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How Does the Striate Cortex Begin the Reconstruction of the Visual World?

Abstract. *The striate cortex transforms the topographic representation of visual space in the lateral geniculate body into a Fourier transform or frequency representation at the complex cell level via the intermediary simple cell stage of "strip integration." Each of these three stages contains essentially the same amount of information, which expresses a conservation of information principle; however, the form of the information is changed. In the transform domain, invariant descriptions of visual objects can be derived to serve as the basic sets required for pattern recognition and memory. We believe that our experimental and theoretical findings are fundamental for understanding the functional organization of the striate cortex.*

Thirty years ago Lashley (*1*) considered the problem of how we see an object as the same object regardless of its position and apparent size. He considered the problem of "stimulus equivalence" as the most elementary problem of cerebral organization and doubted that any progress toward a genuine understanding of nervous integration would be achieved until this problem was solved.

In searching for some invariant description of a visual object, the physiologist is confronted by neurons all along the visual pathways which respond to many variations in stimulus parameters by increases or decreases in firing rate. Kuffler (*2*) and others (*3*) have found that the receptive fields of retinal ganglion cells are organized in a concentric manner; "on" center cells are excited as a function of the size, position, and relative brightness of a test spot within a circular "center" and are inhibited by stimulation over a concentric "surround." Cells with "off" centers and "on" surrounds are oppositely affected. In the lateral geniculate body the receptive field organizations are also concentric, but the topographic representation of visual space becomes more discrete (*4*).

Hubel and Wiesel have shown that layers IIIb and IV of the striate cortex of cats (*5, 6*) and monkeys (*7*) contain sets of "simple" cells that receive information via the geniculo-calcarine radiations and are either excited or inhibited by slits of light selectively oriented and placed in the visual field. Within the cortex each region of visual space is " . . . represented over and over again in column after column, first for one receptive field organization and then another" (*6*). It has not been known what particular advantages are gained by such geometrical and angular organization of the receptive fields, nor how the brain processes the received data to provide invariant descriptions of visual objects at any moment in time.

We carried out experiments in an attempt to find any invariant properties of simple and complex cell responses (in terms of cell-firing rate and response latency) as we varied such stimulus parameters as size, position, and relative brightness. We recorded from 19 cats, each initially anesthetized with sodium thiopental (30 mg/kg, intraperitoneally) with supplemental small doses of Brevital as required. Significant eye movements were prevented by slow intravenous drip of gallamine triethiodide and succinylcholine chloride (*8*). Respiration was maintained with a Harvard pump. Atropine sulfate (4 percent) was used for mydriasis and cycloplegia. Phenylephrine HCl (10 percent) enabled retraction of the nictitating membrane. Corneal contact lenses were selected with the aid of a streak retinoscope to focus each eye at 1.5 m, where a blackboard holding a mat white poster board was placed. A 4-mm artificial pupil was placed before each eye to limit light transmission to the center of the lens.

Light stimuli of various sizes and shapes were projected onto the board from a Leitz Prado universal projector with the aid of a rotatable slit device (*5*). A Compur 3 electronic shutter permitted delivery of rectangular pulses of light for set durations, and the diaphragm settings were changed to produce light stimuli of variable intensity. Background and stimulus light intensities were measured by using an SEI exposure meter. Tungsten microelectrodes were used for extracellular recording (*5*). Recordings were taken from the right striate cortex, and stimuli were presented to the left eye with the right eye covered. In presenting stimuli to one eye, we have reduced the general problem of binocular vision to that of resolving a two-dimensional brightness distribution. A Synax histogram computer 100 (Synax Biomedical) was used to construct poststimulus histograms either on-line or from tape-recorded data.

After each receptive field was mapped, ten stimuli were presented at 5- to 10-second intervals for a number of stimulus sizes and positions, and at each of a number of intensity steps covering a range of 2 logarithmic units above background. For any fixed size of spot or slit within the excitatory field center of simple cells, or in any position across the receptive field of complex cells, the neuronal firing rate was found to increase linearly with the logarithm of the relative light intensity (Fig. 1A). Complex cells respond maximally to slits of a specified width and orientation equally well in all positions across the receptive field (*6*). Elongation of a spot or slit length within the field center of a simple cell or along the preferred direction of a complex cell also caused increases in firing rate, as expected (*6*). However, because of the dual dependence of firing rate upon both relative brightness and area, the data from a single simple cell cannot provide a unique representation of either size or brightness.

Further processing must be carried out until a "reconstruction" (by which we mean the derivation of an invariant description of a visual object) has been achieved in some set of neurons. This information may then serve as a unique determinant for further concept elaboration, comparison with the memory, or other behavior. The data set available at the simple cell stage (Fig. 1B) essentially (*9*) corresponds to data sets

used in a number of fields of endeavor, perhaps most notably in radio astronomy (*10–13*), to specify a solution for a two-dimensional brightness distribution. The radio astronomer uses a long and narrow aerial fan beam to scan across an arbitrary celestial brightness distribution in a number of position angles. The angular resolution of the reconstructed brightness distribution will be equal to the narrow dimension of the elongated apertures doing the strip integrations, provided only that data are available at a sufficient number of orientations or "position angles" (*11, 12*). These scans, which are carried out sequentially for technical reasons, provide the same kind of information that the brain receives simultaneously from adjacent sets of simple cells in vertical, horizontal, and oblique position angles (Fig. 1B). Other similarities in eliminating the surround or background radiation also exist (*14*).

There are at least two mathematical methods by which the two-dimensional brightness distribution can be uniquely specified or extracted from the information contained in a number of its strip integrals. Both of these methods lend themselves well to numerical techniques, and both have been used successfully in radio astronomy (*11–13*). We believe that the available evidence suggests that the brain uses a method similar to that originally described by Bracewell (*11*) and developed more recently by Taylor (*12*). This method requires computation of the Fourier transform of each of the sets of data $[v_i]$, $[h_i]$, and $[o_i]$, and the papers by Bracewell (*11*) and Taylor (*12*) show that these data sets are sufficient to specify the Fourier transform of the original brightness distribution. A Fourier transform expresses the relation between any waveform or amplitude distribution and its frequency spectrum (*15*). For a two-dimensional

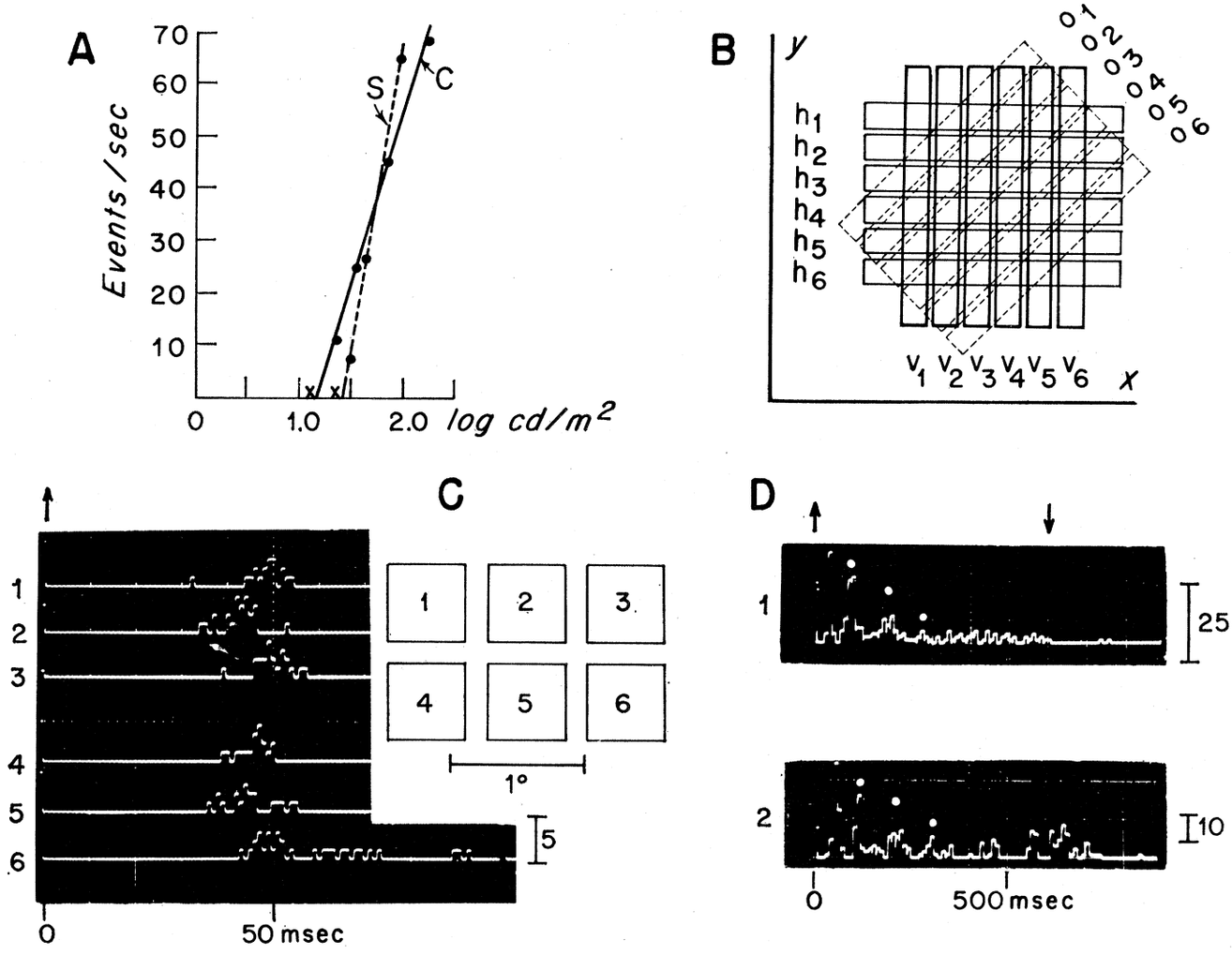

Fig. 1. (A) Average unit response per second for the first 100 msec of response (averaged for ten responses) for a simple cell (*S*) and a complex cell (*C*). A square 20 by 20 minutes of arc at the intensities indicated on the abscissa was used to stimulate the simple cell within its vertically oriented receptive field center, 2 deg by 20 minutes of arc. Stimulus area for the complex cell was 30 by 30 minutes of arc, and the receptive field covered a 3 by 3 deg area. Background illumination for each cell indicated by **X**. (B) Adjacent simple cells selectively respond to stimulation within such receptive field centers as v_1, v_2 . . . v_6. The same region of space is also covered by simple cells with receptive field centers favoring horizontal (h_1 to h_6) and oblique (o_1 to o_6) orientations. In the cat, space is scanned by sets of obliques every 10 to 15 deg in rotation apart (*6*). In radio astronomy one long and narrow aerial beam is used to scan across positions such as v_1 to v_6 and o_1 to o_6 sequentially. (C) Poststimulus histogram (bin width, 1 msec) shows ten responses of a complex cell for stimulation as close as was technically possible to points 1 to 6 as indicated in receptive field insert. Background level is -1.25 log cd/m^2. Stimulus brightness is 1.65 log cd/m^2. (D) Poststimulus histogram responses (bin width, 10 msec) of a simple cell (1) and a complex cell (2) to discrete light stimuli 500 msec long. Dots are placed over the first three secondary peaks occurring at alpha frequency.

distribution of brightness, the Fourier transform represents the distribution of information in the spatial frequency domain. The brightness distribution is effectively decomposed into a set of sine wave gratings at all possible position angles and covering a wide range of cycles per degree of visual angle.

Three of the principal attributes of a Fourier transform are present in the transformation of information from the simple to the complex cells. (i) In the transform or "frequency" domain the amplitudes of the Fourier components are translationally invariant (*16*). For a visual object describable as a brightness distribution in two dimensions, the amplitudes at each and every spatial frequency (*17*) are independent of the position of the object. The work of Hubel and Wiesel (*6*) demonstrates that the responses of a complex cell to a given slit width are independent of the position of the slit, so long as it is oriented in the preferred direction and is within the overall receptive field of the cell. It must also be established that complex cells can encode information according to both (ii) spatial frequency and (iii) "phase."

Rybicki suggested to us that phase information might be coded as a function of the latency of the responses of a complex cell as a function of stimulus position. Phase change as a function of position would be coded by the delay of neural pulses with respect to the shortest possible latency. Our data have confirmed Rybicki's suggestion. He has also suggested that phase shifts would lead to interference when more than one slit is presented.

Complex cell responses were tested as a function of the position of stationary small spots or slits moved sequentially across the receptive field. The primary peak in each poststimulus histogram was found to vary systematically with stimulus position over a total range of about 10 msec. In some cases the latency was briefest at one receptive field border and progressively increased as the slit was moved closer to the opposite border. At the latter position, the primary peaks in the histogram were shifted by about half the normal interpeak spacing. In other complex cells (Fig. 1C), spots or slits in the center of the receptive field gave the shortest latency response; the latency of responses on either side of the center increased until responses at the border were occurring in-phase with each other but out-of-phase with the center responses. Summation of responses occurs as slits are almost vertically presented through points 1 and 4, 2 and 5, or 3 and 6 of Fig. 1C, where the upper and lower responses to small spots are more or less in-phase.

We also inquired as to whether the brain has access to any timing mechanism to allow for the dispersion of phase information for ocular fixation times much longer than the interval (often about 20 msec) occupied by the primary peak. Evidence suggests that an excitability cycle in the alpha frequency band (8 to 12 per second) may provide this mechanism. Unit responses of simple cells (Fig. 1D, top) and complex cells (Fig. 1D, bottom) may be "pulsed" by each stimulus first at about twice and then at or slightly above the alpha frequency. These findings are clearest for the first three or four peaks. The results do not depend upon anesthesia because similar pulsing may be seen in many single records from unanesthetized cats (*18*) and monkeys (*19*). The periodic increases and decreases suggest that the visual system may utilize finite interval scanning (*20*). The identification of stimulus-linked pulsing at alpha frequencies in individual neurons selectively responding to properly placed discrete stimuli confirms Bartley's hypothesis (*21*) that alpha activity may exist in individual cells independently of a grossly recordable alpha rhythm. This was implicit from early work of Adrian (*22*) and Jasper (*23*). Our data suggest (but are not yet enough to prove) that the secondary peaks disperse phase information over 100-msec frame intervals.

An indication of a spatial frequency selectivity is implicit in the work of Hubel and Wiesel, who found that there is a most effective slit width for each complex cell (*6*). Our work suggests that optimum slit width or spatial frequency is related to the rate of change of phase with distance across the receptive field. Widening a slit beyond an optimum width leads to a decreased response (*6*). However, if slits are presented simultaneously through points 1 and 4 and points 3 and 6 (Fig. 1C), thus comprising a two-slit grating, we would expect their responses to be in-phase and therefore to add. The distance over which in-phase and out-of-phase responses would produce cancellation would determine the selected spatial frequency for a restricted region of visual space.

Campbell *et al.* (*24*) have demonstrated that there are cells in the cat striate cortex which are highly selective to the spatial frequency of gratings over a wide range of spatial frequencies. Certain cells such as c 24/6 in their figure 6b show the sharp cutoff on each side of the preferred spatial frequency that would be expected according to a model based on Fourier theory. Campbell and co-workers (*17, 25*) have also demonstrated psychophysically that human visual thresholds are directly related to the spatial frequency components of the visual field. Their findings are sufficient to imply that the brain has at its disposal the two-dimensional Fourier transform of the presented brightness distribution. We believe that the complex cells provide the basis for the spatial frequency selectivity.

Thus the three requirements of a Fourier transform have been met at the complex cell stage. Although it remains for some formal prediction of this model to be demonstrated quantitatively at the complex cell level, the psychophysical studies of Campbell and Robson (*17*) are in the main so consistent with their predictions according to Fourier theory and our findings that we feel it is unlikely that any fundamental discrepancies will occur.

The transformations that have occurred in the visual system at the complex cell stage effectively express a conservation of information principle, and probably answer the question raised in the title. The striate cortex transforms the topographic representation of visual space in the lateral geniculate body into a Fourier transform or spatial frequency representation at the complex cells via the intermediary simple cell stage of strip integration. Each of these three stages contains the same amount of information, but the form of presentation is changed.

The reconstruction in the frequency domain is just beginning, because each complex cell is tuned to one spatial frequency at one position angle for a restricted region of visual space. A unique and complete description of an object is not achieved until some form of "read-out" of the information in all complex cells over the involved region of visual space is established. Because the brain carries out very rapid pattern

recognition despite the very limited firing rate of individual neurons, it must construct its informational equivalent of a Fourier transform of visual space over a number of parallel circuits. Whether neurons further along the visual pathways will encode sequences of spatial frequencies at one position angle or code specific frequencies for some regular sequence of position angles is still unknown.

The recognition of the commitment of the visual cortex to the Fourier transform domain presages a remarkable development for our understanding of pattern recognition. Because Fourier transforms are (except for a phase term) translationally invariant, pattern recognition can be much more efficiently accomplished in the transform domain. Furthermore, a change in size of an object produces only a scale factor change in the set of spatial frequencies represented in the transform domain (*15*). A brighter object will produce a spectrum of the same form, but proportionally stronger. Thus, but for these two scale factors, a reconstruction in the transform domain will uniquely specify any object. However, size and brightness information must also be preserved (*1*); we can judge which of two similar objects is larger or brighter. The fact that size of a viewed object may undergo a rapid apparent increase (macropsia) or decrease (micropsia) following epileptic discharge in the temporal lobe (*26*) suggests that the scaling for size may require processing beyond occipital lobe structures.

Because pattern recognition also implies a match or cross-correlation against the memory, the commitment of the brain to the transform domain also suggests that memory may involve a storage of information easily transferable to a "read-out" in the transform domain. The existence of Fourier transform processes provides additional support for suggestions (*27*) that information may be stored holographically (*28*), a process that is closely related to Fourier transforms.

DANIEL A. POLLEN
JAME R. LEE*
Neurobiology Laboratory, Neurosurgical Service, Massachusetts General Hospital, Boston 02114
JOSEPH H. TAYLOR
Department of Physics and Astronomy, University of Massachusetts, Amherst 01002

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* Present address: Massachusetts Eye and Ear Infirmary, Boston 02114.

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Somatosensory Responses of Bulboreticular Units in Awake Cat: Relation to Escape-Producing Stimuli

Abstract. *In awake, unrestrained cats, bulboreticular neurons respond after electrical stimulation of cutaneous nerve with increasing discharge as stimulus intensity is raised to levels eliciting escape behavior. These cells discharge most vigorously to noxious natural somatic stimuli and are not driven by other sensory modalities. Electrical stimulation through the recording microelectrode also elicits escape, which further suggests bulboreticular participation in pain sensory mechanisms.*

Unlike many of the major mammalian sensory systems, the neural basis for pain sensation is relatively poorly understood. Studies on peripheral nerve show that small-diameter myelinated (A-delta) and, possibly, unmyelinated (C) fiber activity is necessary for pain sensation (*1*), and that a subpopulation of each of these fiber groups includes afferents responding only to mechanical or thermal somatic stimuli which are presumably noxious to the awake animal (*2*). There is less certainty, however, about the central nervous system (CNS) consequences of such stimuli and how these may relate to pain. It has been shown that stimulation of somatic C fibers evokes discharge in the ventrolateral quadrant of the spinal cord (*3*), and that there are cells in the dorsal spinal gray responding exclusively, or primarily, to noxious somatic stimuli and to small-diameter cutaneous afferents (*4*). In the anesthetized rat and in the unanesthetized, decerebrate cat, a population of medullary reticular formation neurons responds maximally or exclusively only to intense mechanical somatic stimulation, and many of these cells apparently receive their excitatory input primarily from A-delta fibers (*5*).

While these studies are clearly important for an understanding of nociceptive mechanisms in the CNS, they were all performed on anesthetized, spinal, or decerebrate animals—conditions that affect responses to somatic stimuli (*6*); moreover, there was no opportunity for a direct correlation between neural activity and behavioral responses indicative of pain. To circumvent some of these problems, the electrical activity of single neurons (units) was recorded in awake cats trained to