The Fourier theory of vision

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Abstract. The historical roots of the Fourier theory of spatial visual perception are traced. The development of the underlying concepts and the psychophysical experiments that led to them, and that they in turn spawned, are examined, as well as their relation to the current knowledge of neural substrates in the retina and primary visual cortex. Allowing nonlinearities or even substituting other types of basis functions does not eliminate the difficulties faced by any theory of visual perception that is built on the notion of fixed spatial filters.

Fechner's premonition of the possibility of discovering functional relationships between the mental or subjective-perceptual world and the material or objective-physical world seemed for a time to have been realized in spatial vision. Whether to place the origin of the movement in 1822 or 1754 is a matter for debate, depending on whether primacy is assigned to experiments or to theory. Empirical knowledge usually precedes theoretical formulation, and so it did in this instance. On 6 April 1754 a paper was read before the Königliche Gesellschaft der Wissenschaften in Göttingen by Professor Tobias Mayer, known primarily for his astronomical observations. In common with physicists and astronomers over the centuries, Mayer was curious about the detecting apparatus used for acquiring his astronomical data, namely human vision. In the paper (Mayer 1754) he gave measurements of how far back an observer had to step before he could no longer recognize various visual stimuli, including gratings of various black/white ratios and checkerboards (figure 1).

In 1822 there finally appeared in print the detailed analysis of the conduction of heat in a solid plate, performed during the preceding 15 years by a French mathematician. Publication was delayed because the author, who had been a member of the Benedictine order and served a prison term during earlier years of the French Revolution,

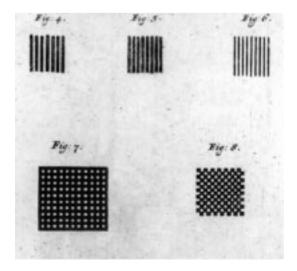


Figure 1. Patterns used by Tobias Mayer to measure visual acuity, including gratings of different black/white ratios and checkerboard patterns. From Mayer (1754); photographic reproduction from the original plates courtesy Bancroft Library, University of California, Berkeley.

had been busy as an administrator in Napoleonic France but then lost his pension for throwing his lot in with the 100-day resurrection (Herivel 1975). Eventually he achieved due recognition with election to the Académie Française and became permanent secretary of the Académie des Sciences. His study contained a novel way of formulating the solution to the partial differential equations of heat flow by means of a series of trigonometric terms, now known by the name of the originator whose full name by then was Baron Jean-Baptiste Joseph Fourier. The Fourier series became a mainstay of functional analysis because, given certain conditions, it allows expression of the performance of physical systems within a framework of accessible orthogonal functions.

Because auditory stimuli are more obviously harmonic than visual ones, hearing researchers had utilized Fourier analysis from the outset (Helmholtz 1863), but in spatial vision there was almost no interaction between the two strands of research for over a century. Grating targets were used on and off for measuring visual acuity, and Shlaer in his notable 1937 study made use of the fact that changing the duty cycle of a square-wave grating changes the modulation of its first harmonic. The idea came to him from a study of diffraction effects in microscope resolution, where Abbe (1873) had introduced an approach which is tantamount to a spatial spectral analysis of images (Rayleigh 1896). But the fateful convergence did not start until the French mathematician Duffieux, in a paperback published in 1946, made explicit the connection between Fourier theory and optics. He pointed to the fact that the equations describing the passage of electromagnetic disturbances through an optical system belong to the class for which Fourier series constitute a solution. The image produced by an optical system has a light distribution that is the convolution of the object with the optical system's impulse function. But convolution is a cumbersome procedure and Duffieux explained how it could be performed in a simpler fashion by recognizing that it becomes multiplication in the Fourier domain: Fourier transformations of the object light distribution and the point-spread function followed by multiplication yield a description of the image. For those who insisted on knowledge of the actual pointby-point distribution of light in the image, an inverse Fourier transformation could be performed, but the light distribution and the amplitude and phase distributions of sine waves of different spatial frequencies are equivalent: they are Fourier transforms of each other.

As a result of Duffieux's thesis, the performance of an optical instrument, including the eye, came to be specified by the contrast transfer function, which describes in the domain of spatial frequencies the change imposed by passage through the instrument. Because at that time manipulations were in the hands of physicists and engineers, expert in the middle-level mathematics involved, there never was the need to stress that transfer functions were complex, in the mathematical sense; that is, both sine and cosine terms had to be specified, or, alternatively, amplitude and phase. The power spectrum, obtained by multiplying the sine and cosine amplitude spectra, is not sufficient, because it lacks phase information.

Armed now with cameras and photocells, modern astronomers were less dependent on the eye for their measurement than their predecessors, but television engineers still preferred to include the observer in their design characteristics. So they became psychophysicists of a sort. The pioneering study by Otto Schade of the RCA Laboratories in 1956 contains every one of the features that later became central to the Fourier theory of vision: targets were sinusoidal gratings superimposed on a uniform field, the modulation depth needed for threshold detectability was determined, measurements were expressed as contrast through Michelson's formula $(I_{\text{max}} - I_{\text{min}})/(I_{\text{max}} + I_{\text{min}})$, and the results were displayed as the reciprocals of threshold amplitude on logarithmic scale of spatial frequency. Schade's curves (figure 2), though somewhat schematic, showed a peak sensitivity near 5 cycles deg⁻¹ and losses at both higher and lower spatial frequencies.

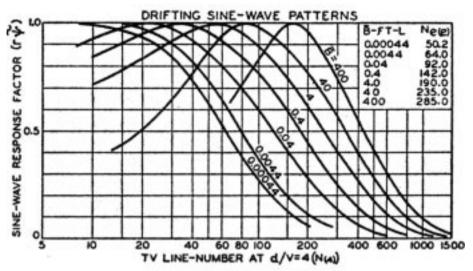


Figure 2. Schade's description of the response of the human visual system to sinusoidal grating targets. All the features prominent in later Fourier studies are already present, including the plotting of the response in reciprocal measure of the Michelson contrast at threshold on a log scale. Reprinted with permission from Schade (1956).

His approach was thoroughly in accord with the systems theory permeating engineering which was then beginning to make inroads into psychology too (Fitts 1951). The idea was to characterize the working of a system by subjecting it to specific kinds of stimuli and examining the resulting responses. One began by postulating the simplest properties of a system, ie linearity, stationarity (invariance with time) and minimum order of complexity (ie obeying differential equations of low order), and testing it with step, pulse, ramp, and sinusoidal stimuli.

Systems theory had a particular fascination for the experimentalist in vision; an almost parallel development took place in temporal vision, where Schade's counterpart, the Dutch engineer DeLange (1954) measured modulation threshold for lights flickering sinusoidally. It is not accidental that the two were contemporaneous, as were equivalent input/output studies in eye movements (Westheimer 1954), the pupil (Stark and Sherman 1957), and accommodation (Campbell et al 1959). At heart was the hope to bring order into what we regarded as a fuzzy state of knowledge by using a rigorous experimental format.

It took a few years for this approach to gain a foothold in the thinking of the spatial-vision research community, but, when it did, it took a singular form. Ordinarily, systems theorists are ecumenical as regards their testing functions. When the eye's optics was first subjected to double-pass measurement of image quality, Flamant (1955) used a slit, ie pulse function, and when Campbell and I extended her work (Westheimer and Campbell 1962), we used both slits and a sine-wave grating. In what turned out to be the most heuristic component in this work, however, Fourier theory was the tool for the calculation and description of the image: in factoring out the reverse path back from the eye to the external measuring device to arrive at the eye's line-spread function, one achieves deconvolution through the use of the Fourier transform, ie the contrast transfer function, which describes demodulation experienced by sinusoidal stimuli in the passage through the eye's optics. All it needed was the further step, one that had been pioneered by Schade, of bringing in the rest of the visual system, and the special variant of system's theory of spatial vision was born which, unlike its role as one of several equivalent tools in the study of temporal visual processing and the oculomotor apparatus, made the sinusoid its centerpiece.

Its success story was launched at the meeting of the Optical Society of America in 1964, when Fergus Campbell and John Robson exhibited a photograph in which a grating pattern of gradually increasing spatial frequency had a logarithmically decreasing contrast along the length of the grating lines. One saw instantly that, at some intermediate spatial frequencies, grating lines could be detected with lower contrast than at the high and the low spatial frequencies. The introduction of the Fourier way of thinking had major consequences for spatial-vision research. Thresholds had, of course, always been a foundation of psychophysicists. But where previously theoretical formulations were built on line (Steinhardt 1936) or patch (Graham et al 1939) targets, stripes with a sinusoidal profile now became the favorite pattern. The reciprocals of the iust detectable modulation as a ratio of the mean luminance, plotted on log-log coordinates against the spatial frequency in cycles deg⁻¹ and called the modulation sensitivity curve, has the virtue that it can be compared, without any dimensional change, with the optical contrast transfer function of optical systems. Working with spatial frequency produced a numerical inversion. Resolution thresholds, more traditionally expressed as small distance differences on the retina, became the highest spatial frequency that elicited an observer's response. Sharp images were described as having a high-frequency content rather than steep intensity profiles in their light distribution. Conversely, blurred objects were characterized as low-frequency.

Another consequence of the modulation sensitivity approach was that it highlighted a phenomenon not easily demonstrated perceptually by other means. The response of the visual system to a stimulus of a critical size is enhanced when its surround has opposite contrast. The peaking of the modulation sensitivity curve near 5 cycles deg⁻¹ is consonant with the spatial opponency demonstrated in certain psychophysical functions (Westheimer 1965) and in neural responses of retinal ganglion cells (Kuffler 1953) and visual cortex simple cells (Hubel and Wiesel 1962). Even the flattening of the modulation sensitivity curves with lowered mean luminance levels fitted in well with the observed dropping out of inhibitory surrounds at low light levels for cat ganglion cells (Barlow et al 1957) and human thresholds (Westheimer 1965).

But these were only superficial signs of a more far-reaching transformation. Spatial reciprocity is central to Fourier analysis: discrete location in one domain is mathematically and practically equivalent to wide (in theory infinite) extension in the other. A sinusoidal grating target extending over the whole retina, and hence covering millions of receptors, is fully specified by the amplitude and phase values in just one place in the Fourier plane. But plotting the eye's modulation sensitivity curve brings no more understanding of how we distinguish objects in space as plotting the eye's luminosity curve does to how we see colors. The more complete articulation of the Fourier theory of vision which was soon published by Campbell and Robson (1968) made this evident. Just as each point pair in the pupil of an optical instrument contains information of the strength of a particular sinusoidal component across the whole image, so, according to Campbell and Robson, the visual system separately evaluates the power of each of the sinusoidal components into which the retinal image could be dissected. They had a specific example. A square-wave grating is actually made up by the superposition of sinusoids with defined frequencies and amplitudes, the fundamental and sinusoids with 3, 5, 7 ... times its frequency and diminishing amplitudes. The higher spatial frequencies are filtered out by the eye's optics (they are represented by point-pairs further and further apart in the pupil and eventually do not enter the eye), but the third harmonic passes through quite well. Campbell and Robson's proposition was that the visual system does not process a square-wave grating edge by separate edge across its width, but spatial frequency by separate spatial frequency as contained in the whole image. Could it be that there exist somewhere in the brain separate mechanisms for

evaluating the strengths of each of the sinusoidal components into which the retinal images could be analyzed, according to their spatial frequencies?

A favorite research strategy in such a situation is analysis by disabling the uptake or processing of one or more constituent components, much the way nature has helped by omitting a visual pigment in some individuals. In optical systems one can overtly display the spatial-frequency spectrum, and filter out defined components by physically blocking their transmission. This is not so easy where the brain is involved and more indirect methods have to be devised. One of them is adaptation, selective fatiguing, in which components can be temporarily desensitized. A typical procedure is to have the observer stare at a grating of a fixed pitch and measure the increase in detection thresholds for gratings of that particular pitch and some of its neighbors (Blakemore and Campbell 1969). The range of desensitization defines the width of a spatial-frequency channel, a necessary construct once it had been decided that the third harmonic component of a square-wave grating had its own sensory life, so to speak, and was not just one of many silent items in a mathematical series expansion.

The concept of channels had actually always been part of the analysis of sensation. The three color primaries are examples, and so are non-overlapping receptive fields of retinal receptors and ganglion cells. Central to it is the issue of independence, mathematically orthogonality, by which is meant that if something is a member of one channel it cannot at the same time be a member of another. A photon, of whatever wavelength, once absorbed by a red cone becomes a signal in the pathway labeled red. Photons absorbed in a cone 3 deg to the left of the fovea in the left retina have that spatial label. True, the signal can interact with one from a cone 3 deg to the right in the right retina to yield a nearer depth impression but, without the retention of the labels of these positions and the eye of origin, the distinction could not be made between nearer and farther. In a pure Fourier theory of vision, the major proposition would be the attribution of a single specific label to each sinusoid and the claim for independence of sinusoids of different spatial frequencies.

The turn that this kind of thinking imposed on the subject cannot be overemphasized. The idea of spatially extended representation—sinusoids in Fourier theory are meant to cover the whole of the field—led the thinking away from a Helmholtzian view (point-by-point analysis and a synthesis at some unknown stage further along) to a view that had been neglected for a while but had a long tradition among followers of Hering and of the Gestalt school: that spatial processing at the earliest stages might be specific for size and shape, decoupled from position. About the same time, James Thomas conducted analogous experiments with disks of various sizes. The general notion in these approaches was to show by adaptation and threshold detection experiments that patterns could act as wholes, beyond their stimulation of each retinal area individually. This was by earnest, rigorous, repeatable psychophysical studies and well beyond the vague, even if true, claims of compelling impressions of connectedness that one finds in the writings of Wertheimer and Köhler of the 1920s.

As the interest in this approach widened, several further strands of enquiry began to emerge. Can the Fourier view be extended beyond threshold experiments? And, indeed, can it satisfy more stringent requirements for object recognition and natural scenes? Furthermore, there is the obverse side of contemporary psychophysics with its slant towards rigor and the laboratory rather than introspection: are there physiological substrates to support it? Phrased succinctly, are sinusoidal stimuli as satisfactory candidates for the basis functions of spatial vision as they are for the physics of optical imagery?

A vast program for empirical and theoretical research was opened up. The properties of the channels and their behavior under various conditions of vision—luminance, adaptation, time, color—were plumbed, and theoretical investigations mounted with

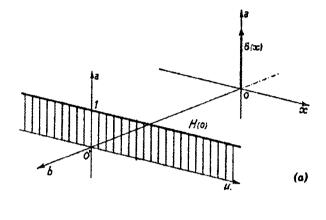
concepts such as masking, noise, and uncertainty. Among the many consequent applications of the Fourier channel mode of thinking, just a couple will be mentioned. Graham and Nachmias (1971) found that when presenting the sum of two low-contrast gratings that differ in spatial frequency by a factor of 3 and increasing the amplitude of one of them to bring the whole pattern to threshold detectability, the relative phase of the two did not matter. Thus near threshold the two gratings were found to act independently. Weisstein and Bisaha (1972), recognizing that, in a Fourier world, a bar has a spatial-frequency spectrum with a defined peak, looked for and found some masking (suprathreshold reduction of apparent contrast) when a subject was shown a grating after the presentation of a bar. But the question of linearity was on everybody's mind.

One way of checking for linearity is to determine whether there is strict proportionality between the responses of signals at the same wavelength that have different input amplitudes. Occasionally one sees reference to the term piecewise linear. Strictly speaking, this term is applied to the case where the gain function (output/input) for a given sinusoidal stimulus is not a straight line but can, over some range of input amplitudes, be approximated by straight line segments. Its use to refer to the analysis by the Fourier method of a limited spatial patch is quite problematic, for in Fourier theory any limitation of the area under consideration has immediate consequences for the whole spectrum. Narrowing the analyzed patch introduces components at other spatial frequencies. This will be discussed later when Gabor stimuli are dealt with. It needs to be stressed that any examination of nonlinear behavior is immediately confined by the initial analytical framework, which in Fourier theory is harmonic. But if the framework is other, the approach might be quite different. The effort by Wiener, during World War II, to study nonlinearities in sonar might be mentioned. Here the probe (stimulus) are pulses which might be emitted at irregular intervals, and the responses are echoes, rather than continuous electromagnetic waves. Wiener invented a method of studying the deviation from complete superposition, ie the nonlinearities of responses to a succession of pulses. The method is now called Wiener kernels, which have found application in, for example, the examination of nonlinearities of electroretinographic responses to light flashes. In vision, nonlinearities are rampant at every stage, and if the method of analyzing them is sensitive to the analytical framework, which it surely is, then the structure of the platform is a significant desideratum. Hence there is need for agonizing whether to remain within the Fourier domain in the face of nonlinearities.

Another deeply searching question concerns the sufficiency of an analytical framework. No one is surprised if complexity has to be introduced in the modeling of a biological system, especially where the brain is involved. But one also has to examine whether in principle a model can account completely for the phenomena under its purview. Whenever an observer can correctly identify some aspect of a visual stimulus, the neural processing mechanism must have available and preserve information of that aspect, regardless of the transformation that the signals have experienced in their passage through the eye to the brain. If it is postulated that visual signals undergo a Fourier transformation in the path to perception, there is need to address how all the features in the natural scenes which we encounter and on which an observer can report are encoded. It is obviously not feasible that separate spatial-frequency channels exist for arbitrarily small steps in the spatial-frequency spectrum, so the question of the number of channels and their bandwidth had to be tackled. Just as in color vision, the channels don't have to be too numerous, as long as there is overlap and a method exists for extracting information of the relative signal strengths.

Fourier arguments in vision that deal only with power spectra fall short of this goal because an image cannot be fully reconstructed from the power, ie the square of the amplitude, in the Fourier spectrum. A complete representation of an image needs both the amplitudes and the phases for each of the constituent spatial frequencies.

The most trivial and at the same time most powerful example of what is meant here is the fact that, in the amplitude domain, the Fourier representations of a single sharp line and of white noise are the same. In white noise the phase is random, whereas for a line the phases of all components are tied: position changes, to which we are exquisitely sensitive, are coded by specific and related phase changes right across the spatial-frequency spectrum (figure 3). In fact a case has been made that in naturally occurring stimuli, which differ surprisingly little in their amplitude spectra, it is the phase from which we predominantly glean the most relevant knowledge (Piotrowski and Campbell 1982). Any Fourier theory of vision that claims completeness has to address how phase information is encoded and read out.



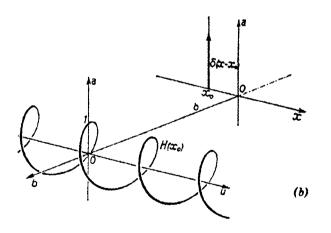


Figure 3. Graphical depiction of the amplitude and phase in the Fourier spectrum of a single line object. (a) A line on the optical axis, the amplitude spectrum is flat, and the phase is zero at all spatial frequencies; (b) lateral shift of the object does not change the amplitude spectrum, but there is now a linear increase in phase angle with increasing spatial frequency. In the two-dimensional depiction, the response vector traces out a helix, ie unit amplitude with phase angles increasing as a function of spatial frequency. Reproduced by permission from P M Duffieux The Fourier Transform and Its Application to Optics 2nd Edition (New York: John Wiley) 1983, figure 58, page 66.

Finally, though it befits the discussion of a theory of visual perception to concentrate on concepts, from the beginning, and certainly these days, the structure and functioning of the eye and the brain as biological tissues have always been part of the story. Where there is complete linearity, there is no need to consider physical realization—all sets are fully interchangeable and equivalent. However, once nonlinearities are allowed threshold, saturation, nonadditivities of all kinds, there is no longer a general theory and assimilation to the particularities of the platform are mandatory. In color vision, for example, the intuitions of trichromacy and of opponency and the evidence from the genetically color-deficient preceded the discovery of three cone pigments and of color-opponent neurons. They are part of the fabric and our understanding would be the poorer without them. In his influential book, David Marr (1982) argued that

real understanding of vision arises from the computational theory and algorithms rather than the implementation hardware. But deep down, most of us are uncomfortable with that idea, witness the widespread invocation of the original Hubel and Wiesel papers as references and starting points of empirical inquiries into spatial vision. If only algorithms and not their hardware implementation mattered, why bother with neural responses in anesthetized cats? Even when inquiring into the basis of our empirical knowledge of the world or into the evolution of the nervous system in conformity with environmental imperatives, the intrinsic structure of the sensory system would be regarded as fundamental.

The most direct physical implementation of a spatial-frequency analysis would be by way of Fourier combs, ie a series of detecting templates that have a spatially sinus-oidal acceptance function and whose output is proportional to the image's content at their spatial frequency. For completeness they would have to be duplicated with 90° phase shift. The eye's optics can certainly be treated in such a manner, but the anatomy of the retina is not in accord. Processing here is strictly local, transduction is compartmentalized in the structural elements, rods and cones, and the generation of neural signals is confined within small neighborhoods. Receptive fields in the LGN and the first stages of the primate visual cortex are similar. Although there have been reports of neurons in the visual cortex with multiply-peaked receptive fields, reminiscent of Fourier combs, the general consensus is that processing in V1 is still very predominantly local, though the receptive field may have interesting properties of orientation- and direction-selectivity, end-stopping, spatial contrast-opponency, and so on.

This is not to say that examination of the visual neural system cannot be performed within a Fourier framework. A grating of the right orientation and moving with the right velocity is, in fact, an excellent target for a first characterization of a neuron in the primary cortex. But the response reflects only the extent to which the relevant portions of the grating match the position, orientation, and center/surround properties of the neuron's receptive field. Non-classical surround zones with complex interacting properties would not be revealed because they are covered by the single overall grating pattern.

The initial phase of enthusiasm for the Fourier analysis in spatial vision in time gave way to a more reflective tone. The realization set in that, as mathematically and conceptually attractive the whole framework might be, the distance between theory on the one side, and the structure and wider actuality of visual functioning on the other, had been widening rather than narrowing. Laying out the state of the art circa 1980 Weisstein and Harris felt that applying Fourier analysis to the visual system has a certain esthetic, and pragmatic, appeal but went on to say: "Even if the visual system doesn't do anything that is uniquely identifiable as a Fourier analysis, we as scientists may find that Fourier analysis is a helpful tool for exploring and comprehending what the visual system is doing" (Weisstein and Harris 1980, page 323).

Eventually, when the limitations of regarding sinusoids as the canonical patterns through which all visual percepts arise became apparent, a compromise developed. It took the form of Gabor functions, ie sinusoids with a Gaussian envelope. Brillouin (1962) has illuminated the situation in an exemplary fashion. If linearity holds, an image can be specified just as well by the point-by-point light distribution as by a distribution of amplitude and phase of sine and cosine functions in the applicable spatial-frequency range. Brillouin explains that in a plane in which the Fourier components represent one axis and the position coordinates the other axis, Gabor functions can be thought of as occupying rectangles, ie limited in extent in both the spatial-frequency and space domains.

Gabor stimuli certainly match the known structure of the visual system well. They are oriented and at the same time have a profile reminiscent of the center/surround

spatial opponency of ganglion cells. Their champions tend again to assign to them the role of canonical functions, just as had been claimed previously for sinusoids. That is, they postulate that the visual system initially filters every image through a bank of Gabor combs. Enter the question that was raised earlier in connection with Fourier series, viz the number, density, distribution of parameters, etc of the population of these detecting units (these have to suffice to catch all the details that observers can report on in a visual scene to which they are exposed). And once again the problems of linearity and completeness have to be faced.

A single thread runs all through this argument: it is the concept, taken over from retinal anatomy, that the optical image passes through a stage of passive spatial filtering, much as that undergone by the wavelength spectrum in being absorbed by the cone pigments and emerging as signal strength with just three color signatures. Debates about linearity and subsequent interactions, eg opponency, can take their natural course once it is conceded that such a framework is applicable. In other words, the discussion has been merely about the kind of spatial filters, not whether in fact such filtering models do justice to the actual processing of optical signals arriving at the retina. A reassessment of such a view, which applies equally to models with functions as diverse as the Fourier, Gabor, Difference-of-Gaussians (Wilson and Bergen 1979), disk (Thomas 1970), Gaussian derivative (Young 1987), or Walsh (Richmond et al 1987), or indeed in terms of Marr's primal sketch, can, however, not be avoided.⁽¹⁾

The usual view of channels in spatial vision and the analytical tools used to characterize them, eg masking and selective adaptation, is that they represent fixed pathways through which the optical image is necessarily passed. Overlapping acceptance functions, nonlinearities, etc, notwithstanding, our perception is based, so it is contended, on the output of these channels. Now, it is true that such a picture does apply in primary optical and retinal processing: the optical image is filtered through receptors with indivisible spatial signatures and visual pigments with univalent chromatic signatures. Especially in the latter case, selective adaptation is a marvelous tool. Strong light at one wavelength will desensitize the acceptance of light at all wavelengths at which a pigment absorbs. It is the uncritical transfer of this world-picture to spatial channels that causes the trouble. If adapting to a grating of one spatial frequency causes a desensitization for gratings of that and related spatial frequencies, does this mean that viewing a totally unrelated object, say a face, generates a signal in that channel proportional to the spatial-frequency contents in the object? Or could it be that channels, of whatever kind, are merely ad hoc, defined by, and at the moment of, the stimulus? In other words, do selective adaptation experiments, at the heart of the channel viewpoint, delineate fleeting footprints in the sand merely to fade and be replaced by the next imprinting pattern, or do they expose the rigid ribs of structures through which all stimuli are inescapably constrained to pass?

The vast number of phenomena described under the rubric of figural aftereffects suggest the answer. On reading Köhler and Wallach's classic (1944), is it thinkable that such a multitude of adaptation phenomena can be forced into a framework of single sets of canonical channels, whatever their nature? This exercise in conceptualization within the confines of perceptual theory can be supplemented—though psychophysics can stand on its own legs without feeling the need for support from these quarters—by consideration of the neural substrate in which the processing takes place. Fixed filtering is tantamount to regarding the response profile and connectivity of neurons in

⁽¹⁾ A distinction must be drawn between a set of basis functions, ie primitives that are canonical descriptors, and the stimuli used to probe the system. Even though a system is taken to have, say, Gabors as primitives, it can be examined by probing with point stimuli. When linearity holds, there is no need to grapple with the distinction, but, where it does not, the situation can quickly get opaque.

the primary visual cortex as immutable except for an amplitude term. Such a limited view may perhaps be read into the earliest studies, carried out under anesthesia, but evidence from current neurophysiology makes it clear that not only the signal strength of neuronal responses but also all sorts of parameters of their receptive field change with context, attention, and learning. The processing apparatus in the brain, if perhaps only minimally that in the retina, changes quite substantially with the stimulus condition, so that any one filtering mechanism, delineated however rigorously with one set of objects, may be rudimentary or even absent when another set is displayed.

To those of us who shared Fechner's vision of mathematical relationships between physical stimuli and the perceptual experience, the realization that the platform of sensory processing is floating rather than firm comes as a disappointment but, of course, also as a challenge. Nor is it a new experience. There had been similar hopes to seek secure roots of spatial vision in geometry. The attempts, from Helmholtz to Luneburg, to anchor space perception to constructs derived from mathematical geometry have proved elusive. They foundered, just as modern models of fixed channels, not just on the subtlety but rather on the overarching malleability and adaptability of the sensorium. The task of creating theories of vision is not over; it just becomes more difficult and more interesting as each generation of researchers contribute their own illumination and their own insight.

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