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Visual Receptive Fields Sensitive to Absolute and Relative Motion during Tracking

Abstract. *Some neurons in the visual cortex of awake monkeys visually tracking a moving target showed receptive fields that were excited only by stimulus motion relative to a background, while other neurons responded to any kind of stimulus motion. This result was found with two methods, one in which tracking eye movements were identical in both relative-motion and absolute-motion conditions, and another in which stimulus motions on the retina were identical in both conditions. This response pattern can differentiate translation of the retinal image during eye movement from motion of objects in the world.*

Image motion across the retina does not necessarily provide information about object motion in the world; information about object motion is generated only when one pattern in the optic array moves with respect to another. To detect motion of objects in the world, some cells in the visual system must respond to motion relative to a background (which indicates object motion) rather than to displacement of the entire visual image across the retina (which indicates eye movement). The two conditions were separated by exploring the visual receptive fields (RF's) of single cells in the monkey's visual cortex (*1, 2*) while the monkey tracked a slowly moving target. In one condition a stimulus was fixed to a screen so that its image scanned the retina during the monkey's slow eye movement; the stimulus moved with respect to the retina but not with respect to the background. In the other condition the stimulus moved with respect to both the retina and the background during identical slow eye movements.

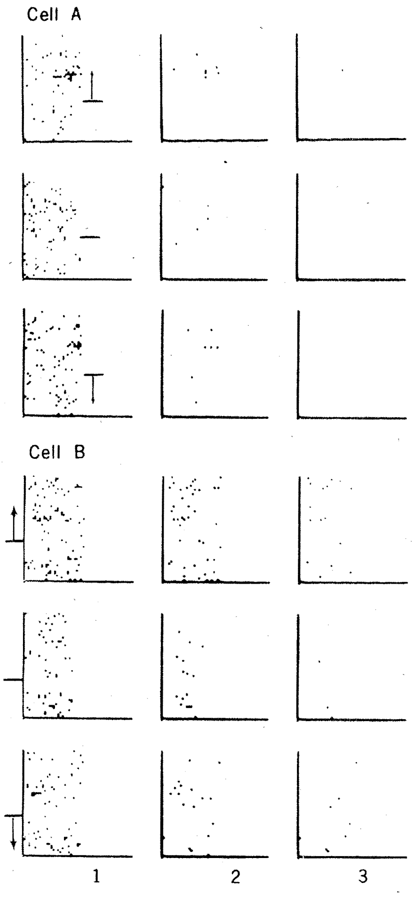

Fig. 1. Two cells with receptive fields responsive only to motion relative to a background. Each row shows a separate map made under visual tracking, and each pair of axes represents the 25° by 25° region of the stimulus screen over which the fixation target could be moved. A map consists of vertical scans separated by 0.5°, beginning at the left. Each scan is divided into 50 segments, each 0.5° (50 msec) long, and a spot is darkened in the display if the cell fired while the fixation target (a 1° disk) crossed the corresponding region of visual space. At levels 2 and 3 a spot is darkened only if the cell fired at least two or three times, respectively. The bar stimuli and their locations in relation to the scanned area are shown in the left column, with the stimuli moving through a 2° by 4° aperture in the directions indicated by the arrows attached to them. Moving bars are depicted in the centers of their apertures. About half of the 25° by 25° stimulus space was mapped in each condition. Receptive fields are apparent when the stimuli are moving but not when they are fixed on the screen. The two cells are from opposite hemispheres of the same monkey. Cell A shows one of the strongest fields found, and cell B one of the weakest. Control maps, with the fixation target moving upward but not tracked, showed only background activity (not illustrated).

Three immature rhesus monkeys were trained to sit in a primate chair and optically track a 1° target moving on a tangent screen. Eye movements were monitored with standard clinical electrooculogram electrodes fixed above and below the orbits, while the eyes were observed with a system based on the Mackworth eye camera (*3*). Because tracking accuracy improves with practice (*4*), each monkey was overtrained for at least 2000 trials before RF exploration began.

For RF determination a 25° by 25° region of the screen was divided conceptually into 2500 blocks, each 0.5° by 0.5° in extent. The fixation target passed through each block in succession, and a point was produced in the display when an action potential occurred. The displays of Fig. 1 are therefore maps of cell firing for corresponding positions of the fixation target on the screen. The target jumped to the edge of the scanned area, moved up and down (or right and left) at 10° sec^{-1}, and jumped back to a hidden origin point. If the monkey followed the downward movement of the target without saccadic eye movements, he was rewarded with apple juice. At any time the experimenter could initiate a new trial 0.5° to the right of the previous one; unsuccessful trials were repeated.

Each RF map was made with two stimuli on the screen, a fixation target and a mapping stimulus. To provide a mapping stimulus that moved relative to the screen, a horizontal bar 0.5° high was moved vertically through a fixed aperture 2° high and 4° wide. As the bar disappeared from one edge of the aperture it was replaced by another on the opposite edge, resulting in a moving display with a contant speed and direction. Light flux at the monkey's eye varied less than 1 percent as one bar replaced another. The aperture was always mounted contralateral to the hemisphere in which the cells investigated were located. With this apparatus, responses were mapped under three conditions of stimulus motion; the bars moved down the screen at 5° sec^{-1}, remained fixed, or moved up at 5° sec^{-1}. When the monkey's eye scanned down the screen during tracking, the upward velocity of the bars across the retina was increased by 10° $\sec^{-1}$, resulting in retinal stimulus speeds of 5°, 10°, and 15° $\sec^{-1}$, respectively. Thus, absolute motion across the retina was present in all three conditions; but at the second, intermediate, speed there was no stimulus motion relative to the background. The hypothesis that relative motion is necessary for RF excitation predicts that some neurons will respond only under the first and third conditions, while a pure retinal-motion hypothesis predicts responses under all three conditions.

Brightness of the fixation target and the mapping stimulus was 60 lu/m^2 on a screen of 4 lu/m^2, yielding 1.2 log units of contrast. The screen was a finely textured black poster board 57 cm from the monkey's eyes (*2*).

A simple system was developed to record from single cells in awake monkeys (*5*). A tungsten microelectrode was advanced slowly into the lateral striate cortex (area 17), 5° to 10° from the foveal projection. When an action potential of a cell was isolated, the RF was first explored with large hand-held stimuli and was then mapped with the tracking method.

In the first experiment, data were obtained from 34 neurons. Of the 18 that were investigated under both relative-motion and absolute-motion conditions, 39 percent responded only to relative motion (Fig. 1), another 39 percent responded to both absolute and relative motion (Fig. 2), and the remaining 22 percent were unresponsive to any of the stimuli used. The lack of response when the mapping bar was fixed on the background (Fig. 1) was not caused by a threshold of stimulus speed across the retina, because retinal motions both faster and slower than the 10° $\sec^{-1}$ of the fixed-stimulus condition elicited clear RF's. [Wurtz (*6*), using a similar recording procedure, found no qualitative difference in response to absolute movements varying from 10° to 40° $\sec^{-1}$ during steady fixation.] Responses were not caused by abrupt appearance or disappearance of a stimulus, because this occurred only once every 0.4 second and was not synchronized with scanning. Responses to unsynchronized events would not appear consistently at the same height in the maps.

These results were tested statistically against a null hypothesis of identical responses to the moving bars and to the fixed bar. A chi-square test was significant ($P < .001$), showing that the results were not due to some uncontrolled factor.

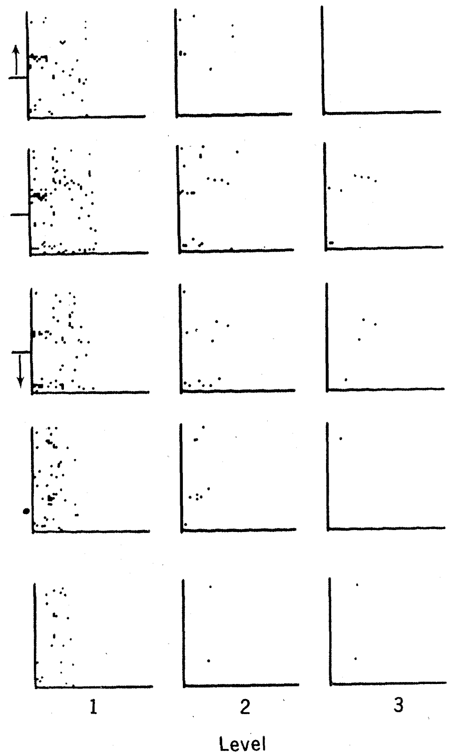

Fig. 2. A cell that responds to any movement of a bar stimulus across the retina. Mapping was done as in Fig. 1. The fourth map from the top (made with a fixed disk 1° in diameter) shows that some of the cells mapped in this experiment had small disk-shaped receptive fields; the bar-shaped response areas result from convolution of the mapping stimulus with the receptive field. The bottom map, a control with a fixation target but no other stimulus, shows no receptive field.

To test the relative-motion hypothesis further, another experiment was performed in which maps made with a fixed stimulus and slow tracking were compared with maps made during anesthesia with the eyes nearly immobile. In the latter condition, the moving spot, instead of being a fixation target, scanned the retina itself. Thus, relative motion was present, but the speed and direction of image motion on the retina was equal to that of the fixed stimulus during tracking. A cell was first examined under the tracking condition, with a peripheral stimulus (a 1° disk) fixed on the screen. The animal was then anesthetized with ketamine hydrochloride, the cell was remapped, and the optic disks were projected onto the screen with an ophthalmoscope to determine retinal position. Some cells showed responses only under anesthesia, when relative motion was present, even when the same mapping stimulus (a 1° disk) scanned the retina in both conditions.

Cells that could not be excited by any stimuli were found in the present experiments with about the same frequency as in a previous study with similar mapping methods (*2*); possible reasons for the inexcitability of these cells was discussed in that report. Inaccuracy of tracking eye movements did not obscure responses, because the presence of small RF's (Fig. 2) showed that the resolution of the mapping technique rather than tracking error was the limiting factor. Inactive cells may have had highly specific trigger properties (*6, 7*); thus, the results may represent a biased sample of motion sensitivities.

The contrast between these results and those of Wurtz (*6*) underscores the differences between slow and rapid eye movements. Wurtz found no differences between responses to stimuli moving at 900° $\sec^{-1}$ during steady fixation and responses to fixed stimuli during rapid eye movements. The Wurtz experiment, designed to search for a corollary discharge at the cortical level, is complicated (in a perceptual context) by retinal blur and saccadic suppression. More than two-thirds of the neurons in Wurtz's sample dramatically changed their responses with a transition from slow to rapid stimulus movement, a result suggesting fundamental changes in response properties.

Cells responding preferentially to relative motion have been found before, both in insect visual systems (*8*) and in direction-selective cells of the superior colliculus (*9*). In the latter system, response to movement in the RF center is reduced when a second stimulus in the inhibitory surround moves along with the first; and directional selectivity is lost with the removal of cortical input. Further work is required to define the relations between the cortical and collicular cells.

The presence of two types of cells in about equal numbers, one responding to any stimulus motion and the other only to motion relative to a background, means that information is available at the cortical level for a comparison mechanism that distinguishes eye movement from object movement. Both types of cells are activated by object movement, whereas only the absolute-motion cells respond to eye movement. This response pattern is consistent with Gibson's theory (*10*) that the visual world is stabilized by defining the optic array as a stable world, leaving motion to be perceived as a result of motion of one part of the array with respect to another.

Gibson (*10, 11*) pointed out that the features to which physiologists have found responses in mammalian visual systems—such as disks, lines, and edges moving on homogeneous screens—are highly ambiguous for perception. An edge in the optic array can specify the edge of an object in the environment, but it can also signal a shadow, a change in contour, or many other things. Useful structure in the ambient optic array comes not from differences in brightness, but from stabilities in optical patterns over time and the lawful transformations of these patterns.

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Object Distance as a Determinant of Visual Fixation in Early Infancy

Abstract. *Data from two experiments show that the duration of visual fixation of solid objects by infants aged 6 to 20 weeks varies as a function of object distance between 30 and 90 centimeters. There was no characteristic habituation of fixation of an object at 90 centimeters but there was a marked increase in fixation time when objects were advanced to 30 centimeters (experiment 1). A linear decline in fixation times occurred as the object distance increased from 30 to 90 centimeters with the real size and the angular size of the object held constant (experiment 2). No evidence for visual size constancy in young infants was obtained by this method.*

During the course of a series of experiments designed to investigate visual size constancy in early infancy, we obtained evidence strongly suggesting that object distance is a critical determinant of the duration of visual fixation, regardless of the object's actual or retinal size. Further investigation confirmed this suggestion, showing that infants between 6 and 20 weeks of age pay little regard to objects located at more than about 1 m away. These results bear closely on theories of the development of space perception and have obvious implications for experiments on infant perception in which visual fixation serves as an index of discrimination. When objects of the same actual or retinal size are presented repeatedly at different distances, infants respond to the variation in object distance rather than to the constancy of actual or retinal size. We report here the results received in our two experiments.

In the first experiment the degree of recovery from habituation (*1*) of visual fixation was used as an index of the apparent size of white cubes. After ten 10-second trials (5-second intervals between trials) with an 18-cm (visual angle, 11°26′) cube at a distance of 90 cm, the same (18-cm) or a different (6-cm) cube was presented for two 10-second test trials at either 90 cm or 30 cm. Thus the four test conditions were as follows: 18-cm object at 90 cm, 18-cm object at 30 cm, 6-cm object at 90 cm, and 6-cm object at 30 cm. These conditions essentially replicate those used by Bower (*2*) but with smaller objects at shorter distances. It was our original intention that the degree of recovery (increments in fixation time) under these four conditions would indicate whether the apparent size is determined mainly by the object's real size irrespective of distance (perceptual constancy) or by the angle subtended by the object at the eye (visual angle). Thus minimum recovery when the same (18-cm) cube was presented at 30 cm would have suggested constancy, whereas minimum recovery when the 6-cm cube was presented at 30 cm would have suggested visual angle. It was assumed that the magnitude of recovery would reflect the magnitude of the perceived change.

A group of 32 healthy, full-term infants viewed the suspended white cubes in an observation chamber 140 cm long, 76 cm wide, and sloping from 64 cm high at the viewing end to 98 cm at the other. The interior was dark blue to provide high contrast with the cubes, the surfaces of which were of different reflectances to give constant luminance when illuminated by two 20-watt fluorescent tubes mounted in the corners behind the infant. Black crosses 18 mm wide for the large cube and 6 mm wide for the small cube were taped on the surfaces facing the subject. The infant was deemed to be fixating on the cube when the center of the corneal reflection of the cross was centered in the pupil as observed from a 7-mm aperture in the side of the chamber in front of, and to the right of, the subject (*3*). Fixation was manually timed by means of a switch which operated a printout timer. Separate groups of eight infants, four boys and four girls in each group, were assigned to each test condition. In each group there were two age levels, 6 to 12 weeks and 13 to 20 weeks, equally distributed between the sexes.

The mean fixation times for each group during the ten habituation trials and the two test trials are shown in Fig. 1A. Appropriate tests of trend (*4*) over habituation trials showed no significant overall decline in fixation time and no differences in trend between the four groups or the two age levels. Contrary to expectation, there was no habituation of fixation over ten trials with an 18-cm object at 90 cm. Using an analysis of variance that took into account groups, age, and sex (*5*), we examined the change in fixation time in the test phase by comparing the mean fixation time of the last two habituation trials with the fixation time during the first test trial. There were significant main effects for groups and for trials ($P < .01$ in both instances), and a significant interaction between groups and trials ($P < .05$). There was no significant increase in fixation time for the two test condi-