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BRAIN AND THE PERCEPTION OF OBJECTIVE REALITY

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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 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; Norman, 1964; Treisman, 1969; Deutsch & Deutsch, 1963) have ultimately opted for a combination or compromise 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 deleted). She surmises, as does almost everyone else, that these elementary processes reflect unitary functions of aggregates or "channels" of neurons which can be characterized according to these elementary processes. This paper reviews additional data that suggest an alternate explanation of Treisman's results. The data come from experiments involving the neurological as well as the behavioral level of inquiry. Some of these

experiments are based on the use of Treisman's paradigm and thus bear directly on the issues she has posed.

In a sense this alternative explanation is more radical than Treisman's. In agreement with her interpretation, one aspect of attention is considered to be a centrifugal 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 five major categories. First, results using the Treisman paradigm are presented. These results show which systems of the monkey and human brain are critically involved in processing conjunctive, and which are involved in processing disjunctive displays. Some data are included that lead to a discussion of what might be the essential differences between conjunctions and disjunctions with respect to differences in their processing.

Second, 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 to already 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. These experimental results are discussed with respect to others which deal with unit responses of other regions of cortex which have been shown by lesion studies to be involved in visual processing.

Third, 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 fields are elongated to show an inhibitory side-band.

Fourth, the suggestion will be offered that perceptual constancies are developed as a function of the 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.

Fifth and finally, the role of attention of the intrinsic "association" cortex of the posterior cerebral convexity and that of the frontal lobe is taken up. Results are reviewed which demonstrate that electrical stimulations of this cortex modify the receptive field properties of neural units in the primary visual receiving system. The pathways involved are described. These data are taken to suggest that attention involves the development of a sensory set which is an extension and differentiation of the motor processes determining object constancy.

1. Disjunctive and Conjunctive Displays

Bolster, Ruff, Cutcomb, Harrington and Pribram (in preparation) used a modification of Treisman's displays to test both humans and monkeys. Reaction times were monitored in humans; in monkeys, event-related electrical activity was recorded by means of concentric bipolar electrodes implanted in the striate visual-receiving cortex, the peristriate cortex, the intrinsic association cortex of the inferior gyrus of the temporal lobe, as well as others implanted in the frontal intrinsic and precentral cortex. Reaction times were forfeited in monkeys in favor of a time-out procedure that would separate sufficiently the onset of the stimulus display from the occasion of the response so that stimulus-produced and response-produced brain potential changes could be clearly distinguished. In most studies the subject had to select a green square from a set of colored squares

and diamonds, each of equal contour and luminance when compared to the rewarded cue. Rewards were banana flavored pellets for the monkeys and a "correct" signal for humans.

The cues were displayed on a set of nine translucent panels which could be individually pressed by the monkeys restrained in a monkey chair. Humans sat in an arm chair which had a modified calculator keyboard on one of the arms to serve as a response panel. The display was under the immediate control of an Apple II microprocessor; behavioral and electrical brain recordings were effected by the PDP 11/34. The entire procedure was under the control of version VI of the Automated Discrimination Apparatus for Discrete Trial Analysis (DADTA VI) which in one form or another has been successfully used for over 20 years (see Pribram, Gardner, Pressman, & Bagshaw, 1963; Pribram, 1969; Drake & Pribram, 1976; Cutcomb, Bolster, & Pribram, 1981).

The following display combinations were used in the experiment described here: a) a simple disjunctive display in which the green square had to be identified in a background of eight red diamonds; b) a more complicated disjunctive display in which the green square had to be identified in a background of red diamonds, white circles and blue triangles (this was the only display in which the contour of the cues was not held identical); c) the conjunctive display in which the green square had to be identified in a background of green diamonds, red diamonds and red squares. The displays lasted for 100 msec; intertrial interval was never less than 3-1/2 seconds, but otherwise determined by the subject who self-initiated each trial. From trial to trial the cues were positioned among the nine display panels in pseudorandom order. All subjects had reached an asymptotic level of behavioral performance before brain electrical recordings were initiated.

Results of these experiments were as follows. In *humans*, Treisman's observations that reaction times are longer in the conjunctive than in the disjunctive task were confirmed. Two interesting additional observations were made: reaction times in the difficult disjunctive task were longer than in the easy disjunctive task, although not as long as in the conjunctive task. Further, in the conjunctive task but not in either of the disjunctive tasks many errors were made and these occurred for the most part on the left display/response

panels. Thus mistakes in conjoining were made mostly "by" the right cerebral hemisphere.

The studies with monkeys also produced some surprises. Pribram (1980) had predicted that the automatic parallel processing—which Treisman had suggested to operate in the processing of disjunctive tasks—would be a function of the posterior convexity of the cerebral hemispheres including the intrinsic association cortex, while the controlled serial search necessary to process conjunctive displays would devolve on the frontal intrinsic cortex. These predictions were only partly confirmed: automatic parallel processing of disjunctive displays involved only the sensory-motor projection systems of the brain: this was shown by the fact that different (simple vs difficult) disjunctive displays evoked different event-related potential changes recorded from striate and peristriate visual cortex but not from the posterior or frontal intrinsic association cortex. Conversely, serial search of conjunctive displays produced no changes in primary sensory-motor projection recordings but did produce changes in potentials recorded from both the posterior and frontal intrinsic association cortex.

Other experiments have allowed a dissociation to be made between the brain electrical activity evoked in the primary sensory projection cortex, the precentral motor cortex, and the posterior intrinsic association cortex of the temporal lobe. In one series of experiments (Rothblat & Pribram, 1972; Pribram, Day & Johnston, 1976; Nuwer & Pribram, 1979; Day & Pribram, in press) four stimulus displays were used: each display was made up of two cues, each of which combined a shape (a square or diamond) with a color (red or green). On any run (a minimum of three days of 100 trials each) one feature (either square, or circle, or red or green) was reinforced irrespective of the other features with which it was displayed. Thus the brain electrical activity could be analyzed with respect to the task on any run (i.e. the reinforced feature) and this analysis could be compared with analyses centered on features per se or location (left panel or right panel) of response per se. Further, the analysis was made both forward from the moment of stimulus onset and backward from the moment of response. These earlier studies as well as the current ones showed that the brain electrical activity evoked in the primary sensory receiving areas was for the most part,

though not exclusively, determined by the features in the stimulus display irrespective of whether they were being reinforced. Brain electrical activity recorded from the precentral motor area was for the most part, though not exclusively, determined by the location of the response, irrespective of whether it was being reinforced. [There are event related potentials from some electrode sites within these primary sensory and motor projection areas from which recordings did show reinforcement related potential changes in all of these studies and more specifically when recordings were made with small macroelectrodes (Pribram, Spinelli & Kamback, 1967) and microelectrodes (Bridgeman, 1982).] The electrical potential changes evoked in the posterior intrinsic (temporal lobe) cortex were primarily related not to the cues displayed nor to the response emitted but to the cognitive operations (categorizing, pigeon holing) (Broadbent, 1974) evoked by those cues which were reinforced. In the results of these experiments there was no clear and consistent involvement of the electrical activity recorded from the frontal intrinsic association cortex except on occasions when the task was novel or the reinforcing contingencies were shifted between runs. This relationship to novelty is confirmed in another current series of experiments (Bolster, Harrington, Tunis & Pribram, in preparation) in which runs of stimuli are differentiated by the probability with which two cues appear in a task in which the cues are irrelevant. Thus in one run a blue circle appears on 90% of the trials while a red diamond appears sporadically on 10%. Then, on another run the appearance of cues is reversed—now red diamond makes up the bulk (90%) of the presentations while blue circle is pseudorandomly interposed (on 10% of the trials). In this experiment dramatic changes occur in the recordings made from frontal cortex whenever the low probability cues are presented. No such changes appear in the recordings made from posterior intrinsic cortex except near the polar tip of the temporal lobe which is intimately related to the frontal cortex in function (Fulton, Pribram, Stevenson & Wall, 1949; Pribram & Bagshaw, 1953) by virtue of its connection via the uncinate fasciculus (McCulloch, 1944; Kaada, Pribram & Epstein, 1949; Pribram & MacLean, 1953).

These results indicate that the frontal intrinsic cortex becomes especially involved when changes in situations occur, a conclusion supported by the results of neurobehavioral studies involving lesions

(Pribram, 1959, 1962; Luria, Pribram & Homskaya, 1964; Konow & Pribram, 1970; Brody, Ungerleider & Pribram, 1977; Brody & Pribram, 1978). Response to change is a function of processing a novelty/familiarity dimension in which the probability of the occurrence of the non-familiar is processed within the context of the familiar. Frontal cortex has been shown to be necessary to setting such contexts both with regard to spatial (Anderson, Hunt, Vander Stoep & Pribram, 1976) and temporal variables (Pribram & Tubbs, 1967; Pribram, Plotkin, Anderson & Leong, 1977).

By contrast, the result of the current (and to some extent, the earlier) experiments indicates that the serial search involved in processing conjunctive displays (defined by the markedly increased reaction times of humans on the conjunctive task) is a function of the posterior not only the frontal intrinsic association cortex—bilaterally in monkeys and left hemispheric in man. In fact the changes in electrical brain activity related to (serially) processing conjunctive displays are considerably more consistent (and show greater amplitude) for posterior than for frontal electrode placements. Thus a common prediction that involves primarily frontal cortex in serial processing (see e.g. Pribram, 1954, 1958, 1962, 1978; and Fuster, 1980) is *disconfirmed*. Once again this result is consonant with those obtained when frontal resections have been made (see Anderson et al.; Brody & Pribram, 1978). All intrinsic cortex but especially that of the *posterior* cortical convexity serves serial processing.

The results obtained in the current series of experiments also suggest that one important aspect of processing conjunctive displays, though by no means the only aspect, concerns the number of discriminable features in the display. Reaction time does increase as a function of the number of features disjunctively displayed in these tasks, contrary to the results obtained using simpler-for-humans alphanumeric "same-distractor" and "different distractor" sets by Shiffrin and Schneider (1977; Schneider & Shiffrin, 1977). Nonetheless, both the error score data on humans and the electrical brain recordings made on monkeys indicate a dissociation between the processing of disjunctive and the processing of conjunctive displays suggesting that factors other than the number of features displayed operate to make conjunctive displays more difficult to search.

There is thus nothing in these results that would contradict the

essentials of Treisman's bottom-up model of the object perception process. What is added is that the constructive aspects of conjunctivity depend on the operations of the posterior intrinsic association systems of primates—especially those of the left hemisphere in man.

Nonetheless, a slight misgiving arises from the fact that easy disjunctive displays are automatically processed so completely by the primary projection cortex.¹ In a sense, disjunctivity is as much if not more of a characteristic of object identification than is conjunctivity. From studies in form perception (e.g. Hochberg, 1968) and movement perception (e.g. Gibson, 1965; Johansson, 1973) there is no reason to suspect that object perception depends essentially on serial processing—quite the contrary, a great many objects can be simultaneously made out of configurations of moving dots. It is this phenomenon that has given rise to the view that perception can be direct, and need *not* be constructional. How then are we to reconcile the indications for a serial bottom-up process with these top-down observations?

2. Classification of Receptive Field Properties

Reconciliation 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 1950's, cells had been assigned to categories such as concentric, simple, complex, and hypercomplex (1959, 1962). In a series of studies begun in our laboratory during the mid 1960's (Spinelli & Barrett, 1969; Spinelli, Pribram & Bridgeman, 1970; Phelps, 1973, 1974) 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 result of these and subsequent experiments (Pribram, Lassonde & Ptito, 1981) was the fact that each cell in the primary visual projection cortex has *multiple* selectivities and that the cells differed in the combinations of these selectivities. 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, Finlay and Volman (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 me repeat this point once again for it is critical to any understanding of the issue of whether object perception is constructed by conjoining features which are initially isolated or whether features are abstracted from objects. 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 selective, directional selective, 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 selectively tuned to acoustic frequencies (Spinelli, Starr & Barrett, 1968) and groups of neurons and even single cells show late responses (ca 300-400 msec after a stimulus is presented) only to a rewarded cue in a problem solving situation (Pribram et al., 1967; Bridgeman, 1982).

This conjoining of properties in a receptive field of a neuron does not mean however that each neuron represents those conjunctions which characterize any particular object. No pontifical "grandfather" or "grandmother" cell has been found 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, the perception of objects must be constructed much as Treisman suggests—but not exactly. Object perception results not only from processes which *conjoin* properties but which simultaneously *select* these properties from a pool in which they are already to some extent haphazardly conjoined.

A simultaneous selection/conjunction would account in a novel fashion for the distinction between objects 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—objects for bottom-up; objects—elements for top-down. The sensory-motor reciprocity model being developed here differs from both these alternatives in that *both objects and elements are formed from some more primitive matrix in which conjunctions already abound. Input to this matrix from the senses "abstracts" sensory qualities; perception of objects are formed by the operations of the motor 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/conjunction 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 & 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 & Hubel, 1965a, 1965b; Pettigrew, 1974). And there is some additional tuning that can occur as a result of specialized environmental inputs (Hirsch & Spinelli, 1970; Blakemore, 1974). In the context of object perception these data can be taken to indicate once again 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 my 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, Kuhnt & Benevento, 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 perceptual process appears to

reflect invariances in the relationship between input and receptor variables and cortical system variables. The invariants can be perceived either as properties of the receptor surface or the properties can be projected onto the environment.

What determines projection? Bekesy's ingenious experiments (1967) with artificial cochleas hold the clue to an answer. By lining up five vibrators on one's forearm, Bekesy 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. I feel the paper on which I am writing at the tip of my 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. Constancy and the Motor Systems of the Brain

It is the importance of movement to object perception that provides the key to an answer to the second question posed earlier: how does the selection/conjunction process proceed to emphasize some features to the exclusion of others? Try the following demonstration. Have someone touch you with a pencil or other object. You feel the touching, rubbing, pressure, etc. These are elementary qualities of tactile sensibility. Now grasp and rotate the same object in your palm by active manipulation. Suddenly the object, e.g. a pencil, has materialized!

There is an intermediate perception that can be achieved when the passive touching is performed in a reasonably regular fashion. Thus an X or a T may be identified as a pattern—somewhat intermediate between a passive sensation and an object. Auditory perceptions are based on the relative frequencies of vibratory stimuli—

movement in time is involved. It is likely that a similar mechanism based on relationships among spatial frequencies, one of the feature properties of the receptive field matrix of the visual cortex (Campbell, Cooper & Enroth-Cugell, 1969; Campbell & Robson, 1968; DeValois, Albrecht & Thorell, 1978a, 1978b; Glezer, Ivanoff & Tscherbach, 1972, 1973; Maffei & Fiorentini, 1973; Movshon, Thompson & Tolhurst, 1978a, 1978b, 1978c; Pollen & Taylor, 1974; Pribram et al. 1981; Schiller et al. 1976). In this case, movement is provided by the constant tremor-like displacements of the eyeball. When an image is artificially stabilized on the retina, pattern vision ceases within seconds (Ditchburn & Ginsborg, 1952; Riggs, Ratliff, Cornsweet & Cornsweet, 1953; Heckenmueller, 1968).

How are such patterns generated? Recall that direction of movement and orientation as well as frequency characterize the spatial properties of the receptive field network. These properties can combine into geometric (Fourier) descriptors which designate contours of patterns. Desimone (1980) has analyzed the spatial frequency spectra of receptive fields in the inferotemporal cortex and decoded them in terms of Fourier descriptors: a variety of stick figure contours emerge. The inferotemporal cortex does more than develop contours as we shall see below, but contours are a prerequisite to its function in object discrimination and choice. Where contours are developed—in the striate or prestriate cortex—is at present unknown.

Pattern perception based on contours is not identical with object perception however. *The characteristic which identifies the perception of objects is constancy across changes in the sensory patterns they elicit. Constancy is achieved by a connectivity which allows the variety of images and their contours which characterize an event to be correlated so that only invariances remain. The averaging procedure used in analyzing event related brain electrical potentials is an example which extracts constancies from noise. Edelman and Mountcastle (1978) have detailed a model of connectivities which achieve constancies by eliminating irrelevant information. Mathematically such "degenerative" procedures are non-linear and irreversible. An important question for research is whether non-linearities are introduced at the object level of processing. Sensory-motor reciprocity theory is based on the suggestion that constancies are developed by the*

functions of motor programs initiated in systems interwoven with and adjacent to the sensory projections in the brain. 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 the Edelman type of degenerative connectivity for the more locally symmetrical connectivities (Barlow, 1981; Pribram, 1960) of the projection cortex *per se*. This is especially true in the somatic modality. But to some extent it is also true of the other senses (see Pribram, 1982, for review). Thus, electrical excitation of the peristriate cortex (which surrounds the visual projection area) of monkeys produces eye movements and the question arises whether perhaps object constancy in the visual mode is a function of this visuomotor system. No immediate answer can be given but a beginning has been made toward such an answer. In one experiment (Ungerleider, Ganz & Pribram, 1977) size constancy was shown to depend on this system. After extensive damage, monkeys respond exclusively to the retinal image size of an object, ignoring the contextual environmental and organismic factors responsible for constancy.

Sperry (1947), Held (1968), and Festinger (1967) have each 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 the environment—whether with his eyes, hands or whole body.

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

Once this has been accomplished, the variety of movements stabilizes the spatiotemporal location of the object, establishes a perimeter around the imaged figure and explores the area within that perimeter. Recall that the Treisman experiments were undertaken in order to distinguish parallel (automatic) from serial (search) processing. And recall that in our evoked response experiments that parallel processing was shown to be a function of the sensory-motor systems of the brain. Helmholtz, in a well-known demonstration, had suggested that parallel processing results in 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. Voluntary movement stabilizes that world. Helmholtz reasoned that two simultaneous signals went out, one to the eye muscles and a corrective signal to a central location that counteracts the first. It is as if the screen upon which the retinal image projects is moved simultaneously with the retinal image. Teuber (1960) has called this second signal a "corollary discharge."

The origin and destination of this corollary discharge is as yet unknown despite several studies to locate them. An excellent remaining possibility is that the cerebellum is somehow involved in calculating the discrepancy between the "image now" and the "image then" which would be produced by the signal that moves the eye.

Meanwhile, eye movement studies (e.g. Mackworth & Otto, 1970; Stark & Sherman, 1957) have demonstrated both a perimeterizing and a concentration of eye fixations on "informative" aspects of an image. Blum (1973, 1974) and Gauthier (1977) and others (Schwartz, Desimone, Albrecht & Gross, in press) have devised precise mathematical models which can extract geometric (e.g. Fourier) descriptors of shape (invariances) from such figure-ground perimetry. Whitman Richards and Lloyd Kaufman (1969) have pointed out the relevance of this type of model to "center of gravity" tendencies to 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 imagination, 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).²

They 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 I 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 wave fronts and vectors) which constitute selection within the feature matrix of the cortex. Note here that the direction of control is from the peristriate to the striate cortex. Control can be effected via corticofugal efferents to subcortical loci which in turn influence the geniculo-striate system, or control may be exercised directly via peristriate to striate corticocortical connections.

As in the Richards and Kaufman experiment, flow patterns can originate in the environment or, as so often occurs naturally, they are initiated by movement of the organism. Movement can consist of directional displacement or it can be oscillatory as in the spontaneously occurring eye movements which prevent the fade out which occurs when retinal images are experimentally made stationary. In either case, the peristriate cortex becomes involved in fixating the "whirlpool" of the flow patterns.

In the olfactory mode such oscillatory movements are produced by respiration. As Freeman (1981) has elegantly demonstrated, oscillatory movements create the formation of wave packets which interact in terms of their spatial frequency. Both Freeman (1981) and Grossberg (1981) have presented mathematical models of the development of perceptual constancies based on such interactions.

That illusory feature conjunctions due to faulty vector calculations dependent on movement might occur comes therefore as no surprise.³ Rather, it is one of those awesome masterpieces of the design of nature that conjunctions are ordinarily veridical (i.e. validated consensually and by others).

5. Attention and the Intrinsic Association Cortex

Note, however, that in our event related brain potential experiments (reported in Section 1) serial search was related to the intrinsic association systems of the brain, not to the sensory-motor systems which were shown involved in parallel automatic processing. Serial search requires a motor program, an active central motor-like (cerebrofugal) process which can be considered an extension of the type of movement involved in fixating the "center-of-gravity" or "whirlpool" of a flow pattern. Now however, instead of a figure-ground relationship it is a relationship among alternative figures that must be "fixated." Eye movement studies (Bagshaw, Mackworth & Pribram, 1972) have shown that in the absence of posterior intrinsic association cortex visual search becomes disrupted. This may be related to the fact that behavioral choice among alternative visual stimuli is drastically impaired (see e.g. reviews by Pribram, 1954, 1958, 1974; Gross, 1973; Mishkin, 1958). In one experiment (Pribram, Spevack, McGuinness & Blower, 1980) it was shown, using Response Operator Characteristic (ROC) curves, that such lesions enhance the amount (flow?) of noise in which the stimuli are processed. Wilson (1975) has shown that the impairment of choice among alternatives resulting from lesions of the posterior intrinsic cortex impair categorization. She has suggested on the basis of her experiments that categorization of alternatives depends on the "adaptation level" to those alternatives. "Adaptation level" and "noise" are related concepts—perhaps the evidence for increased noise in the system can be taken as the basis for failures to categorize and thus respond appropriately to alternatives. In the language of cognitive operations, categorizing or pigeon holing (Broadbent, 1974) is thus shown to depend not on stimulus filtering nor on response selection but on vectors operating in the brain's phase space. This was demonstrated in one experiment in which event related brain electrical potentials were recorded from occipital, temporal and precentral sites and analyzed in the frequency domain. During performance of categorizing tasks the phase of brain electrical activity led in the occipital region when analyzed with respect to the stimulus presented, in the precentral region when analyzed with respect to panel pressing, but in the temporal region when analyzed with respect to the rein-

gained by such preprocessing so that constancy is achieved in the presence of flux whether that change originates from the organism or from its environment.

Sensory-motor reciprocity is therefore necessary for object constancy and selective attention in the face of an everchanging organism-environment relationship. Initially perhaps this necessity was inaugurated by the motility of animals. Currently, the mechanisms developed to handle the problems posed by motility have made possible perceptual constancy and selective attention to the complex of conjunctions which we identify as objects.

FOOTNOTES

1. Treisman, as well, notes and presents evidence for parallel automatic processing of groups. In a personal communication she states that "I believe that we can attend to groups as well as to single items when a group behaves in correlated ways; the group is then treated as one object"—see Treisman, 1982. The neurophysiological question that is raised, of course, is how "behavior" in correlated ways "can be" perceived—i.e. what might be the mechanisms that allow correlations to be computed. It is this question which section 4 attempts to address.
2. The formation of such "whirlpool" stabilities in a variety of far from equilibrium physical and biological conditions has been amply documented by Prigogine (1980) and is the basis for the development of self-organizing (autopoietic) systems (Varela, 1979).
3. Illusory conjunctions of "central" origin can be of an even more bizarre nature as in a subject under hypnosis recently reported by Hilgard (1981). The hypnotized subject was told that post-hypnotically he would see the person sitting in a chair on his right also occupying the chair on his left. The subject did so observe and had great difficulty in finding out which was the illusory until he hit on the device to silently instruct both images to lift their right arm. Only the illusion obeyed.

4. By "wave-forms" is meant a propagated excitatory and/or inhibitory neural activity which can be recorded as event-related slow potentials and analyzed by means of wave equations. The origins of propagated excitation/inhibition are to be found in patterns of nerve impulses and in the pre and post synaptic graded potentials they engender.

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