L. Zeigler, in *Aspects of the Development of Competence*, W. A. Collins, Ed. (Erlbaum, Hillsdale, N.J., 1981), vol. 14, p. 1] to accommodate the longer latency of the visual blink reflex (mean onset latencies: acoustic, 60 msec; visual, 180 msec). For details of scoring program, see F. K. Graham, L. E. Putnam, and L. A. Leavitt [*J. Exp. Psychol: Human Percept. Perform.* **1**, 161 (1975)] or B. D. Strock [thesis, University of Wisconsin (1981)].
10. B. J. Anthony and F. K. Graham, unpublished data.
11. S. A. Hackley, M.A. thesis, University of Wisconsin (1981).
12. J. A. Deutsch and D. Deutsch, *Psychol. Rev.* **70**, 80 (1963); D. A. Norman, *ibid.* **75**, 522 (1968); R. M. Shiffrin and W. Schneider, *ibid.* **84**, 127 (1977); M. I. Posner and D. R. Snyder, in *Information Processing and Cognition*, R. L. Solso, Ed. (Erlbaum, Hillsdale, N.J., 1975), p. 55.
13. Supported by the W. T. Grant Foundation, NIH grant HDO1490, NIMH fellowship MHO1798 (to B.J.A.), and research scientist award K3-MH21762 (to F.K.G.). We thank B. L. Zeigler for assistance in programming and circuit design and K. M. Levin and C. H. Wang for serving as observers.

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Single Visual Neurons Code Opposing Motion Independent of Direction

Abstract. *Cells in intermediate and deeper layers of the pigeon optic tectum respond best when a textured background pattern is moved in the opposite direction to a moving test spot. Complete inhibition occurs when the background moves in the same direction as the test stimulus. Most noteworthy is the invariance of this relationship over a wide range of test spot directions. These cells represent a higher level of abstraction in a motion-detecting system and may play a role in figure-ground segregation or the discrimination of the motion of an object from self-induced optical motion.*

One of the fundamental tasks required of any sensory system is to "parse," or decompose, patterns of stimulation into clusters of attributes that represent the distal sources giving rise to them. In audition, this entails segregating the neural patterns produced by the complex pressure wave reaching the ears into separate "streams" representing their separate sound sources. This "auditory stream segregation" (*1*) is complex, involving spatial, temporal, and harmonic relationships. Nevertheless, our experience in the everyday world of sounds attests to their efficiency. They enable us to untangle many concurrent sounds, even when their spectra seem hopelessly intertwined.

In vision also, the neural patterns produced by complex retinal images must be parsed into objects, and their three-dimensional locations and motion characteristics preserved separate from ambient variations. Figure-ground segregation has been studied extensively in relation to stereopsis (*2*) and computer "scene analysis" (*3*). Gibson's early work (*4*), however, has been followed by a growing awareness that image motion characteristics may play a key role in this process. For example, visual psychophysical experiments with coherently moving dots show vivid emergence of figures among other incoherently moving dots (*5*). Differentially moving dots also lead to compelling and accurate sensations of depth (*6*). Recent theoretical accounts have also shown that retinal flow patterns, generated by an observer moving through space, can provide, in principle, information about object rigidity, boundaries, and orientation (*7, 8*), also suggesting how neural mechanisms might make some of these computations (*8*).

In this report we describe single cells that might perform such functions. These units, which have very large inhibitory receptive fields, are inhibited by the in-phase movement (same direction, same velocity) of a test stimulus and background and are often facilitated by anti-phase movement (opposite direction, same velocity) (*9*). We have demonstrated that these results hold, within an individual cell, for test spot directions

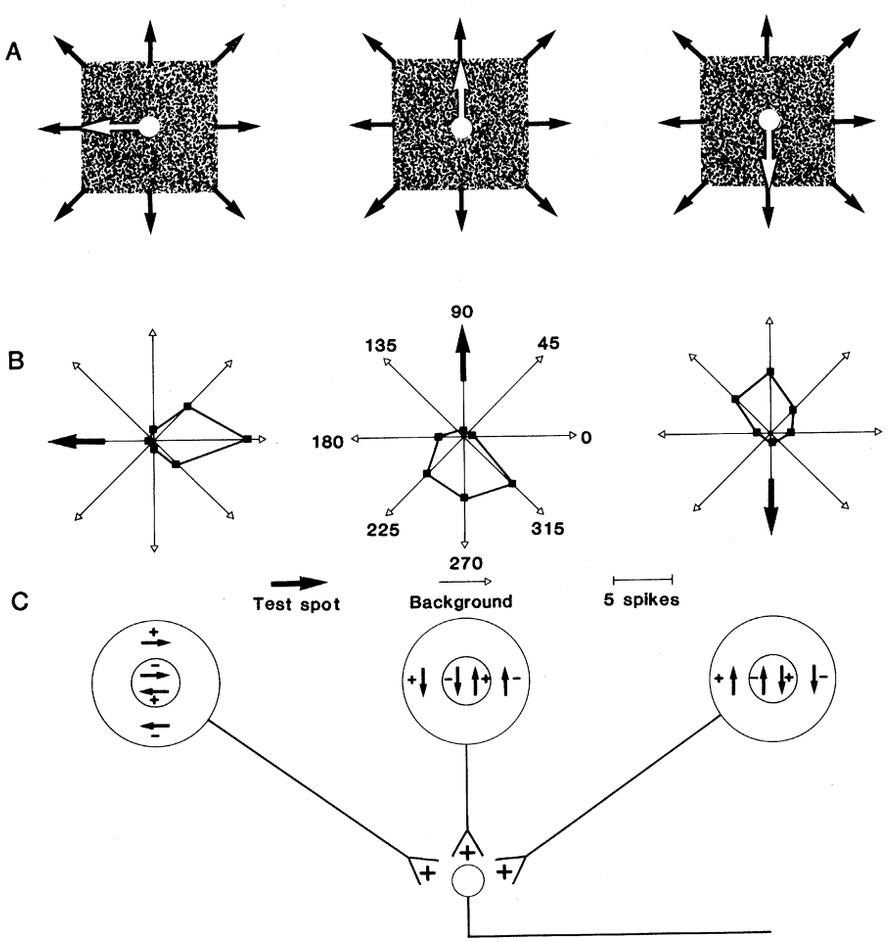

Fig. 1. (A) Schematic diagram representing visual stimulating conditions presented to individual pigeon tectal cells. The white spot indicates the test stimulus, and the textured pattern represents the background. Arrows indicate the direction of motion of these components used to measure the responses portrayed in the corresponding polar plots. (B) Polar response plots obtained from a single cell showing the mean number of impulses as a function of background direction. Each plot was obtained by choosing a fixed test spot direction (bold arrows) and varying background direction. Despite changes in test spot direction, cells responded best when the background motion was opposite test motion in all three cases. (C) Hypothetical scheme to account for the results. Concentrically overlapping subunits having different preferred directions and with opponent center-surround organization converge onto a cell of higher order.

differing by 180°. That is, it is the relationship between the motion directions of the test stimulus and the background, rather than the absolute directions, that determines the responsivity of the cell.

Conventional extracellular recording techniques were used to study tectal cells of anesthetized white Carneau pigeons. Details of preparation, recording, and stimulus control have been reported (*9*). Upon successful isolation of a cell, the optimal size and velocity of a single test spot was chosen and swept in several different directions through the excitatory receptive field (ERF). In agreement with previous studies (*10*), these cells exhibited broad directional tuning curves. After qualitative assessment of their directional selectivity, large textured background patterns (101° by 47°) were back-projected onto a tangent screen, while the test spot was front-projected. As reported previously (*10*), the in-phase movement of a test spot and background pattern produced profound inhibition, whereas anti-phase movement often produced facilitation.

Since the primary focus of this study was the relationship between test spot and background directions of movement, we assessed the effect of background direction for one particular test spot direction and obtained a polar tuning function. We then altered the test spot direction and again varied background direction (Fig. 1A) and obtained other polar tuning functions. Poststimulus time histograms for eight sweeps of the test spot, for each direction of background movement, were obtained with the total spike count for each separate condition. The mean number of spikes per condition was computed to form the polar plots.

A total of 119 cells below a depth of 0.4 mm from the tectal surface have been studied in 37 birds. Full sets of quantitative data were obtained for 40 cells and partial or qualitative observations made on the remainder. All 40 cells responded as illustrated in Fig. 1B, where it can be seen that when the background patterns were moving in the opposite direction (anti-phase) to the test spot, the cell responded strongly. When the background pattern was moved in the same direction (in-phase) as the test spot, the response was inhibited. This relationship held for three different directions of the test spot motion through the ERF. For example, in Fig. 1B the test spot was moved up through the ERF (middle panel); downward or near downward movement of the background movement resulted in a clear response to the test spot. When the test spot was moved down, (right panel of Fig. 1B), it was the upward directions of background movement that permitted a clear response, whereas downward directions of the background inhibited the response. Forward motion of the test spot required backward motion of the background for the best response (*11*). The remaining 79 cells showed the same qualitative characteristics. Each shared the selective in-phase inhibition of background for test spot motion, which was preserved when the direction of test spot motion was reversed.

These cells were also exposed to other conditions not shown here. For example, the central portion of the rear-projected textured pattern was occluded through a large stationary mask attached to the back of the screen; this treatment produced identical results to those described above, which indicates that background inhibition and facilitation is mediated by processes outside of the excitatory receptive field center. The response produced by the moving test spot was the same whether it was presented alone or swept over stationary background patterns. Furthermore, no excitatory responses were ever produced in any of these cells by any direction of movement of the textured background patterns themselves. In previous studies we showed that no eye movements are produced in anesthetized animals by any of these stimulus conditions.

Figure 1C illustrates a possible mechanism to account for these results. Lower order, directionally specific neurons are assumed to have an antagonistic, center-surround organization with respect to motion (*9*). If several units of this type, each with a different preferred direction, were to converge on a higher order neuron (*8*), it would have response characteristics similar to those found in this study.

These results indicate a new level of complexity and abstraction in the processing of motion information by single neurons. Because this characterizes the response properties of all tectal neurons recorded in the deeper layers, they must perform an important visual function.

Two possibilities seem most likely. (i) Nakayama and Loomis (*8*) suggested the possible existence of center-surround cells (Fig. 1C), which could play a critical role in delineation object boundaries for a moving observer in a stationary environment. The cells we recorded from could perform this function if aided by compensatory head and eye movements that occur during walking (*12*). (ii) Retinal image motion resulting from the birds' own movements must be segregated from that produced by actual moving objects. Translation of the retinal image produced by eye, head, or body movement would result in similar motion patterns (in-phase) in the center and surround regions of these receptive fields and thus inhibit any response. In contrast, movement of an object relative to its surround would be signaled by these units over a wide range of object directions.

B. J. FROST
Departments of Psychology and *Physiology, Queen's University, Kingston, Ontario K7L 3N6*
K. NAKAYAMA
Smith-Kettlewell Institute of Visual Sciences, 2232 Webster Street, San Francisco, California 94115

References and Notes

1. A. S. Bregman, in *Attention and Performance*, J. Requin, Ed. (Erlbaum, Hillsdale, N.J., 1978), vol. 7; C. L. Dannenbring, *Percept. Psychophys.* **24**, 369 (1978); J. Rasch, *Acoustica* **40**, 21 (1978).
2. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
3. D. Waltz, in *Psychology of Computer Vision*, P. H. Winston, Ed. (McGraw-Hill, New York, 1975); D. Marr, *Vision* (Freeman, San Francisco, 1982); D. H. Ballard and C. M. Brown, *Computer Vision* (Prentice-Hall, Englewood Cliffs, N.J., 1982).
4. J. J. Gibson, *The Perception of the Visual World* (Houghton Mifflin, Boston, 1950); *The Senses Considered as Perceptual System*, (Houghton Mifflin, Boston, 1966).
5. O. Braddick, *Vision Res.* **14**, 519 (1974).
6. B. J. Rogers and M. Graham, *Perception* **8**, 125 (1979).
7. J. J. Koenderink and A. J. van Doorn, *J. Opt. Soc. Am.* **66**, 717 (1976); S. Ullman, *Proc. R. Soc. London Ser. B* **203**, 405 (1979); H. C. Longuet-Higgins and K. Prazdny, *ibid.* **208**, 385 (1980).
8. K. Nakayama and J. M. Loomis, *Perception* **3**, 80 (1974).
9. B. J. Frost, *Brain Res.* **151**, 599 (1978); _____, P. L. Scilley, S. C. P. Wong, *Exp. Brain Res.* **43**, 173 (1981).
10. B. J. Frost and D. E. DiFranco, *Vision Res.* **16**, 1229 (1976); D. Jassik-Gerschenfeld, F. Minois, F. Condecourtine, *Brain Res.* **24**, 407 (1970). We have shown that the directional tuning curves for tectal cells is generally broad and often has a cardioid shape when plotted on polar coordinates. The most notable feature of these units is a "backward notch" or lack of responsiveness to stimuli moving from anterior to posterior in the visual field. This backward notch may filter out flow patterns produced by forward locomotion.
11. For the cell illustrated here, the test spot subtended 4.5° and was swept along a 36.9° path through the ERF, at 11.8° per second. The background was a random noise pattern, with element sizes ranging from 0.08° to 1.7°. Luminance of the spot was 2.3 cd/m^2 and of light areas in the textured pattern, 1.4 cd/m^2.
12. M. B. Friedman, in *Neural and Endocrine Aspects of Behavior in Birds*, P. Wright, P. Caryl, D. M. Vowles, Eds. (Elsevier, Amsterdam, 1975); B. J. Frost, *J. Exp. Biol.* **74**, 187 (1978); D. W. Pratt, *J. Exp. Biol.* **97**, 217 (1982).
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