Visually Guided Locomotion: Psychophysical Evidence for a Neural Mechanism Sensitive to Flow Patterns

Abstract. *Inspecting a radial flow pattern depressed visual sensitivity to changes in the size of a small test square, but only when the square was located near the focus of the flow pattern. This result suggests that precise visual judgments of one's direction of forward motion with respect to the outside world may be mediated by an already known neural organization sensitive to changes in the size of small objects.*

Each time we fly or travel by automobile we rely on the human visual system's ability to signal the precise direction in which the pilot or driver's head is moving with respect to the outside world. The importance of visual cues in landing is evidenced by the number of accidents whose cause has been identified as inadequacy of visual cues (*1*). Even so, one-eyed airplane pilots, such as Wiley Post, and many less-famous one-eyed automobile drivers continue to demonstrate that such visual judgments do not require binocular vision (*2*). The necessary information must therefore be represented within a single retinal image which, being two-dimensional, cannot directly portray three-dimensional motion.

Gibson's (*3*) subjects viewed a movie that had been filmed from an airplane in flight. He found that pilots and nonpilots alike were able to estimate the point toward which the airplane was flying. Gibson noted that this judgment was achieved without any binocular visual cues whatsoever and pointed out that, for geometrical reasons, the retinal image is necessarily distorted in a specific way when the observer's head moves forward. Contours flow radially away from a focus *F*, and that focus is the point toward which the observer is moving. Gibson proposed that this flow pattern can be regarded as a visual stimulus in itself, and would constitute an adequate basis for estimating the direction in which one was moving (*3*).

In principle, a subject could use knowledge of the position of the flow pattern's focus to guide the direction of locomotion toward a desired target even without information as to the position of the eye in orbit. For example, a crawling infant (Fig. 1) continually correcting the direction of locomotion so as to keep the focus of the flow pattern centered on the teddy bear could look around the room while crawling, confident that with forward progress, the toy would eventually be reached (*4*).

Gibson's proposal could be taken as a hint that the human visual system might contain a neural organization sensitive to flow patterns but relatively insensitive to local motion and local changes of luminance that accompany them, since these local effects can also occur in the absence of flow patterns. One way of attaining preferential sensitivity to flow patterns would be by responding only to certain relationships between local motion in different regions of the visual field. At first sight this seems to demand interactions across considerable distances in the visual field. However, we will argue that visual sensitivity to flow patterns can be explained without invoking long-range interactions.

We have proposed elsewhere that the human visual pathway contains channels that are preferentially sensitive to changing size (*5*). We subsequently found neurons in the visual cortex of cat that might provide a physiological basis for such channels (*6*). These changing-size channels operate when a pair of edges move in opposite directions, but are not responsive to movement per se since they

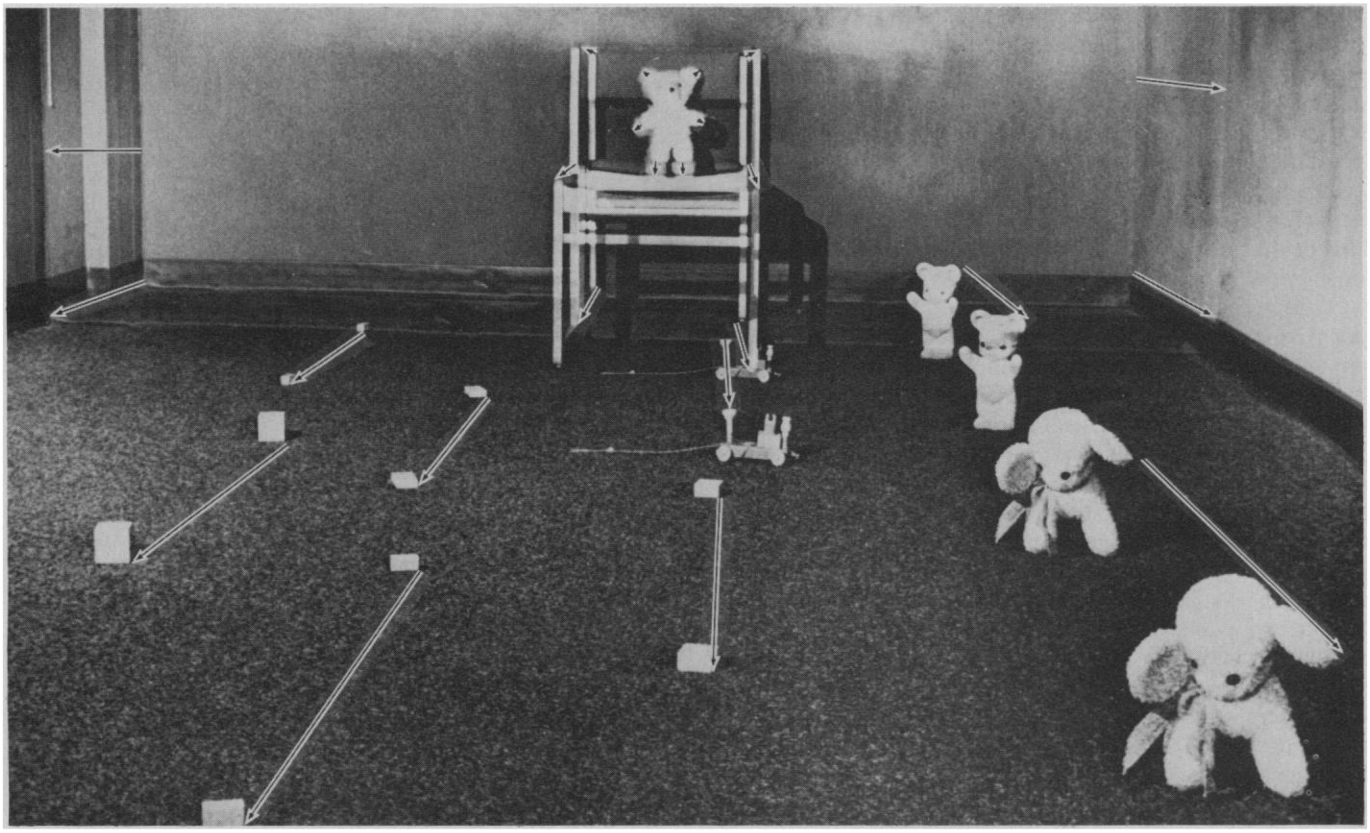

Fig. 1. An infant's motion toward a target (the teddy bear's nose) creates a radial flow pattern in the visual field with the target as its focus. The radial velocities of contours increase (arrows), and texture becomes progressively coarser as the angular distance from the target increases. The flow pattern enables the infant to judge its direction of motion precisely even when not looking directly at the target.

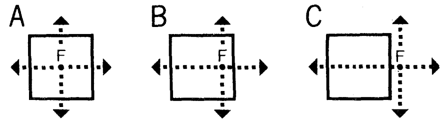

Fig. 2. The human visual system contains channels sensitive to changing size. A changing-size channel will respond to the flow pattern when the flow pattern's focus *F* falls inside the channel's receptive field (represented by the square) but not when *F* lies outside the receptive field. This response could provide a basis for judging the position of a flow pattern's focus. Such judgments would be precise, since the receptive field of a changing-size channel is no more than 1.0° to 1.5° in diameter.

are not active when the edges move in the same direction. They do not respond to a change in light flux. Changing-size channels do not operate when the pair of stimulating edges are too far apart: their separation must not exceed 1.0° to 1.5° (*7*).

We propose that a flow pattern could stimulate a changing-size channel and that the relative activities of changing-size channels fed from adjacent regions of the visual field could provide a basis for locating the focus of a flow pattern. For simplicity the receptive field of a changing-size channel is shown in Fig. 2 as a square (*8*). We suppose that the flow pattern would stimulate a changing-size channel sensitive to expansion when the focus *F* fell within the receptive field (Fig. 2, A or B). On the other hand, the changing-size filter would be stimulated much more weakly (or not at all) when *F* lay outside its receptive field (Fig. 2C). Therefore, a neural mechanism that compared the outputs of changing-size filters fed from nearby regions of the visual field would provide a basis for estimating the position of the focus precisely. The smaller the dimensions of the changing-size receptive field, the more precisely could the position of the focus be estimated (until, for very small receptive fields, eye movements set a limit to precision).

We tested this hypothesis by finding whether gazing at a flow pattern for some time preferentially reduced visual sensitivity to changing size and, if so, whether this effect was greater in the immediate neighborhood of the flow pattern's focus than in remote regions. We measured visual sensitivity to changing size by stimulating the eye with a test rectangle whose horizontal edges were stationary but whose vertical edges oscillated from side to side at 1 Hz in antiphase (that is, moved in opposite directions at any given instant) (Fig. 3A) (*9*). Control experiments differed only in that the test rectangle's vertical edges oscillated in phase rather than in antiphase (that is, the edges moved in the same direction at any given instant, so that the rectangle's size remained constant, but its position oscillated). Subjects adjusted the amplitude of the oscillation so that it was just visible. We recorded these threshold settings before and after 10 minutes of inspection of the flow pattern (Fig. 3B). By calculating the percentage of changes of thresholds we obtained a measure of the changes in visual sensitivities to the antiphase and in-phase test rectangles caused by inspecting the flow pattern.

Threshold elevations for the antiphase (changing-size) test rectangle were plotted against the distance *X*° between the center of the test rectangle and the focus of the adapting flow pattern (Fig. 3C). Inspecting the flow pattern produced clear depressions of visual sensitivity to the antiphase test rectangle, but this adapting effect fell to insignificant levels when the center of the 0.5° test rectangle was located only a little more than 0.25° from the point in the visual field previously occupied by the focus of the adapting flow pattern. Our findings are consistent with the prediction illustrated in Fig. 2 that threshold elevations should fall to zero when the focus of the flow pattern was located outside the receptive field of the changing-size channel (neglecting the effect of fixation variations due to eye movements) and suggest that the receptive field of the channel tested had approximately the same width as the 0.5° stimulus rectangle.

Threshold elevations for in-phase oscillations of the test rectangle's edges (Fig. 3D) were much smaller than those for antiphase oscillations (Fig. 3C). Furthermore, the in-phase elevations did not depend upon the distance *X*° from the focus. Data from all four subjects led to similar conclusions, even though there were marked intersubject differences in absolute sensitivity to changing size and in percentage of threshold elevation (*10*).

A possible objection to the experiment is that the focus of the flow pattern fell on the fovea, and the retina is, to a first approximation, radially symmetrical about the fovea. Therefore, we repeated the experiment with the focus of the flow pattern displaced 2° horizontally to the right of the fovea. We measured threshold changes both to the left and to the right of the position of the flow pattern's focus. The results were essentially similar to those shown in Fig. 3, C and D. Similar results were also obtained when we repeated the experiment with the in-

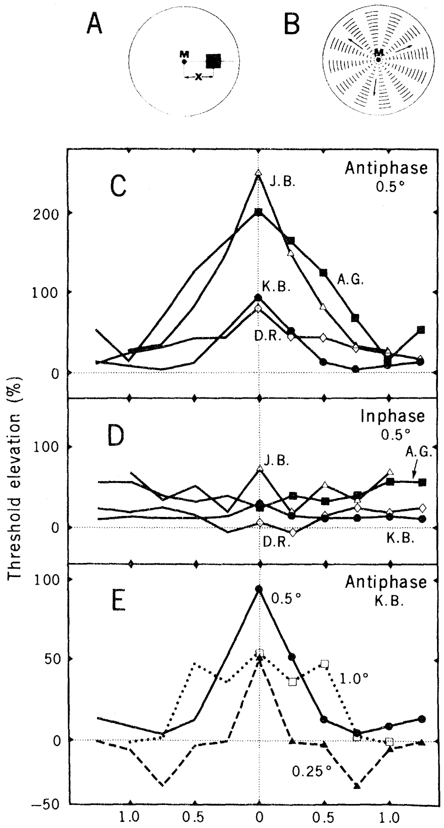

Fig. 3. (A) The vertical edges of the test rectangle oscillated from side to side in antiphase (changing size) or in phase. Oscillation thresholds were measured as a function of *X*° before and after a 10-minute inspection of the flow pattern. The edges were moved by a triangular waveform, that is, at constant speed. Three test rectangles were used in separate experiments. Their widths were 0.25°, 0.5°, and 1.0°. All were 0.5° high. Total light flux was constant. (B) Flow pattern of 3.5° diameter consisting of 48 equally spaced sectors, alternate sectors containing 13 line segments. The line segments flowed radially outward from the focus for 5 seconds, then reversed their directions of motion for 5 seconds, and so on. The flow pattern and the test rectangle were never visible at the same time. Subjects were allowed to inspect the test rectangle for 10 seconds to make a setting. Exposure to the adapting flow pattern for 60 seconds intervened between successive postadaptation settings, and exposure to the stationary flow pattern for 60 seconds intervened between successive preadaptation settings. Test rectangle luminance was 3.0 cd m^{-2}, and the innermost ring of the flow pattern was 34 cd m^{-2}. The test square and the flow pattern were generated on a cathode-ray tube (Hewlett-Packard model 1321A) (green phosphor, type 31) viewed from a distance of 4.3 m; they were superposed on a 6° by 6° green adapting background of luminance 1.6 cd m^{-2}. A green light-emitting diode of luminance 13 cd m^{-2} was the fixation mark (*M*). The right eye only was used. The radial velocity of flow was 0.75 deg sec^{-1}, and was constant across the screen (*12*). (C) Threshold elevations (*13*) for the antiphase test rectangle versus distance. (D) Threshold elevations for the in-phase test rectangle versus distance. (E) Threshold elevations for the antiphase test rectangle versus distance for three widths of test rectangles.

nermost annuli 0.8 log unit brighter and 0.8 log unit dimmer than the outermost annuli.

As a further test of the prediction illustrated in Fig. 2, we measured threshold elevations for two additional test rectangle widths, namely, 0.25° and 1.0°, for three of our four subjects. Figure 3E shows how the antiphase threshold elevation curves progressively broadened as the width of the test rectangle increased from 0.25° to 1.0°.

We conclude that visual sensitivity to the location of a flow pattern's focus could be mediated by channels that respond to changes in the size of small objects. The relative activities of these changing-size channels might be one basis on which the brain computes the direction in which the head moves with respect to the external world (*11*, *12*).

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References and Notes

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3. J. J. Gibson, *The Perception of the Visual World* (Houghton Mifflin, Boston, 1950), pp. 117–144.
4. If some part of a subject's ability to use flow patterns to guide locomotion depends on neural development, and if this neural development depends on early experience in visually guided locomotion, a major increase in visual sensitivity to flow patterns might not occur until the time an infant starts to crawl alone. Furthermore, adults who had been unable to travel normally under their own volition early in life might, consequently, have abnormal responses to flow patterns so that their ability to guide their locomotion by retinal flow patterns might be impaired. This discussion amounts to a special case of the more general proposal of R. Held and A. Hein [*J. Comp. Physiol. Psychol.* **56**, 872 (1968); *Sci. Am.* **213**, 84 (November 1965)].
5. D. Regan and K. I. Beverley, *Vision Res.* **18**, 415 (1978); *ibid.*, p. 209; ______ and M. Cynader, *Proc. R. Soc. London Ser. B*, in press.
6. D. Regan and M. Cynader, *Vision Res.*, in press.
7. K. I. Beverley and D. Regan, *ibid.*, in press.
8. Receptive field measurements have been reported (*7*).
9. We chose oscillatory stimulation for test rectangles (and therefore for flow pattern) because the chief evidence for the existence of changing-size channels was obtained with stimulus rectangles whose edges oscillated either in phase or in antiphase (*6*). This enabled us to show more clearly that selective adaptation to antiphase (changing-size) stimuli could not be explained in terms of the classical motion channel since the movements of the rectangle's edges were identical for in-phase and antiphase stimuli: the only difference was in the relationship between the motion of opposite edges. We could not have used this argument had we used asymmetric (ramping) movements.
10. For the 0.5° test rectangle, preadaptation sensitivity to changing size at 1 Hz was 1.6, 0.7, 2.8, and 1.5 minutes of arc per second (central foveal stimulation); peak threshold elevations (Fig. 3C) were 94, 250, 202, and 80 percent; and half-widths of curves (Fig. 3C) were 12, 17, 35, and 14 minutes of arc for subjects K.B., J.B., A.G., and D.R., respectively. If visual sensitivity to flow patterns is important in landing aircraft and in automobile driving, and if this visual capacity proves to be relatively uncorrelated with the results of standard visual tests, there may be flying and driving tasks for which tests of sensitivity to flow patterns or to changing size might profitably be added to present screening tests.
11. Our finding that changing-size channels are not sensitive to pairs of edges more than about 1.5° apart make sense in the light of our proposal that a major function of changing-size channels might be to provide a basis for judging the location of a flow pattern's focus, since changing-size channels sensitive to narrow objects would signal the location of the focus more precisely than those sensitive to wide objects. D. Regan and K. I. Beverley, *Vision Res.*, in press.
12. Since the radial velocity in our flow pattern did not depend on the distance from the focus, our stimulus differed from a real-world flow pattern. In a real-world flow pattern, the angular velocity of flow for an object point located along a direction $\theta°$ from the point toward which the eye is moving is proportional to $(\theta v/D)$, where D is the distance between the eye and the object point and v is the linear velocity of locomotion.
13. Threshold elevations were calculated as follows:
$$TE = \frac{T_a - T_b}{T_b}$$
where T_a was oscillation threshold after adaptation and T_b was oscillation threshold before adaptation.
14. Photograph (Fig. 1) by G. Castle, Dalhousie University. We thank J. Raymond, M. Cynader, A. Ginsburg, L. Harris, and W. K. Honig for their critical comments and N. Beattie for assistance in preparing this report. K.I.B. was supported by National Research Council of Canada grant A-0323 to D.R. Sponsored by the U.S. Air Force Office of Scientific Research, Air Force Systems Command under grant AFOSR-78-3711.

21 November 1978

Noradrenergic Innervation of Cerebral Cortex: Widespread Effects of Local Cortical Lesions

Abstract. *The trajectory of the intracortical noradrenergic fibers has been characterized by histochemical analysis following the production of cortical lesions in the rat. A large group of noradrenergic fibers enters the cortex at the frontal pole and proceeds caudally through the deep layers of dorsolateral cortex. Branches arise from these longitudinally directed fibers and form a uniform pattern of innervation throughout lateral cortex. Because these fibers travel long distances rostrocaudally within the gray matter, a large area of cortex can be deprived of noradrenergic innervation by a relatively small lesion of frontal cortex. The medial and lateral cortex can be selectively and differentially denervated of noradrenergic fibers, and there is a medial to lateral topographic relationship between deep longitudinally running fibers and overlying cortex.*

The ascending noradrenergic (NA) projection from the locus coeruleus appears to be the most divergent system in the brain, originating from a few thousand cells in the pons and innervating a large portion of the diencephalon and the entire cerebral cortex. Predictably, the projection does not mediate modality-specific sensory information but has been implicated in more general functions such as attention, mood, and vigilance (*1*). To achieve a better understanding of the role played by the coeruleo-cortical system in cortical circuitry, we have studied the morphological organization of the terminal and preterminal NA axons within the cortex of the rat. Our previous observations (*2*) indicate that the coeruleo-cortical projection is geometrically orderly throughout the lateral neocortex and that its organization differs considerably from that of other cortical afferents. Two noteworthy features of the NA innervation are the high density of fibers throughout all cortical layers and the predominantly tangential orientation of axons within the cortical gray matter. We now offer experimental data that further clarify the intracortical route of the NA fibers and that demonstrate the tangential organization of this major cortical afferent.

Throughout all areas of the lateral neocortex, a qualitatively uniform pattern of NA innervation has been found (*2*) through the use of immunocytochemical staining with antibodies directed against dopamine-β-hydroxylase (DBH) (*3*). The NA fibers in layer VI are largely oriented in the anteroposterior direction, and they form a continuous, intracortical sheet of longitudinal fibers overlying the white matter. Although tangential fibers are also seen in layers IV and V, the prevalence of short, tortuous axon segments suggests that an NA terminal field is present in these layers. Layers III and II are traversed by radially oriented axons with minimal branching, whereas layer I contains numerous tangential fibers with both anteroposterior and mediolateral orientations.

The pattern of NA innervation in the medial (cingulate) cortex differs from that of the lateral cortex. Within the medial cortex, striking differences exist between the anterior cingulate and the retrosplenial regions (*4*). The anterior cingulate cortex has a low density of NA fibers, particularly in layers II and III, in contrast to the retrosplenial cortex, which has an extremely high density of NA innervation, most evident in the middle layers, where there appears to be an NA terminal field similar to that in layer IV of lateral cortex.

0036-8075/79/0720-0313$00.50/0