus, it always transmits a signal of stimulus movement in its own best direction—the assumption of the labelled line; 2) that the PVN population is related to a neural network able to sum the activity of all active PVNs in a vectorial manner; and 3) that when a PVN is suppressed by a stimulus, it provides a positive signal of a stimulus moving in a direction opposite to the best direction for that PVN. The analysis proceeds as shown for one stimulus movement in Figure 13, a vectorial summation constructed from data obtained in study of many single cells (n = 90). The discharge of each cell in the PVN population is indicated by the length of a vector in Figure 13, which indicates the intensity of response by its length, and the best direction by its vectorial angle. Many cells responded only weakly or not at all to this particular, downwardly moving, visual stimulus; their vectors are scarcely visible in the figure. It is clear however that the summed population vector is a powerful and accurate signal of the direction of
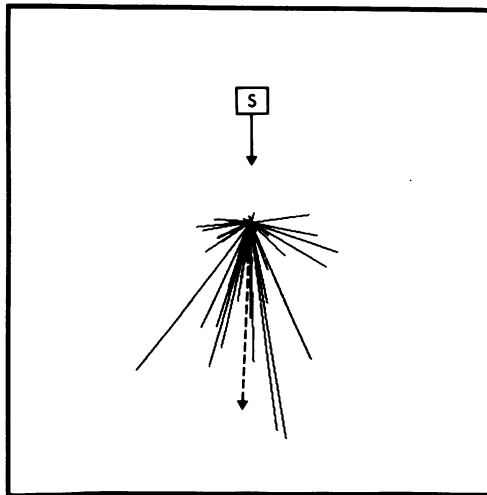

Fig. 13. A model to illustrate the application of the linear vector summation analysis to the responses of parietal visual neurons to moving stimuli. See text for description.
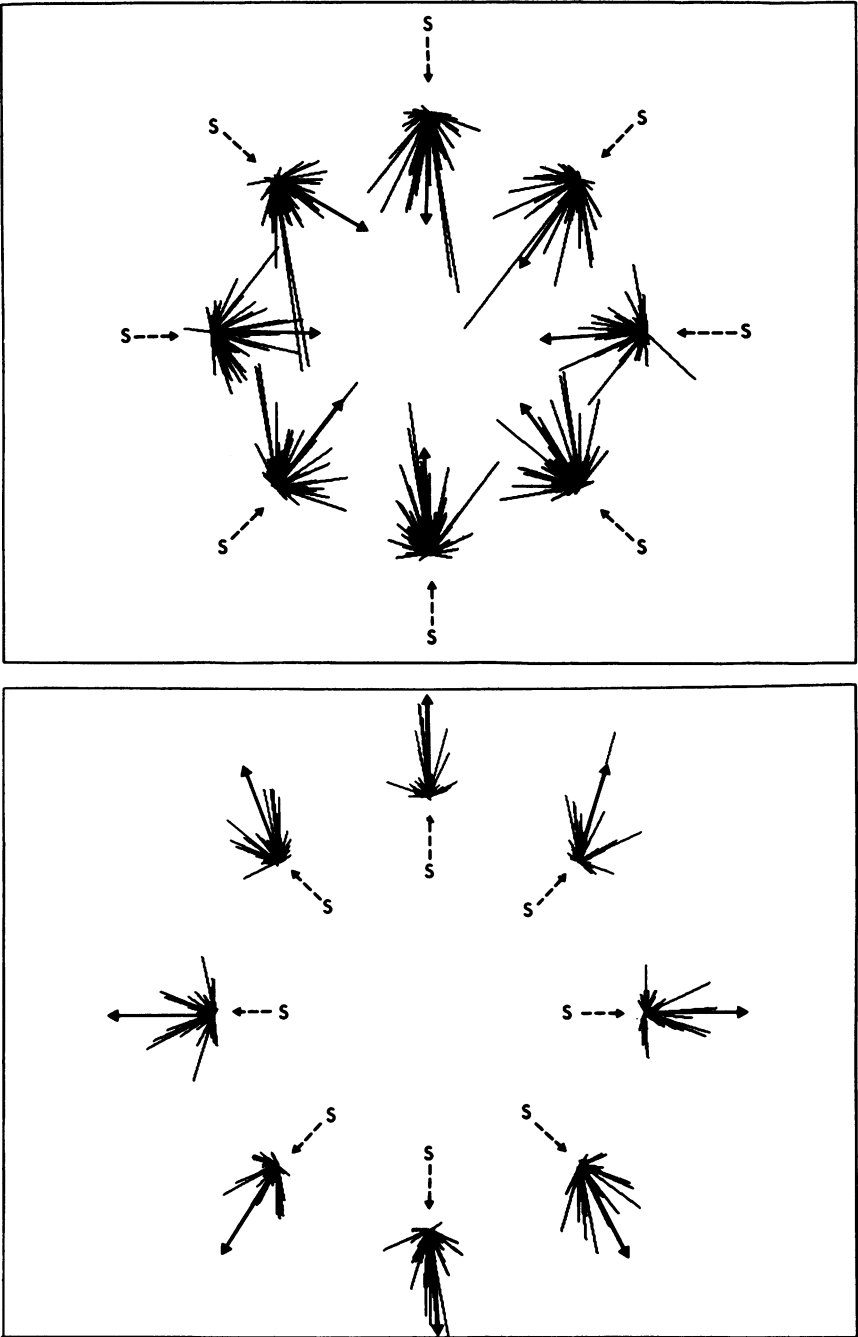
Fig. 14. Individual response vectors and the resulting population vectors (arrows) for the population of parietal visual neurons studied in each of the 8 directions of stimulus motion. Above, for cells responding to inward stimulus motion from the periphery towards the central line of gaze; below, for cells responding to outward stimulus motion. Insets show the distribution of the best directions for the populations analyzed. See text for further description. From Steinmetz, et al (23).

stimulus movement. We repeated this analysis for each cell in the population for each of the eight stimulus directions tested, for our sets of inwardly and outwardly sensitive PVNs. The results are shown separately for the two populations in Figure 14. They suggest the remarkable possibility that the same set of cells, e.g., the inwardly sensitive PVNs, can provide a strong signal of the angle of stimulus movement regardless of the angle. How accurately such a population signal reflects the true angles of stimulus movement is shown by the graph of Figure 15.

Thus the parietal view of the surrounding world is a special one, a central construction of the visual flow-by, one for which there are no counterparts in the quasi-isomorphic representations of the visual world at the levels of optic nerve or striate cortex. The head of a mammal is surrounded by a halo of marked sensitivity to the movement and to the direction of movement of objects into or out of his visual fields, particularly in the periphery. The parietal system provides a continuously updated image of the apparent movement of the surrounding environment during forward or backward locomotion, or during head turning. It is important to emphasize that a host of behavioral studies have shown that we use information from the flow fields in a *pre-conscious mode of processing* for the control of posture and locomotion; and, by a lucky adaptation, in driving high-speed vehicles and landing airplanes.

We discovered a paradoxical effect of attention upon the parietal visual
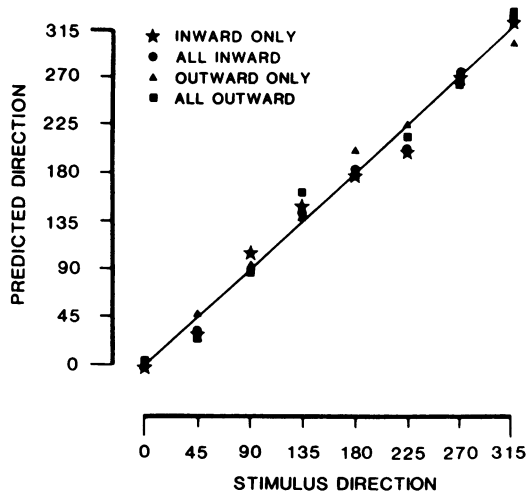

Fig. 15. Population vectors (predicted directions) shown as functions of the actual stimulus directions, for the populations of parietal visual neurons studied. The near-identity relation indicates the accuracy of the population signal derived by the vector summation analysis, in contrast to the signal of a single neuron, shown in Fig. 12. From Steinmetz, et al (23).

system (25). During interested fixation of a target dead ahead, as might occur during walking or running or during eye-hand manipulation, there is a three-fold increase in excitability in the parietal system. The adaptive value of such a facilitation is obvious, for a primate engaged in closely attentive foveal work is markedly at risk to the predator's strike across the periphery of his visual field. The effect of attention upon the temporal lobe system for the perception of contour and color is exactly the opposite, for with interested fixation there is a drop in the capacity for the conscious processing of contour and color in the extra-foveal visual fields.

CONCLUSIONS

Each of us lives in the center of his own perceptual space, and from that central position we each experience the functioning of his own brain. That capacity for internal self-conscious experience is surely one of the most perplexing phenomena in all of biological science. Through your sensory systems you gain some abstracted images of what is outside. Complexing these with stored expectations and memories, you construct in neural space and time a continually updated image of the surrounding environment, of objects and events within it, of your movement through it.

You construct—that is my central theme. It is only rarely that our representations of the external world at central neural levels are iso-morphic with physical reality. Let temporal cadence and two dimensional structure stand as examples, though even for them one can predict that as we probe more central levels of the brain isomorphisms will fade away, to be replaced by constructions. Indeed the majority of representations are central neural constructions, and for the more interesting cases of which we know they depend upon but cannot be derived directly from peripheral afferent input. Let the visual flow fields, or stereognosis, or the concept of body image stand as examples.

Our concept of reality as expressed by representations at the neural level is thus enlarged. It includes the successive and parallel transformations imposed by the microstructure of sensory systems and cerebral cortex. This brain microstructure is in the first instance set genetically, but it is maintained dynamically, and is continually modified by life experience. Thus each of us constructs, stores and recalls his own uniquely private image of the world and events within it. Your images and mine may at times be identical and viridical as regards physical reality. More often they are abstracted constructions that differ between individuals, differences determined by the different structure and dynamic processing mechanisms within each of our individual brains. Thus we may glimpse even at these rather primitive levels of brain function neural mechanisms thought to contribute to the uniqueness of each individual human personality.

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