

The role of disparity-sensitive cortical neurons in signalling the direction of self-motion

Jean-Pierre Roy* & Robert H. Wurtz

Laboratory of Sensorimotor Research, National Eye Institute, National Institutes of Health, Bethesda, Maryland 20892, USA

MOVEMENT of an observer through the environment generates motion on the retina. This optic flow provides information about the direction of self-motion¹, but only if it contains differential motion of elements at different depths^{2,3}. If the observer tracks a stationary object while moving in a direction different from his line of sight, the images of objects in the foreground and in the background move in opposite directions. We have found neurons in the cerebral cortex of monkeys that prefer one direction of motion when the disparity of a stimulus corresponds to foreground motion and prefer the opposite direction when the disparity corresponds to background motion. We propose that these neurons contribute a signal about the direction of self-motion.

Consider an observer translating rightwards while tracking a stationary object in front of him (Fig. 1). Images of objects in the foreground (closer than the fixation point) will move to the left, while images of objects in the background (farther than the fixation point) will move to the right (Fig. 1). Without a signal indicating the depth of the two opposite motions, the direction of self-motion cannot be ascertained: the movement of the observer could equally well be to the left or the right. However, if the direction of flow could be tagged with a depth signal, the ambiguity about the direction of self-motion would be removed.

One depth signal is binocular horizontal disparity. In a frontal-eyed animal, the relative position of the images of an object on the two retinæ indicates the depth of that object relative to the point of fixation. It has been proposed that the medial superior temporal area (MST) of the rhesus monkey cerebral cortex analyses optic flow^{4,5}, and we found in earlier experiments that direction-selective neurons in MST, the cells that respond to fronto-parallel motion in one direction but not the other, carry a disparity signal. When presented with stimuli moving in their preferred direction, their discharge rate was higher when the stimuli were of one sign of disparity (for example, crossed disparities, foreground neurons) or the other (uncrossed disparities, background neurons) (J.-P.R. and R.H.W., manuscript in preparation). To test whether this disparity signal was appropriate to determine the direction of self-motion from the two opposite motions shown in Fig. 1, we presented a set of disparity stimuli moving first in the preferred and then in the non-preferred direction for the neuron under study.

We studied 65 cells. Their receptive fields were large (mean of 27° on a side, s.d. ± 12°) and often crossed the vertical meridian (57%). Of these 65 cells, 39 (60%) preferred the same sign of disparity for the two opposite directions of motion. In all these cells, however, one direction elicited a much stronger response to the preferred disparity than the opposite direction (Fig. 2a). These neurons could then detect the direction of motion of the foreground (as in Fig. 2a) or background. The relative depth signal added to the direction signal could provide information about the direction of self-motion. Under certain conditions, however, these neurons will fail to provide that information. If the observer looks at a very close object, for example, there will be only background motion, and a foreground responsive cell (such as the one in Fig. 2a) will be silent. These neurons then seem to signal the direction of self-motion only under certain conditions.

We found other neurons in MST that could play a more general part in signalling the direction of self-motion. Twenty-six

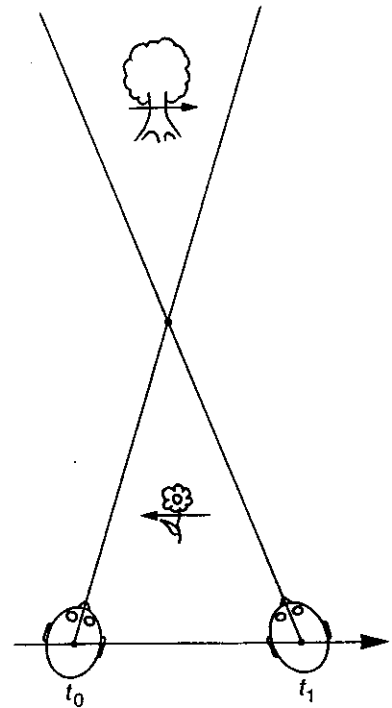


FIG. 1 Opposite motions of the background and foreground during self-motion (top view). As an observer moves to the right (large right-pointing arrow) while tracking an object, the direction of motion of the images of objects will depend on their depth relative to the point of fixation (the dot). An object in the background (behind the fixation point) 'moves' in the direction of self-motion; at time t_0 , the image of the tree is to the left of the line of gaze, at time t_1 , it is to the right: relative to the line of gaze, its image has moved to the right (small right-pointing arrow). An object in the foreground (in front of the fixation point) 'moves' in the opposite direction; at time t_0 , the image of the flower is to the right of the line of gaze, at time t_1 , it is to the left: its image has moved to the left (small left-pointing arrow). These opposite motions of the background-foreground will be generated when the observer does not look in the direction of his self-motion.

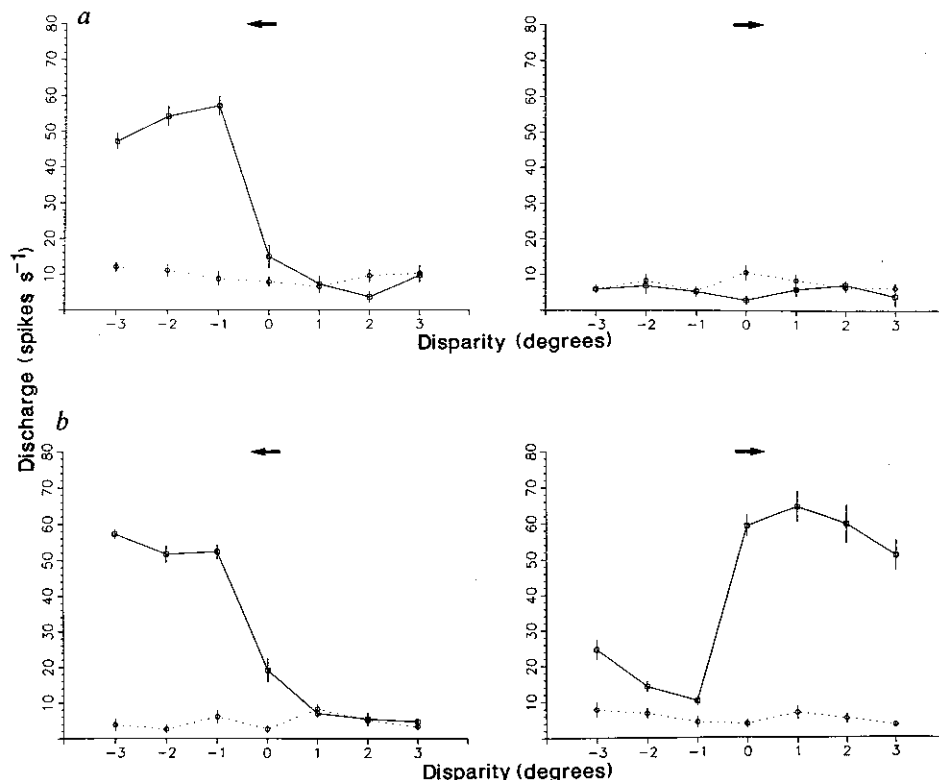
cells out of the 65 tested (40%) preferred one direction of motion when the monkey was presented with visual stimuli of one sign of disparity and the opposite direction of motion for visual stimuli of the opposite sign of disparity (Fig. 2b). This disparity-dependent direction selectivity means that the cell would respond during self-motion in one direction, irrespective of where in depth the animal is fixating. The neuron will respond when the foreground moves to the left or when the background moves to the right or both. These neurons then seem to signal the direction of self-motion relative to the object fixated under any conditions of viewing, as long as the direction of gaze and the direction of self-motion are different.

Most disparity-dependent directional selective neurons responded above the spontaneous level for one direction of motion when the disparity was 0° (as illustrated in Fig. 2b for rightward motion). This response could be associated with the foreground motion (4/20), background motion (9/20), both (5/20), or neither (2/20). This finding is consistent with the observation that rhesus monkeys are not able to track with perfect accuracy⁶. Their gaze either overcompensates for the self-motion causing the object tracked to 'move' with the background, or undercompensates causing the object tracked to 'move' with the foreground.

The relation between direction and disparity was not affected by varying the speed of motion of the visual stimuli: a disparity-dependent direction neuron did not become non-disparity-dependent when the stimuli moved at different speeds (6° s⁻¹, 16° s⁻¹ and 26° s⁻¹). Also, the sign of disparity (crossed or uncrossed) for a given direction remained the same for all speeds tested. When other physiological properties of these neurons

* Present address: Department of Neurology and Neurosurgery, Montreal Neurological Institute, Montreal, Quebec H3A 2B4, Canada.

FIG. 2 In *a*, an MST neuron discharges (continuous line) above the spontaneous rate (dotted line) for crossed disparities (indicated by a minus sign) when the stimuli move in one direction (left) but does not respond when the stimuli move in the opposite direction (right). Speed of motion for both directions is 6° s^{-1} . In *b*, another MST neuron discharges above the spontaneous rate for crossed disparities when the stimuli move in one direction (left), and discharges above the spontaneous rate for the opposite uncrossed disparities when the stimuli move in the opposite direction (right). Speed of motion for both directions is 6° s^{-1} . Random dot red/green anaglyph stimuli were presented at seven disparities: crossed: $-3^\circ, -2^\circ, -1^\circ, 0^\circ$; uncrossed: $1^\circ, 2^\circ, 3^\circ$. These stimuli were presented five times, randomly interleaved, in the central $20^\circ \times 20^\circ$ region of the neuron's receptive field. Receptive field size and eccentricity, preferred stimulus, preferred speed and preferred direction were determined, after which the disparity stimuli moving in the preferred and non-preferred direction were back-projected on a screen where the monkey fixated on a spot of light. The distance of fixation was maintained at 86 cm throughout the experiment. The position of both eyes was monitored using the search coil technique⁸ and the monkeys (two *Macaca mulatta*) had to maintain fixation within a $0.3^\circ \times 0.3^\circ$ electronic window throughout the stimulus presentation to receive a liquid reward. Single-cell discharges were counted in a time window of 400–1,000 ms after stimulus onset to



were compared, the only difference found was a predominance of disparity-dependent direction-selective neurons preferring horizontal motion (rightwards or leftwards) as opposed to oblique or vertical motion: 62% responded preferentially to a horizontal axis of motion, whereas only 36% of the non-disparity dependent direction neurons responded preferentially to horizontal motion. This preference of disparity-dependent direction-selective neurons for horizontal motion supports our interpretation of a role for these cells in indicating the direction of self-motion: macaque monkeys are primarily terrestrial animals and so their locomotion will most often be horizontal⁷. Other physiological characteristics were equally distributed among the two types of neurons: preferred disparity, preferred direction, receptive field size, receptive field eccentricity, and frequency of receptive fields crossing the vertical meridian.

The disparity-dependent direction-selective neurons described here could provide a signal about the direction of self-

remove the non-directional on-response, and a time window of $-600-0$ ms was chosen for the spontaneous condition. Vertical lines indicate standard error over the five trials. Other experimental conditions were as before⁹.

motion when the observer moves in one direction while tracking an object in another direction. This corresponds to the condition where the direction of self-motion relative to the object tracked has a horizontal component. When there is no horizontal component to the self-motion, such as when the observer moves directly towards the object tracked, the optic flow is a pure expansion and the disparity-dependent direction-selective neurons, then, are unlikely to respond. Other neurons that do respond specifically to expansion have been described in MST^{4,5}. We propose that just as the expansion neurons could indicate the forward component of self-motion, the disparity-dependent direction-selective neurons could indicate the horizontal (rightward or leftward) component of self-motion. As the angle between gaze and self-motion changes during locomotion, these two cell types would provide a continuously changing signal about the direction of self-motion relative to the object tracked. □

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