

HOLONOMIC BRAIN THEORY IN IMAGING AND OBJECT PERCEPTION *

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Image processing in the visual system is described utilizing some basic neurophysiological data. We propose that both sensory and cognitive operations address features already conjoined in critical receptive fields. As both sensory perception and further processing stages are critically dependent upon movement, the theory emphasizes sensory-motor reciprocity in imaging and in object perception.

'If we could find a convenient way of showing not merely the amplitudes of the envelopes but the actual oscillations of the array of resonators, we would have a notation (cf. Gabor 1946) of even greater generality and flexibility, one that would reduce under certain idealizing assumptions to the spectrum and under others to the wave form ... The analogy ... [to] the position-momentum and energy-time problems that led Heisenberg in 1927 to state his uncertainty principle ... has led Gabor to suggest that we may find the solution [to the problems of sensory processing] in quantum mechanics.'

(Licklider 1951: 993)

1. Introduction

An age-old problem in philosophy is the origin of knowledge. In recent times two opposed views have dominated not only the philosophical scene but psychology as well: there are those who see knowledge as built of more elementary events to which the organism has access through his senses. Then, in opposition to this elementarist view are those who emphasize the fact that we perceive what we are set to

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perceive, that specific events are differentiated out of some more global tacit knowing. Today, in cognitive psychology those two approaches have given us bottom-up *vs* top-down models, although most investigators (e.g., Broadbent 1977; Deutsch and Deutsch 1963; Norman 1964; Treisman 1969) have ultimately opted for a combination between the two extreme positions.

Anne Treisman has presented a superb demonstration that, under certain conditions, illusory conjunctions can occur between 'features' or 'channels' of visual sensory experience (1977). She interpreted her results to indicate that object perception is due to a conjoining of elementary processes – a bottom-up type of organization (although elsewhere, e.g., 1980, she addresses the use of top-down information in constraining the conjunctions among elementary features). She surmises, as does almost everyone else, that these elementary features reflect the results of activity in separate classes, 'channels', of neurons which can be characterized according to these elementary features. However, the actual data indicate that features are already, to some considerable extent, conjoined in the receptive field properties of neurons which makes it necessary to develop an alternative explanation of her results.

In a sense this alternative explanation is more radical than Treisman's. In agreement with her interpretation, one aspect of perception is considered to be a centrifugal or centripetal process that actively selects particular conjunctions of features to form objects. In contrast to Treisman, however, this selection of features or properties of objects is made by cognitive operations akin to motor programs from pools of properties *already* neurally conjoined. Furthermore, input from the senses also addresses these conjoined pools of properties to provide the psychological phenomena we identify as more 'elementary' sensory events. This *sensory-motor reciprocity model* is thus neither exclusively bottom-up nor top-down, but more of an amalgam in which a *match* between bottom and top is critical.

The research to be reviewed falls into several categories. With regard to imaging, results are reviewed of microelectrode analysis of the feature response of units in the primary visual receiving area of the monkey cortex. The results of these experiments are critical in that they show each neuron in this primary sensory system already to conjoin several feature selectivities: i.e., each neuron is selectively sensitive to several features and cannot therefore be conceived as a detector for any one feature.

Further, data are reviewed which demonstrate that feature selectivity is a function of neural units in the visual (and auditory) system and not necessarily of the physical stimulus display presented to the system. These data are obtained when visual (and auditory) 'white noise' is presented and units in the visual cortex continue to display 'simple' properties: i.e., their receptive (i.e., functional dendritic) fields are elongated and show at least one inhibitory side-band.

These experimental results are discussed with respect to a mathematical model which forms the basis for additional models of higher-order visual processing that lead to perceptual constancies as a function of the perisensory motor systems of the brain. Data are reviewed that show that size constancy depends on the peristriate visual system from which eye movements are obtained when electrically stimulated. Perhaps other constancies such as color and shape, etc., are also developed as functions of this cortex - a suggestion based on the discovery that cell pools in these areas of cortex can be characterized by a predominance of one or another such feature constant. This suggestion is discussed within the context of the somatic and auditory sensory-motor systems.

Movement provides the key. Try the following demonstration: have someone repeatedly touch the palm of your hand with a pencil or other object while your eyes are closed. You feel the touching, rubbing, pressure - sensory qualities and perhaps sensory patterns. Now grasp and manipulate the same object and suddenly its 'objectivity' materializes.

Sperry (1947), Festinger et al. (1967), and Held (1968) each have suggested that perception is a motor process. In part this suggestion stems from the fact that neurons are sensitive to transients, and movement produces transients. However, their analysis has failed to account for our inability to basically alter images of scenes, despite occasional illusory conjunctions. In sensory-motor reciprocity theory, the motor systems are assigned a more restricted role, that of developing object constancies. Objects are perceived as invariant when the organism actively moves about in the environment - whether with eyes, head, hand, or whole body - with the consequence that a *set* of images results. Invariances must then be extracted from the set in order for object constancy to take place.

The characteristic which identifies the perception of objects is constancy across changes in the sensory patterns the objects elicit. Gibson

(1979, 1980) and more recently Turvey et al. (1978) have emphasized the view that such constancies result when the several parts of the distal stimulus of the optic array – the layout – move with respect to one another in such a way as to provide an invariant input to the organism: in this scheme invariance, 'information', resides in the environment and the major contribution of the organism to object perception is that he is moving: movement produces the relative displacement of portions of the layout with respect to one another. Bernstein (1967) and Johansson (1973) have developed techniques which clearly demonstrate the effects on perception of coordinated motion of one set of features (dots) with respect to another.

Johansson's demonstrations indicate that the trained observer can process short exposures (e.g., 1/2 sec) of such coordinated patterns. In neural terms, this is a considerable processing time and indicates that the contribution of the organism to object perception is somewhat more than just moving.

There must be some mechanism within the perceptual system of the organism which aids the extraction of invariances. The environment of the senses contains all sorts of invariant patterns, only some of which are processed. To repeat an old adage, trees fall in the woods and perturb their surroundings but the making of a *sound* by a falling tree depends on having a sentient organism within earshot. Sentience depends on being endowed not only with the appropriate sense organ but also a central processing competence.

For object perception, this central processing competence must, at a minimum, be composed of a connectivity that allows the variety of sensory patterns which characterize a series of events to be correlated so that only invariances remain. The averaging procedure used in analyzing event-related potentials is an example which extracts constancies from noise.

Let us repeat in order to make this argument clear. According to Gibson (and Turvey), certain invariances are produced when coordinated parts of the environmental layout move with respect to one another. Gibson's, Turvey's and Johansson's experiments demonstrated this beyond any reasonable doubt. At the same time, however, retinal excitation and striate cortical processing, as we have seen, do not at any point in time single out the invariant from the variety of sensory inputs. Subjectively, one can simultaneously perceive the differences between the sensory patterns produced by an object *and* the extracted invariant

which identifies the object as one moves about it. According to Gibson, only the invariant should be perceived (because there is no retinal image, even momentarily) and this is not so.

In short, invariants in environmental inputs are produced by movement, but these invariants must vie with the variety of sensory (retinally and cortically produced) images for special treatment. This paper addresses the neural mechanism which make such special treatment possible.

Sensory-motor reciprocity processing achieves its result by impressing on the primary visual cortex sets of samples which eliminate those aspects of images (patterns) which are irrelevant to the production of each constancy. With regard to imaging we describe how the visual cortical representation of the retinal image is effected by the Gabor transform, modeled as a function of both retinal position and two-dimensional spatial frequency on an abstract four-dimensional retina-spatial frequency product manifold which we have called the visual perception manifold. Similar models for the functional organization of striate cortex based on the description of simple cell receptive field profiles by Gabor functions have been proposed by Sakitt and Barlow (1982), Kulikowski et al. (1982), and Varela (1982). However, none of these models has fully developed for object perception the form of the mathematical structure implied by the Gabor transform.

2. Classification of receptive field properties

The sensory-motor reciprocity approach to imaging depends on understanding clearly the results of microelectrode analysis of the receptive field properties of neurons in primary sensory areas such as the visual cortex. Many attempts have aimed to classify units, cells, in the visual cortex according to their properties. Beginning with the seminal work of Hubel and Wiesel in the late 1950s, cells have been assigned to categories such as concentric, simple, complex, and hyper-complex (1959, 1962). In a series of studies begun in our laboratory during the mid-1960s (Phelps 1973, 1974; Spinelli and Barrett 1969; Spinelli et al. 1970) we attempted to make a quantitative assessment of the nature of the properties defining these categories by using a computer-controlled experimental situation in which single, double, and multiple spots and lines were drifted across the visual field of cats

and monkeys. In this way the receptive field of a cell could be accurately mapped because the computer 'knew' where the spots or lines were located and could assign the response of the unit to that location in a set of bins that represented the possible locations in which the spot(s) or line(s) might appear. In addition, elementary sensitivities of the cells to such stimuli as color, and the direction and velocity of movement, were assessed.

The most striking results of these and subsequent experiments (Pribram et al. 1981) was the fact that each cell in the primary visual projection cortex has *multiple* propensities, and that the cells differed in the combination of these propensities. Thus it became impossible to classify the cells – only the properties of a network of receptive fields were amenable to specification and classification. These properties were to a large extent, though not exclusively, characterized by the elementary stimuli that were used to study the receptive field network. In short, each neuron in the primary visual cortex has already conjoined elementary sensory properties in some characteristic combination.

Here are some examples: G.H. Henry (1977) has noted, in several thousand explorations, hypercomplex properties (i.e., an inhibition when elongation of the receptive field extends beyond certain limits) were found only rarely and that when present, the receptive field also showed either complex (i.e., responsive to an elongated stimulus anywhere within its receptive field) or simple (i.e., showing excitatory and inhibitory regions within its receptive field) properties. Schiller et al. (1976) found so many properties for each neuron examined that they attempted classification via a multidimensional statistical analysis. Though not undertaken by them, Henry's and Schiller's approach, drawn to its logical conclusion, results in a classification of field – or network – properties rather than a classification of single neurons (Pribram et al. 1981).

Thus any conceptualization based on the idea that sensory feature elements are kept isolated in the primary visual projection systems must take these data into account. Whatever the nature of feature analysis and of channel separation, it is *not* due to a limited line, neuron-to-neuron mechanism.

Let us repeat this point once again, for it is critical to any understanding of the issue of whether imaging results from the conjoining of features which are initially isolated, or whether features are abstracted

from images. According to the current findings, *neither* hypothesis is correct. Were the cell rather than the property the basic unit to be classified, a cell might for example be complex *or* hypercomplex, but not both. The fact that a cell can simultaneously be both, and in addition be color sensitive, directional sensitive, velocity and luminance specific, indicates that these properties, features, are already conjoined within the receptive field of the cell. Some of these cells in the visual cortex are even differentially tuned to acoustic frequencies (Spinelli et al. 1968) and groups of neurons and even single cells show late responses (ca. 300–400 msec after stimulus is presented) only to a rewarded cue in a problem-solving situation (Pribram et al. 1967; Bridgeman 1982). Thus a cell is defined by a congerie of properties, not a single feature.

This conjoining of properties in a receptive field of a neuron in the primary visual cortex does not mean, however, that each neuron represents those conjunctions which characterize any particular image or object. No pontifical 'grandfather' or 'grandmother' cell has been found at this initial processing stage whose output is *uniquely* specified by an object. It remains possible that such specificity becomes encoded in the pattern of the output of a neuron – a pattern which can be specified by an interresponse interval histogram or burst profile. But to date this has not been accomplished. How then can we account for illusory conjunctions? Most likely, images must be constructed much as Treisman suggests – but not exactly. *Sensory perception results not from processes which conjoin properties, but which simultaneously select these properties from a pool in which they are already to some extent conjoined.*

Selection would account in a novel fashion for the distinction between perception and more elementary sensory processes. Both bottom-up and top-down theories admit readily to such a distinction, and in fact are based upon it: elements → percepts for bottom-up; percepts → elements for top-down. The sensory-motor reciprocity model being developed here differs from both these alternatives in that both percepts and elements are formed from some more primitive matrix in which conjunctions already abound. Sensory input to this matrix from the senses 'abstracts' sensory qualities; perceptions of objects are formed by the operations of the systems associated with the senses.

Two questions immediately come to mind. First, how do the properties of the receptive field matrix originate; are they more or less stably set phylogenetically? Second, if they are, how does the selection process

proceed to emphasize some features to the exclusion of others? We turn to an examination of the first of these questions.

3. Features extracted from noise

There is a considerable body of evidence which supports the conception that at least some feature properties of the receptive field matrix are inborn (see, e.g., Wiesel and Hubel 1965a, 1965b; Chow 1961, 1970; Ganz 1971). True, these properties must be exercised in an ordinarily rich environment lest they deteriorate and/or develop abnormally (Wiesel and Hubel 1965a, 1965b; Pettigrew 1974). And there is some additional tuning that can occur as a result of specialized environmental inputs (Hirsch and Spinelli 1970; Blakemore 1974). In the context of perception, these data can be taken to indicate that a feature matrix is a relatively stable property of the organism's sensory (receptor to cortical) system. Tuning of elements in that matrix by sensory input from the environment is feasible, but the elements to be tuned are characteristic of the organism.

An additional experimental result bears on this issue; Sutter (1976) identified a cortical unit with simple receptive field properties and then stimulated it with visual white noise (by presenting many spots appearing and disappearing on a TV monitor). The experiment was undertaken to determine whether the response of the cell was linear (i.e., whether all of the variance of the stimulus-response relationship could be accounted for by the first kernel of a Wiener polynomial). Much to our surprise he found that within 30 msec the cell mapped only those spots within its receptive field, as determined by conventional means (shining a line at a particular orientation). Ten msec later an inhibitory flank became evident, as would be predicted for simple receptive field properties on the basis of intracellular recordings (Creutzfeldt et al. 1974). In short, the cell actually extracted the features 'elongation' and 'orientation' from noise on the basis of its own propensities. Similar results were obtained for frequency selection in the auditory system (Hosford 1977). Clearly, the cells are *selecting* from the multiform sensory input only those properties to which they are sensitive.

The potential combinations of selectivities and multiform inputs appear to be legion. The result of the sensory process appears to reflect invariances in the relationship between input, and receptor variables

and cortical system variables. The invariants can be sensed either as properties of the receptor surface or the properties can be projected onto the environment.

What determines projection? Von Bekesey's ingenious experiments (1960, 1967) with artificial cochleas hold the clue to an answer. By lining up five vibrators on one's forearm, Von Bekesey was able to produce the feeling of a single spot which could be moved up or down by changing the phase of vibrations between the vibrators. When a second artificial cochlea was placed on the opposite forearm, the feeling of a spot could be made to jump from one arm to the other, and with practice the spot was finally 'projected' away from the receptor surface of the skin much as sound is projected from two stereophonic speakers.

But bilaterality is not a necessary condition for projection. When phase relations between fingers are adjusted, a spot can be projected outward from them. One feels the paper on which one is writing at the tip of one's pencil, not at the tip of the fingers which hold it. Whenever conditions are 'right', projection occurs. 'Rightness' appears to be maximized by movement in time, such as vibration or movement in space.

4. Pattern sensing

Given a feature space in the primary sensory systems, how are images, i.e., selected patterns of features, formed? According to the sensory-motor reciprocity approach proposed here, patterns emerge when invariants are selected from the conjoint receptive field properties of cortical neurons by the sensory input which addresses them. Selection occurs when the motor apparatus of the organism provides a scan over a limited portion of the sensed environment. With respect to the first stage of perception, oscillatory movements of receptor surfaces are critical; tremors for touch, respiration in olfaction, the movement of cochlear hair cells in hearing, nystagmoid displacements of the retina in vision. When such oscillatory movements are stopped or counteracted, sensory adaptation takes place and sensations fail to be registered. In vision, producing 'stabilized retinal images' by scleral mirrors and other devices (Ditchburn and Ginsborg 1952; Riggs et al. 1953; Heckenmueller 1968) has proved to be a powerful research tool for analyzing visual processes.

Our analysis focuses on cells in the visual cortex which display 'simple' receptive fields, which by virtue of their excitatory and inhibitory elongated subfields, are especially sensitive to such micrometer movements. However, the analysis holds as well for cells with complex receptive fields since Movshon et al. (1978a, b, c) have shown them to be composed of subfields each of which shows simple properties.

There have been three fundamentally different approaches to modeling the neurophysiology of imaging: D.C. Field; Feature Hierarchy; and Interference Pattern (for review see Pribram (1971)). Several sets of experiments ruled out the D.C. Field theory forwarded by Wolfgang Köhler (1958). Among these were the implantation of gold foil (Lashley et al. 1951); the cross hatching of the visual cortex and insertion of mica strips into the cuts (Sperry 1947); and the injection of minute amounts of aluminum hydroxide cream to produce epileptic foci (Pribram 1971).

Currently, Feature Hierarchy models comprise what Horace Barlow has called the neurophysiological 'dogma' in perception (Barlow 1965). Such models are bottom-up in approach and implicitly assume a Euclidean geometry. Thus, a convergence of outputs from cells with concentric receptive fields results in simple receptive fields; convergence of outputs from cells with simple receptive fields results in complex fields; and convergence of the outputs of cells with complex receptive fields results in hypercomplex fields, etc. until a 'pontifical' or 'grandmother' cell is reached whose receptive field corresponds to the perceived image.

Though there is considerable merit to some aspects of the hierarchical approach, as already indicated there are also some grave difficulties. Diverse receptive field properties are already conjoined in early stages of processing; latency of response of cells with complex receptive fields are often shorter than latencies of response of cells with simple fields (Henry 1977); the end-stopping which characterizes hypercomplexity can be found in cells with either simple or complex fields.

In addition, there is a computational awkwardness in composing the rich texture of a percept from simpler line sketches. Nonetheless, this approach has been developed in a sophisticated fashion by David Marr and his associates, Poggio and Ullman (see Crick et al. (1981) and Marr and Poggio (1977) for a review). We will make use of sketches in our modeling as well; but we reserve this aspect of perception to a later stage when categorization takes place (Pribram and Carlton 1987).

For the early, image processing, stage considered in this paper, we have chosen a modification of the third approach: a manifold composed of a microstructure of patterns of synaptic and dendritic graded potential changes which can be conceived of either as a spectrum composed of continuously fluctuating potentials or in terms of a matrix of momentary non-propagated dendritic minispikes.

Whereas both the D.C. Field and the Feature Hierarchy approaches to the neurophysiology of perception imply geometric isomorphism between the brain process and an experienced percept, the approach taken here, pioneered by Lashley in physiological terms (1952) and by Gabor mathematically (1946), eschew geometrical for algebraic isomorphism. Thus, the computations involved are not immediately, intuitively, understood without recourse to engineering instantiations of the mathematics. Fortunately, the optical hologram as developed in the early 1960's (Leith and Upatnicks 1965; Leith 1966) has provided an image processing device which makes the mathematics palpable for us.

At the same time the use of the optical hologram has led to some misunderstanding of 'the Holographic Approach to Brain Function in Perception and Memory' which is grounded in Gabor's mathematics, not in the optical artifact (see Pribram 1966; Pribram et al. 1974). Perhaps the most critical misunderstanding is that holographic theory is a version of Field Theory, which it is not. As Pribram stated (1971: 113), 'Arrival and departure patterns conceived as microstructures thus become a third force in the cell vs. "floating" field argument ...'

5. The Gabor elementary function

This third force is Gabor's use of the mathematics of the quantum theory to develop holographic image processing. But as Gabor points out: 'The foregoing references are merely an acknowledgement to the [quantum] theory which has supplied us with an important part of the mathematical methods' (1946: 432). It is not implied that events at the quantum level are necessarily responsible for the process, although this remains a possibility.

Gabor's insight devolved on noting that:

¹Fourier's theorem makes of description in time and description by the spectrum, two mutually exclusive methods. If the term "frequency" is used in the strict mathematical sense which

applies only to infinite wave-trains, a "changing frequency" becomes a contradiction in terms, as it is a statement involving *both* time and frequency.

The terminology of physics has never completely adapted itself to this rigorous mathematical definition of "frequency." For instance, speech and music have for us a definite "time pattern" as well as a frequency pattern. It is possible to leave the time pattern unchanged, and double what we generally call "frequencies" by playing a musical piece on the piano an octave higher, or conversely, it can be played in the same key, but in different time. Evidently both views have their limitations and they are complimentary rather than mutually exclusive.

Let us now tentatively adopt the view that both time and frequency are legitimate references for describing a signal and illustrate this - by taking them as orthogonal coordinates. In this diagram harmonic oscillation is represented by a vertical line. Its frequency is exactly defined while its epoch is entirely undefined. A sudden surge or "delta function" (also called "unit impulse function"), on the other hand, has a sharply defined epoch, but its energy is distributed over the whole frequency spectrum. This signal is therefore represented by a horizontal line' (1946: 431).

Gabor then goes on to point out that other signals such as a sine wave of finite duration can be plotted within the confines of the orthogonal Fourier coordinates. It is this description which we now refer to as the 'Gabor elementary function'. (See fig 1.)

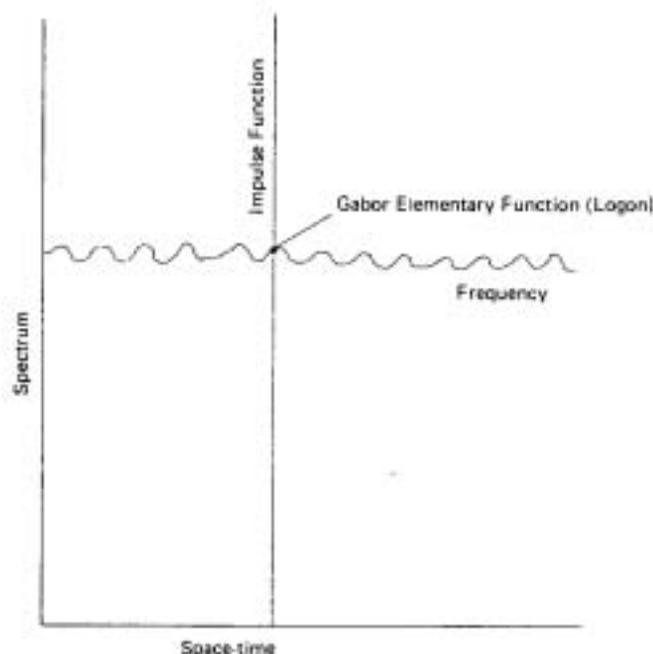


Fig. 1. Spectrum (i.e., frequency) by space-time diagrammatic representation of the position of the Gabor elementary function.

Gabor's analysis of the complementarity of time and frequency leaves unsettled the fact that there is a time-like dimension to frequency which is responsible for the physicists' and popular view of what is meant by frequency. A resolution to this problem comes by way of the fact that frequencies are cyclic and that cycles have a *duration*. Thus in the Fourier theorem sine and cosine are employed: the sine and cosine referring to the angles of a triangle drawn within the circle that describes the cycle of the wave form. We shall use the term 'duration' to describe this time-like quality of cycles within the spectral domain. The necessity on other grounds, for making such a distinction between time and duration was thoroughly discussed by Bergson (1911, 1911/1959) and Pribram and Carlton (1987).

With the advent of frequency analysis in studies of the visual system pioneered by Campbell et al. (1969b), the term 'spatial frequency' has become a commonplace in the visual sciences. This term, as does the more usual 'temporal frequency' used in physics and ordinary discourse collapses the mathematical separation of spectrum and space/time devised by Gabor.

Gabor notes that, because he has

'... made of a function of one variable - [space]/time or frequency - a function of two variables - [space]/time and frequency - we have the strange feature that, although we can carry out the analysis with any degree of accuracy in the [space]/time direction or the frequency direction, we cannot carry it out simultaneously in both beyond a certain limit. In fact, the mathematical apparatus adequate for treating this diagram in a quantitative way has become available only fairly recently to physicists, thanks to the development of quantum physics.

The linkage between the uncertainties in the definition of "[space]/time" and "frequency" has never passed entirely unnoticed by physicists. It is the key to the problem of the "coherence length" of wave trains, ... But these problems came into the focus of physical interest only with the discovery of wave mechanics, and especially by the formulation of Heisenberg's principle of indeterminacy in 1927. This discovery led to a great simplification in the mathematical apparatus of quantum theory, which was recast in a form of which use will be made in the present paper' (1946: 432).

In the following pages Gabor develops his theme. He substitutes the complex exponential for operations with simple sine and cosine functions. The introduction of complex variables is necessary because:

'If we had operated with the real signal $s(t)$ instead, the weight function would have been even, and the mean frequency f always zero. This is one of the points on which physical feeling and the usual Fourier methods are not in perfect agreement. But we could eliminate the negative frequencies only at the price of introducing a complex signal' (1946: 434).

Finally, Gabor proceeds to define his elementary function, the 'logon':

'The signal which occupies the minimum area $\Delta t \Delta f = 1/2$ is the modulation product of a harmonic oscillation of any frequency with a pulse of the form of a probability function. Because of its self-reciprocal character, the probability signal has always played an important part in the theory of Fourier transforms. But its minimum property does not appear to have been recognized. It is this property which makes the modulated probability pulse the natural basis on which to build up an analysis of signals in which both [space]/time and frequency are recognized as references' (1946: 435).

As noted, simple receptive field profiles closely approximate the Gabor elementary functions. Specifically, these are formed by the product of a sinusoid and a Gaussian, i.e., a sinusoid which is limited by a Gaussian envelope. The sinusoid is determined by the spatial frequency response of the receptive field; the Gaussian reflects lateral inhibition which limits the otherwise more or less limitless extent of overlapping dendritic fields.

At this point, a basic question arises: are the spatial frequency characteristics, i.e., the frequency components of the Fourier relation in the Gabor elementary function to be considered 'real' or are they to be regarded simply as a mathematical tool useful to the investigator of sensory functions. The question arises because of the very nature of the Fourier relationship: its invertibility. Thus the receptive field profile can be expressed in 'space/time' coordinates just as readily and more clearly since it is the ordinary language of neuroanatomy. Thus many neuroscientists are arguing that there is no difference between the 'spatial frequency' and the 'line feature' descriptions of the receptive field properties of visual cortical neurons (see, e.g., MacKay 1969).

There are two arguments against such a view. The first is that the richness of the Gabor complementarity analysis which was reviewed above, is ignored. Gabor took the problem of the Fourier relation a step beyond the Fourier theorem and in doing so invented image processing by holography.

Second, we have obtained evidence (Spinelli and Pribram 1966, 1967; Lassonde et al. 1981) that electrical stimulation of posterior and frontal cortex and of the putamen and caudate nucleus, can change the receptive field profile of neurons in the striate cortex. We have interpreted such changes as being the result of changes produced in lateral inhibition. Thus posterior cortical and putamen stimulation produce

smaller receptive fields presumably because of enhanced lateral inhibition; while frontal cortex and caudate stimulations produce the opposite effect.

It is thus feasible that at the limit, as a result of excitation of the posterior (and putamen) systems of the brain, a maximum shift would occur in the Gabor elementary function toward the space/time coordinate, i.e., toward an impulse function which is spread over many frequencies. Equally feasible is that at the limit, excitation of the frontal (and caudate) systems of the brain, a maximum shift would occur in the Gabor elementary function toward the frequency (spectral) coordinate, i.e., toward a function described in the Fourier domain.

6. Implementation

How then do the Gabor elementary functions that characterize receptive fields in the visual cortex become organized? There is now ample evidence that the junctional potentials occurring in dendritic networks (see Pribram 1971) interact to produce the receptive field properties mapped during single-neuron recording. Dendrites are fitted with spines which resemble little cilia, or hairs, protruding perpendicularly from the dendritic fiber. These spines have heads at their endings, knob-like heads which make contact with branches of axons to form synapses, branches which are also fitted with such spines. The axons bring in signals to the dendritic network and transmission is ordinarily enhanced via chemical transmitters whose action can be modified by other chemicals which act as regulators and modulators.

Shepherd, Rall and their colleagues (see, e.g., Shepherd et al. 1985) and Perkel (Perkel and Perkel 1985; Coss and Perkel 1985) have modeled this process whereby these synaptic events occurring in spine heads interact. The issue is this: the stalks of the spines are narrow and therefore impose a high resistance to conduction (active or passive) toward the dendritic branch. Spine head depolarizations (as well as hyperpolarizations) must therefore interact with one another if they are to influence the action potentials generated at the axon hillock of the parent cell of the dendrite, action potentials by means of which the signal becomes effective at the next stage of processing: '... active propagation beyond branch points to a parent dendrite generally did

not occur unless there was summation with activity in the sister or parent branch' (Shepherd et al. 1985: 2194).

The virtue of this mechanism is that the potential for complexity in processing is enhanced:

'First the relative efficacy of distal dendritic inputs would be greatly enhanced. Second, ... the transients within the model spines and dendrite are rapid and do not have the slow, low amplitude time course of synaptic potentials recorded experimentally at a distance from the cell body. Within the distal dendrite, information might thus be processed through precise timing of specific inputs to different neighboring spines (cf. ref. 20). These precise interactions would greatly increase the complexity of information processing that can take place in distal dendrites' (Shepherd et al. 1985: 2194).

An example of the nature of this enhanced complexity is the potential for selective learning which such a mechanism allows:

'... it has been shown that synaptic polarization in a spine head can spread passively with only modest decrement into a neighboring spine head. If the neighboring spine is pre-synaptic, transmitter release could be evoked' (Shepherd et al. 1985: 2192).

Thus, effects on the presynaptic neuron can occur, effects which are critical if selective learning is to take place (see Freud 1895; Hebb 1949; Cooper 1974).

'Active spines appear to provide a basis not only for multiply contingent processing of synaptic inputs as outlined above but also for storage of information. The spine stem resistance as a parameter for varying the effectiveness of spine input to parent dendrite has been recognized as a locus for plasticity underlying learning and memory' (Shepherd et al. 1985: 2192).

And the spine stems have actually been seen to change their length and thickness under different processing conditions (Perkel and Perkel 1985).

What is important for the thesis presented here is that the active propagation of the signal is discontinuous: 'Thus, the active propagation ... was discontinued and resembled in this respect the saltatory conduction that takes place from node-to-node in myelinated nerve' (Shepherd et al. 1985: 2193). In our model of visual processing such discontinuous processing is described in terms of Hilbert mathematics which proved so useful in modeling the paradox of discontinuous properties of continuous elements in quantum mechanics. The non-local aspects of the mechanisms of image construction and reconstruc-

tion, and thus of memory storage, partake of this paradox (see Pribram 1986). It may yet turn out that this mathematical similarity between the quantum mechanics and neural mechanics has a basis in neurophysiological reality: suggestions (e.g., Hameroff et al. 1982) have been made that microtubules can serve as conductors of soliton waves and the medium within which spine heads are immersed is often glial. Changes in the microtubules of glial cells may well be the locus of the effects of experience on RNA discerned in the experiments of Hyden (1969). For now, all of this is speculation: what we do wish to convey here is that the mathematics used to describe quantum events is also useful in describing receptive field properties that are produced by the junctional interactions occurring in dendritic networks.

7. The mathematical model

Formally, the neural activity corresponding to visual pattern sensing can be modeled as a mathematical function on an abstract manifold determined by the microstructure of synaptic and dendritic events which determine receptive field profiles. Marcelja (1980) showed that simple receptor field profiles closely approximate Gabor elementary functions which consist of the product of a sinusoid and a Gaussian:

$$g(p, u)(x) = \exp(-(x-p)^2/s^2) \exp(-iu(x+p)), \quad (1)$$

where

$p = (p_1, p_2)$ and $x = (x_1, x_2)$ denote retinal points measured in distance units from origin at the foveola;

$u = (u_1, u_2)$ denotes two-dimensional spatial frequency; and

$s = s_1(p, u)s_2(p, u)$ is the product of the horizontal and vertical Gaussian standard deviations.

(In the calculations that follow, as a first approximation, s will be taken equal to one.) Functions of this form were introduced as an overcomplete set in the discrete case by Gabor (1946), generalized to the continuous case by Helstrom (1966), and used by Glauber (1963) to represent coherent states of the electromagnetic field. As discussed above, those functions minimize the product of uncertainties in posi-

tion and spatial frequency: $\Delta p \Delta u = 1/2$. Here, the Gaussian $\exp(-(x-p)^2)$ models spatial localization at retinal position p of the receptive field. The sinusoid $\exp(-iu(x+p))$ describes two-dimensional spatial frequency selectivity with maximal sensitivity to two-dimensional spatial frequency u . Thus the receptive field described by the elementary function $g(p, u)$ is centered at retinal point p and, by virtue of lateral inhibitory mechanisms, has sinusoidal excitatory and inhibitory regions with scalar frequency equal to the magnitude of the two-dimensional vector u and orientation (the angle of the orthogonal to the elongated regions) equal to the angle of u with the horizontal axis ($\arctan(u_2/u_1)$).

Note that two-dimensional spatial frequency, in polar coordinates, includes both orientation (radians) and scalar spatial frequency (number of cycles per unit length) in that orientation. Thus the spatial frequency parameter u in the Gabor functions represents both orientation selectivity (Hubel and Wiesel 1962) and spatial sinusoidal selectivity (Campbell et al. 1969a; DeValois et al. 1978; 1979; DeValois 1984 seminar; Maffei and Fiorentini 1973) of visual cortical cells. In fact, assuming spatial summation over the retina, the spatial frequency tuning curve of the cell is equal to the Fourier transform of its receptive field profile (Andrews and Pollen 1979; Marcelja 1980). Indeed, Marcelja's evidence for the approximation of receptive fields by Gabor elementary functions is the excellent fit of the inverse Fourier transform of the best-fit Gaussian curve in the frequency domain to the experimentally measured spatial receptive field. In other words, if the cell's receptive field profile is described by the Gabor function

$$g(p, u)(x) = \exp(-(x-p)^2) \exp(-iu(x+p)),$$

then its spatial frequency profile is predicted by the Fourier transform

$$g(p, u)^{\wedge}(v) = c \exp(-(v-u)^2/4) \exp(ip(v-2u)),$$

again a product of a Gaussian and a sinusoid. In spatial frequency response measurements, only the Gaussian envelope $\exp(-(v-u)^2/4)$ is observed and corresponds to the reported tuning curves having bandwidth about one octave about the preferred frequency u (Movshon et al. 1978a, b, c). (We have chosen the somewhat arbitrary sign in the

complex exponential factor of the Gabor elementary function so as to facilitate later calculations.)

To construct a visual cortical representation of an instantaneous retinal image $f(x)$, where $x = (x_1, x_2)$ denotes retinal position measured in distance units from the foveola, let us consider first the response of a cortical cell with simple receptive field profile $g(p, u)$. The contribution from retinal area dx about the point x to the cell's response to the signal f is the product $g(p, u)(x)f(x) d^2x$. Assuming the cell adds linearly over the retina (Movshon et al. 1978a, b, c), the cell's response to f is given by the integral

$$Gf(p, u) = \int_{R^2} g(p, u)(x)f(x) d^2x, \quad (d^2x = dx_1 dx_2), \quad (2)$$

which is the inner product of the stimulus function f with the Gabor elementary function $g(p, u)$ in the Hilbert space of square-integrable functions of two real variables. For appropriate f , this inner product is the (p, u) th component of a functional transform of the image f , which we shall call the 'Gabor transform' and denote Gf , an element in the Hilbert space of square-integrable functions of four real variables (two in p plus two in u).

Next let us consider the set of all cells in primary visual cortex with simple receptive field $g(p, u)$ for fixed retinal position p and two-dimensional spatial frequency u . Since u represents both orientation and scalar spatial frequency selectivity, these cells may be grouped in a cortical column formed by the interaction of an orientation column (Hubel and Wiesel 1962) with a scalar spatial frequency column (DeValois and DeValois 1980; DeValois et al. 1978; Pollen and Feldon 1979). Now fixing the retinal point p and letting the spatial frequency vary, we obtain a collection of such cortical columns, whose distribution throughout the primary visual cortex depends on the anatomical projections from retinal location p to the cortex.

Assuming spatial frequency sampling is sufficiently fine, at each retinal point p we associate an abstract two-dimensional continuous manifold, denoted M_p , each point of which represents a particular scalar spatial frequency and orientation, and which may correspond to a cortical column. DeValois (1984 seminar) has indeed found such two-component spatial frequency columns. If the anatomical projection from the retina to the primary visual cortex is continuous, the cortical columns represented by M_p are in the same cortical region.

Finally, the collection of all such manifolds M_p as p varies over the retina constitutes a Cartesian product manifold, denoted $R \times M$, assuming each M_p is equal to the same two-dimensional spatial frequency manifold M . We will call this four-dimensional real manifold the 'visual perception manifold'.

The distribution throughout the simple cell population of V1 of activity corresponding to the retinal image f is represented on the abstract product manifold $R \times M$ by the Gabor transform Gf . Each component $Gf(p, u)$ of the 'Gabor spectrum' of f represents the activity in the cortical column tuned to spatial frequency u and connected anatomically to retinal position p . The form of the Gabor transform

$$Gf(p, u) = \int_{R^2} f(x) \exp(-(x-p)^2) \exp(+iu(x+p)) d^2x,$$

shows that the cortical activity pattern in each column is represented as a function on M_p by a shift in phase of the Fourier transform of the product of the image f with the Gaussian centered at p :

$$Gf(p, u) = \exp(+iup) (fn_p)^{\wedge} (+u),$$

where

$$n_p = \exp(-(x-p)^2), \text{ and}$$

' \wedge ' denotes Fourier transform.

The Gaussian n_p reflects localization at p of the receptive fields of the cells represented by M_p . The Fourier term $\exp(+iu(x+p))$ reflects the effect of lateral inhibition in the neural pathway from retinal location p to cells represented by M_p (Pribram et al. 1974; Bridgeman 1982).

We have just described how the distribution of activity in the dendritic (i.e., receptive) fields of cells with simple receptive field profiles resulting from an instantaneous static retinal image may be represented on a retina-by-spatial-frequency product manifold by the Gabor transform of the retinal image. This is a highly redundant representation because of the overlap of the Gaussians, reflected in the overcompleteness of the Gabor elementary function (which are not

orthogonal in the Hilbert space of square-integrable functions of two real variables). The Gabor representation has enough information to give essentially the Fourier transform with recovery of the retinal image (inverted) simply by projection to a cortical region whose activity is proportional to spatial summation of simultaneous inputs.

The intermediate visual pattern perception corresponds to the neural slow potential pattern resulting from the cumulative effect of continuous microtremor displacements of the retinal image during fixation between saccades. Formally, if $GF(p, u; t)$ denotes the instantaneous activity pattern at time t on the visual perception manifold $R \times M$, then the fixation pattern perception is represented by the fixation-time average

$$\langle GF(p, u) \rangle_T = 1/T \int_0^T GF(p, u; t) dt,$$

where the fixation T is approximately 500 msec (Ditchburn and Foley-Fisher 1967). Averaging of the instantaneous patterns produced by fine intra-fixation eye movements reduces inherent noise (Barlow 1965) as well as preventing fade-out during fixation.

This representation of striate activity patterns by functions on the visual perception manifold $R \times M$ takes formalization of the receptive field data on scalar spatial frequency and orientation and retinal localization to its limit, and provides insight into possible modes of processing beyond the primary sensory stage. Similar models for the functional organization of striate cortex based on the description of simple cell receptive field profiles by Gabor functions have been proposed by Sakitt and Barlow (1982), Kulikowski et al. (1982), and Varela (1982). However, none of these models has fully developed for object perception the form of the mathematical structure implied by the Gabor transform. We assume linearity. For each point p there is enough phase information in the activity pattern on the spatial frequency manifold associated with p , M_p , to obtain, at a next level of activity, an inversion of the retinal image, which is itself an inversion of the perceived visual form. Let us assume that the cortical columns' output is directly proportional to their activity pattern and that the columns associated with p project to a certain set of cells, say C_p , perhaps in V2. The contribution to C_p from spatial frequency element du about u is $Gf(p, u) du$. If cells in C_p add over M_p , then the

resulting activity in C_p is represented by the integral over M_p of $Gf(p, u)$:

$$\begin{aligned} \int_{M_p} GF(p, u) du &= \int_{M_p} \int_{R^2} f(x) e^{-(x-p)^2} e^{+iu(x+p)} dx du \\ &= \int_{R^2} f(x) e^{-(x-p)^2} \left(\int_{R^2} e^{+iu(x+p)} du \right) dx \\ &= \int_{R^2} f(x) e^{-(x-p)^2} 2\pi\delta(x+p) dx \\ &= 2\pi f(-p) e^{(-4p^2)}. \end{aligned}$$

Thus the Gabor transform representation provides a means of re-inverting the retinal image in the activity pattern of the collection of all the sets C_p . This integration of the Gabor transform over M_p is essentially the Fourier transform.

Thus the projection to peristriate (PS)_p of the hypercolumn corresponding to M_p gives essentially a second Fourier transform with recovery of the (inverted) retinal image by integration over M_p . Independently, projection to another peristriate region (PS)_u of the cells sensitive to given spatial frequencies essentially extracts the Fourier transform of the retinal image by integration over R_u , eliminating retinal position dependency of the Gabor transform. (This integration is shown below in the discussion of contour development.)

For scale invariance, a Fourier-Mellin transformation to still another set of prestriate neurons would provide size constancy (see, e.g., Altes 1984). We have not as yet completed our explorations of this theoretical line (but hope to do so shortly) because we felt that invariant responses to a variety of forms (images, contours) are more critical to a full understanding of object constancy.

What is the evidence? One of the characteristics of the development of the mammalian brain is the progressive separation of motor from sensory cortex which may allow a substitution of asymmetric connectivities for the more locally symmetrical connectivities (Burgess et al. 1981; Pribram 1960) of the projection cortex per se. This is especially true of the somatosensory-motor system (see Pribram (1982a, b) for a review). But even in the visual mechanism, it is electrical excitation of

the peristriate cortex (which surrounds the primary visual projection area) of monkeys which produces eye movements. Thus the question arises whether perhaps object constancy in the visual mode is a function of this visuomotor system. No complete answer can be given, but a beginning has been made toward such an answer. In one experiment (Ungerleider et al. 1977), size constancy was shown to be dependent upon this system. After extensive damage to the peristriate system, monkeys respond exclusively to the retinal image size of an object, ignoring the contextual and organismic factors responsible for constancy.

The process by which object constancies come about can be suggested to arise out of the Bekesey experiments on projection. For example, we have already noted that fine oscillating movements in the visual system in conjunction with the property of spatial frequency selectivity (receptive fields are tuned to approximately an octave of spatial frequency) account for pattern sensing. The same properties, when engaged by gross movement, can be expected to produce parallax, thus lifting figure from ground. An image is formed.

Once this has been accomplished, the variety of movements stabilized the spatiotemporal location of the object, establishes a perimeter around the imaged figure, and explores the area within that perimeter. Weisstein and Harris (1980) have found that accuracy in identifying lines was greater when the lines were enclosed by overlapping squares – a function they have labeled an 'object-superiority effect', because accuracy is even greater when lines are presented as part of object-like pictures.

Eye movement studies (e.g., Mackworth and Otto 1970; Stark and Sherman 1957) have demonstrated both a perimeterizing and a concentration of eye fixations on 'informative' aspects of the image. Blum (1973, 1974) and Gauthier (1977) and others (Schwartz et al. 1983) have devised precise mathematical models which can extract geometric descriptors of shape from such figure-ground perimetry.

The 'Fourier descriptor' (FD) method of coding shape proposed by Gauthier (1977) and Schwartz et al. (1983) may be a necessary result of two-dimensional spatial frequency analysis of a two-valued image defined by its closed, piecewise smooth boundary:

$$f(x) = 1 \quad \text{if } x \text{ is inside the boundary} \\ = 0 \quad \text{if } x \text{ is outside the boundary.}$$

As described by Gauthier and by Schwartz et al., the Fourier descriptor method is essentially a one-dimensional Fourier analysis of the 'boundary orientation function' of a bounded planar region.

Fourier descriptors are the Fourier coefficients of the one-dimensional Fourier series expansion of the periodic complex function defined by the given closed contour (Persoon and Fu 1977), so that they are obtained by taking the one-dimensional Fourier transform of the boundary function. By Green's theorem for the plane, the one-dimensional Fourier analysis of the boundary function is related to the two-dimensional Fourier transform of the two-valued function of two variables, defined to be 1 inside the boundary and 0 outside:

$$\begin{aligned} f(u_1, u_2) &= \int_R \int_R f(x_1, x_2) e^{i(u_1 x_1 + u_2 x_2)} dx_1 dx_2 \\ &= \int_{\text{Region}} \int f(x_1, x_2) e^{i(u_1 x_1 + u_2 x_2)} dx_1 dx_2 \\ &= \int_{\text{Region}} dw = \int_{\text{Boundary}} w, \end{aligned}$$

by Green's theorem for the two-form

$$dw = e^{i(u_1 x_1 + u_2 x_2)} dx_1 dx_2,$$

and one-form

$$w = [1/i(u_1 - u_2)] e^{i(u_1 x_1 + u_2 x_2)} (dx_1 + dx_2),$$

$$\hat{f}(u_1, u_2) = \int_{\text{Boundary}} w,$$

corresponding to the one-dimensional Fourier transform of the boundary function, which is the Fourier descriptor.

Thus the two-dimensional Fourier transform $\hat{f}(u_1, u_2)$ designates the contour outside of which such a two-valued function vanishes, and the Fourier descriptors for the contour result from two-dimensional Fourier analysis of the planar function.

Schwartz et al.'s finding in the inferotemporal cortex (which as we shall see in the following paper, takes advantage of the results of earlier

processing stages) of selectivity of neurons for 'frequency' (number of lobes) of two-dimensional 'Fourier descriptor stimuli' can be explained in terms of the Gabor representation by assuming that the cells in the primary visual cortex associated with a particular two-dimensional spatial frequency, say u , project to a certain set of cells, say PS_u in the peristriate cortex. Again, assuming linear summation of input, we can represent the activity of PS_u cells by the integral

$$\begin{aligned} \int_{R_u} Gf(p, u) dp &= \int_{R^2} \left(\int_{R^2} f(x) e^{-(x-p)^2} e^{+iu(x+p)} dx \right) dp \\ &= \int_{R^2} f(x) \left(\int_{R^2} e^{-(x-p)^2} e^{+iu(x+p)} dp \right) dx \\ &= \pi e^{-((u^2)/4)} \int_{R^2} f(x) e^{+i2ux} dx = \pi e^{-((u^2)/4)} \hat{f}(+2u), \end{aligned}$$

essentially the two-dimensional Fourier transform of the retinal image f , which (as shown above) corresponds to the Fourier descriptor for the contour specified by the Fourier descriptor stimulus. Since the Fourier descriptors of 'Fourier descriptor stimuli' defined by Schwartz et al., as obtained from Fourier transforms of functions of the form

$$e^{-(2\pi i/N)n_0 j}, \quad j = 0, \dots, N-1,$$

are delta functions $\delta(n - n_0)$ centered at frequency n_0 , the $(PS)_u$ cells of peristriate cortex would be expected to respond maximally when the two-component spatial frequency $u = (u_1, u_2)$, and the integer n_0 specifying the number of lobes of the Fourier descriptor stimuli were related by

$$u^2 = u_1^2 + u_2^2 = cn_0^2, \quad c = \text{constant of proportionality.}$$

Whitman Richards and Lloyd Kaufman (1969) have pointed out the relevance of this type of model to 'center of gravity' tendencies which occur for spontaneous optic fixations onto figures in the presence of

flow patterns of visual background noise (ground). They suggest that each pattern boundary:

' - sets up a wave [in the cortical receptive field matrix] which is propagated at a constant velocity. The point at which all waves converge together will be the apparent position of the whirlpool [the fixation point]. For simple figures with no invagination, this position will be the center of gravity of the figure. The positions of the whirlpool for more complex figures can be calculated as outlined by Blum (1967).'

Richards and Kaufman conclude by stating that they would like to consider the possibility that a 'center of gravity' analysis 'which regulates oculomotor activity may be occurring at the same time that the form of the pattern is analyzed ... Thus, it is the flow pattern and not the form of the pattern which is the principal correlate of the fixation behavior.' And we will add, the flow pattern in a natural setting is, of course, largely determined by movement. It is movement-produced flow patterns which initiate the emphases and de-emphases (conceptualized as vectors) which constitute selection within the feature matrix of the cortex. Note that *the direction of control is from the peristriate to the striate cortex*. Control can be initiated and effected via corticofugal efferents to subcortical loci, which in turn influence the geniculostriate system, or control may be exercised directly via extrastriate to the primary visual cortex via cortico-cortical connections.

Helmholtz (1924), in describing a well-known demonstration, had suggested that visuomotor control operates by virtue of what today we would call an open-loop, feedforward process. His demonstration involved pushing one's eyeball with one's finger as opposed to moving the eyes 'voluntarily'. The finger-pushing results in a sharp movement - a jumping about of the visual world. Helmholtz reasoned that two simultaneous signals went out, one to the eye muscles and a coordinating signal to a central location that 'informs about the first. Teuber (1960) called this second signal a 'corollary discharge'.

This corollary discharge is most likely initiated in the frontal eye fields, and their projections to the superior colliculus. In addition, the cerebellum may be involved in calculating the discrepancy between the 'image now' and the 'image then', which would be produced by the signal that moves the eye.

The visual perception manifold $R \times M$ provides the locus upon which the operations of the corollary discharge converge. As described by the observations of Richards and Kaufman (1969), their 'center of

gravity' fixations tend to coincide with foci of zero velocity in contour-directed flow patterns of visual noise in small figures (less than 5°). This indicates some sort of symmetry seeking by the saccadic control system. In another study involving angular patterns outlined by dots, Kaufman and Richards (1969) obtained the same fixation tendencies as with line figures. From this, they concluded that

' - it isn't simply the discontinuity of brightness at a corner which reduces the effect on fixation ... It might, therefore, be concluded that cortical representation of shape, rather than local properties of the shapes, is the determiner of fixation ... It is the already organized cortical representation of shape which governs fixation, rather than peripheral input per se' (1969: 85-88).

We suggest that the cortical representation of the retinal image by the Gabor transform on the visual perception manifold $R \times M$ provides the information used by the frontal eyefield-superior colliculus system to direct saccades, which in turn give continuously changing activity patterns on $R \times M$. The independent, simultaneous analysis of this flow of activity patterns on $R \times M$ by projection to and from the peristriate cortex (as described above) with summation of the resulting frequency domain primary visual cortex patterns, results ultimately in the perceived invariances which constitute an 'object'.

We follow Richards and Kaufman (1969) in considering that 'pattern recognition processing' and 'fixation tendencies' are simultaneous, reciprocal processes. Both Pitts and McCulloch (1947) and Richards and Kaufman (1969) have suggested that the superior colliculus does a 'center of gravity' analysis to direct saccades. Pitts and McCulloch proposed that the superior colliculus calculates the spatial coordinates (x, y) of the center of brightness of the visual field and moves the eyes to bring (x, y) to the 'origin of the visual axes' (1947: 142-146). Richards and Kaufman (1969: 83) also suggest that patterns of contours are 'translated into directional apparent movement', perhaps perpendicular to the contour, which orients the fovea to the point of zero velocity. They relate this type of analysis to Blum's (1973) 'symmetric disc coordinates', which are the two-dimensional coordinates of maximal discs centered on an axis equidistant from the boundaries of a given figure.

These calculations in terms of spatial coordinates of the visual field or retinal position are inordinately complicated. By contrast, the structure of $R \times M$ proposed here suggests that the saccadic system may

seek the center of maximal symmetry of the Fourier transform of the retinal image in the following sense. Recall that the activity pattern in each spatial frequency manifold M_p is the Fourier transform of the product of the retinal image with a Gaussian centered at p multiplied by a phase factor.

Corticofugal projection of each M_p to superior colliculus would permit selection by a peristriate-superior collicular system of the retinal point p such that the Gabor transform Gf on M_p has maximal symmetry with respect to an appropriate transformation group, called a selection group, denoted G . The source of such a transformation group may be input from peristriate cortex to the superior colliculus. Thus the role of the superior colliculus would be to select maximal symmetry in the spectral domain rather than to calculate spatial center of gravity coordinates in the spatial domain. Then gaze is directed so that the part of the retinal image that was centered on the point, say p_0 , such that M_{p_0} had maximal symmetry before saccade is centered on the foveola after the saccade:

$$(S_{p_0}f)(0) = f(p_0),$$

$$(S_{p_0}f)(x) = f(x + p_0),$$

where S_{p_0} denotes the saccade which translates the before-saccade retinal image f so that the after-saccade retinal image $S_{p_0}f$ has value at the foveola equal to the value of f at p_0 . The Gabor transform of the translated retinal image is:

$$\begin{aligned} (GS_{p_0}f)(p, u) &= \int_{R^2} (S_{p_0}f)(x) e^{-(x-p)^2} e^{iu(x+p)} dx \\ &= \int_{R^2} f(x + p_0) e^{-(x-p)^2} e^{iu(x+p)} dx \\ &= \int_{R^2} f(x) e^{-(x-p_0-p)^2} e^{iu(x-p_0+p)} dx \\ &= e^{iu(p-p_0)} \int_{R^2} f(x) e^{-(x-(p_0+p))^2} e^{iux} dx \\ &= e^{iu(p-p_0)} (f \mathfrak{N}_{p_0+p})^*(+u). \end{aligned}$$

Projection along the retinal fibre R_u over u (which we have assumed) is realized by linearity in the primary visual cortex and is described by

$$\begin{aligned} \int_{R_u} (GS_{\rho_0} f)(p, u) dp &= (\text{as before}) \\ &= \pi e^{-((u^2)/4)} (S_{\rho_0} f)^{\wedge}(2u) \\ &= \pi e^{-((u^2)/4)} e^{-2iu\rho_0} \hat{f}(+2u), \end{aligned}$$

a rotation of the Fourier transform of f by the phase factor $e^{-2iu\rho_0}$. Summation of the spatial frequency domain activity patterns projected to the primary visual cortex during each successive fixation would permit the construction in primary visual cortex of a maximally invariant activity pattern:

$$\sum_{\rho_0} \int_{R_u} (GS_{\rho_0} f)(p, u) dp = If(u),$$

a function of the original retinal image f in the frequency domain. An 'ideal' image could be obtained by execution of another Fourier transform on $If(u)$, and though such a transform is not necessary for object perception, it is necessary if behavior is to be appropriately directed toward the object. It is the precentral classical motor systems that are proposed to be involved in this additional transformation (Pribram et al. 1984). It is interesting to note in connection with Richards and Kaufman's patterns that the center of symmetry of the Fourier transform of open and closed squares and triangles is the same, since only two edges are needed to determine the center of symmetry of the Fourier transform of such figures.

More research is needed to determine what the symmetry group is. The basic hypothesis is that the object is defined by its invariance under the operations of a transformation group which acts through the superior colliculus. In particular, a rigid body is defined by its invariance under the group of translations and rotations of three-dimensional physical space, the so-called Euclidean group. Each movement (eyes, head, body) affecting vision corresponds to an element of the Euclidean

group acting via the colliculus on the distributed striate representation of the retinal image. Invariances that constitute the object are extracted by the various projections and summations discussed above.

8. Conclusion and summary

We set out to describe image processing in the visual system, utilizing some basic neurophysiological data. In contrast to other available theories, we have proposed that both sensory and cognitive operations address features already conjoined in cortical receptive fields. As even sensory perception depends on micrometer movement (i.e., adaptation occurs when the retinal image is stabilized), and as further processing stages are critically dependent upon movement, the theory emphasizes sensory-motor reciprocity in imaging and in object perception.

Mathematically, the conjoined feature space is described as a four-dimensional real vector space determined by the receptive field properties of position and spatial frequency sensitivity. Spatial frequency sensitivity when combined with orientation selectivity (Hubel and Wiesel 1959, 1962), can be plotted as two-dimensional spatial frequency components (DeValois 1984 seminar). These features responsible for processing spatial patterns had been shown by Barlow (1965), Pollen and Feldon (1979), and by Marcelja (1980) to be described by Gabor elementary functions.

Whereas retinal processing is best described in terms of convolving pupillary input with receptor activity (Rodieck and Stone 1965), the cortical process is found to be more appropriately modeled in Hilbert space. The Hilbert space activity is characterized by the inner product (which is the integral of the product) of the receptive field profiles of the cortical cells and the incoming sensory input signals. This produces, in the cortex, a highly redundant distributed representation of that input.

What has occurred between retina and primary visual cortex is a transformation into Hilbert space, not a filtering operation. The transformation is akin to that which characterizes the quantum domain in physics, and is thus in keeping with the suggestion by Gabor and Licklider in the quotation which introduced this paper.

Sensory-motor reciprocity becomes clearly evident in object percep-

tion. What is difficult to grasp in the approach taken here is the fact that a distinction between sensory image and perceived object must be maintained (since we can observe several images of a single object) and at the same time realize that both imaging and object perception are the resultants of processes going on in the manifold of receptive fields in the primary visual cortex: sensory input on the cortical manifold. Object perception, constancy, results from the selection operation of the perisensory motor systems (peristriate, frontal eye field and collicular) which, while producing variety in the sensory input, set additional processing limits on the same cortical manifold.

As in the case of imaging, the processing which yields object constancy is described to occur in Hilbert space. In this domain centers of symmetry, Fourier descriptors of contours, and the extraction of invariances by cross-correlations among patterns are more readily achieved than if such computations were performed in the spatial (and temporal) domains. The end result of these computations – object perception – is, however, readily retransformed by the execution of another Fourier transform into an 'ideal' image of the object. It is thus that, by movement, objectivity is extracted from the subjectivity of imaging.

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