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RESEARCH NOTE

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Velocity invariance of preferred axis of motion for single spot stimuli in simple cells of cat striate cortex

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Abstract Directional tuning for motion of a long bar and a spot was compared quantitatively over a wide range of velocities in 23 simple cells of cat striate cortex whose "on" and "off" receptive field subregions had been mapped with optimally oriented, stationary flash-presented bars. Tuning curves were derived using stimuli whose polarity of contrast was appropriate for the dominant receptive field subregion of each cell (i.e. light stimuli for on-subregions and dark stimuli for off-subregions); stimulus sweep was centred accurately on the centre of that subregion. Bar stimuli were of optimal width, and spot diameter was equal to the width of the bars. In all simple cells, preferred axis of motion for a long bar was invariant with velocity, being orthogonal to preferred orientation, as assessed with a stationary flash-presented bar. In 20 of 23 simple cells, preferred axis for spot motion was approximately orthogonal to that for bar motion (i.e., parallel to preferred orientation) at all velocities tested, including those just above threshold for spot stimuli. However, tuning for the spot became sharper as velocity was increased, due to an increase in response to the spot moving along the preferred axis and a decrease in response to spot motion along other axes, including the preferred axis for the bar. Both preferred and upper cut-off velocity were consistently higher for spot than for bar motion. The remaining 3 simple cells showed no response to spot motion at any velocity, and their preferred axis of motion for the shortest bar which evoked a consistent response was the same as that for a long bar. We conclude that simple cells respond to motion of a spot *per se* and not just to its oriented components, and that in most simple cells preferred axis for spot motion is genuinely approximately orthogonal to that for motion of a long bar. A spatio-temporal filter model incorporating intracortical feedforward facilitation along the long axis of the receptive field can account for the observed differences in axis preference and velocity sensitivity for spot and bar motion.

Key words Striate cortex · Simple cells
Single spot stimuli · Axis preference
Influence of velocity · Cat

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Introduction

Henry et al. (1974a, b) reported that in simple and complex cells of cat striate cortex (area 17) preferred axis of motion was invariant with stimulus length. It was subsequently shown that in areas 17 and 18 the preferred axis of motion for a long bar and a spot could differ radically in the same complex cell (Crook 1987, 1990). This finding was obtained independently for area 17 complex cells by Wörgötter and Eysel (1989, 1991), who additionally showed that in most striate simple cells the preferred axis for spot motion was approximately *orthogonal* to that for motion of a long bar. Previous assessments of preferred axis of motion for bar and spot stimuli in cat visual cortex have been made on the basis of directional tuning curves derived at a single velocity. However, theoretical considerations related to the fact that a moving spot stimulus contains a wide range of component orientations and velocities (Movshon et al. 1985; Nakayama 1985; Gizzi et al. 1990; see Discussion) introduce the possibility that the preferred axis of motion for spot stimuli in cat striate cortex might be velocity dependent. Additionally, with particular reference to simple cells in area 17, it has been suggested (G.A. Orban, personal communication) that the orthogonal preferred axes of motion for bar and spot stimuli might be seen only at high velocities when spot motion along the long axis of the receptive field causes greater temporal summation than motion along the axis orthogonal to it. Simple cells might then show similar preferred axes for

bar and spot stimuli at low velocities which are most effective for bar motion. In view of the above considerations, we thought it important to investigate the influence of velocity on axial tuning for spot motion in striate simple cells. We found that, in those simple cells which responded to a moving spot, the preferred axis for spot motion was approximately orthogonal to that for motion of a long bar at all velocities tested, even at velocities just above threshold for the spot, although tuning for the spot became sharper as velocity was increased.

Materials and methods

Full details of physiological preparation and monitoring, visual stimulation and recording have been published elsewhere (Crook et al. 1991), and only aspects of experimental procedure specific to the present study are reported in detail below.

Extracellular recordings were made from single cells with receptive fields within 12° of the area centralis projection, in area 17 (Horsley-Clarke co-ordinates: P4.0–6.0, L1.5–2.0) of lightly anaesthetized (70:30% N_2O/O_2 plus 0.4–0.6% halothane), paralysed (0.06 mg/kg per hour alcuronium chloride) cats, which had been prepared conventionally. Electroencephalogram (EEG), electrocardiogram (ECG), heart rate, arterial blood pressure, end-tidal CO_2 (3.8–4.0%) and body temperature (near 38.5%) were monitored continuously. Neutral contact lenses were applied to the dilated natural pupils, and the cat viewed stimuli at a distance of 28.5 cm or 57 cm, via 5-mm-diameter artificial pupils and supplementary lenses for focal correction.

Cells were classified as "simple" if they possessed at least two adjacent and parallel on- or off-subregions in response to stationary flashedbar stimuli, and spatially separate light and dark discharge centres for moving bar stimuli (Hubel and Wiesel 1962; Bishop et al. 1971; Henry 1977). All simple cells in this report had relatively narrow receptive fields, sharp orientation tuning, little or no resting discharge, and were typically dominated by one or other eye. The lateral borders of the receptive field and on- and off-subregions were mapped with a stationary light bar flashed at optimal orientation, onto a removable, clear Perspex screen slotted immediately in front of the visual display. The locus of maximal response along the receptive field axis was determined by the conventional minimum response field method, using a moving bar; this method, however, typically seriously underestimated receptive field length, which was routinely assessed by qualitative length summation tests, in which the length of a moving bar centred on the dominant receptive field subregion was progressively increased. Simple cells with strong end-inhibition were excluded from the present study.

After a cell's receptive field had been mapped, a post-stimulus time histogram (five consecutive presentations; bin-width 100 ms) was compiled in response to a 10°- or 20°-long stationary bar of appropriate polarity of contrast flashed at optimal orientation on the dominant receptive field subregion (a light bar on an on-subregion or a dark bar on an off-subregion) for 1 s every 2.5 s for 2 s every 5 s. Bar width was adjusted to be slightly smaller than the width of the dominant subregion. Background luminance was 0.25 cd/m^2 and stimulus contrast, 0.3–0.5. Directional tuning curves were then derived for a bar and a spot stimulus in turn moving at the same velocity, with polarity of contrast, background luminance and stimulus contrast unchanged. The dimensions of the stationary and moving bars were identical for each cell, and the diameter of spot stimuli was equal to the width of the bars. Stimuli were swept in opposite directions along each axis of motion, with stimulus sweep centred accurately on the centre of the dominant subregion. Amplitude of motion (typically 20°) was identical for bar and spot stimuli and always substantially exceeded receptive field length, as assessed by qualitative tests of length summation. Axis of motion (always orthogonal to bar orientation) was varied in pseudo-random sequence by multiples of 22.5°; the axes of motion tested were identical for bar and spot stimuli and always included the qualitatively determined preferred axis of motion for the bar and the axis orthogonal to it. Stimulus dimensions were chosen so as to restrict the traverse of the spot stimulus to the dominant subregion when it moved along the long axis of the receptive field. Since the tuning curves for spot stimuli were susceptible to even small residual eye movements, the centring of the stimulus with respect to the centre of the dominant receptive field subregion was checked repeatedly. Peri-stimulus-time histograms (PSTHs) were compiled from five forward and reverse sweeps along each axis of motion, with a period preceeding stimulus motion and an inter-sweep interval each equal to one-fifth of the total histogram cycle (see Fig. 1). Cycle duration was spread over a fixed number of bins (250). Velocity was systematically varied in a random manner by keeping stimulus amplitude constant and changing bin-width (range 3–160 ms) and hence cycle duration. PSTHs were smoothed by combining an appropriate number of bins (range 2–10) and polar diagrams derived by plotting peak firing frequency as vector length and direction as vector angle. Polar diagrams were compiled at typically five velocities, which included the velocity just above threshold for spot motion and that just below upper cut-off for bar motion. Presentation was monocular throughout, with the non-dominant eye occluded.

Results

The experimental paradigm and essential result of the present study are illustrated in Fig. 1, for a simple cell whose hand-plotted receptive field consisted of a dominant on-subregion and an adjacent, parallel off-subregion. When tested quantitatively with a stationary light bar flashed at optimal orientation on the on-subregion of the receptive field, the cell gave a sustained response to stimulus onset, but no response to stimulus offset (Fig. 1A). The directional tuning of the same cell for a light spot moving at three different velocities is shown in Fig. 1C–E, with tuning for a light bar moving at the preferred velocity for the spot (26.7°/s) shown in Fig. 1B for comparison. These directional tuning curves were selected from a series of tuning comparisons for bar and spot motion derived at five velocities. The preferred velocity for the bar (around 10°/s) was lower than that at which the illustrated tuning curve was derived, but axis preference and tuning for bar motion were invariant with velocity (not shown). Preferred axis of motion for the bar was orthogonal to preferred orientation. The preferred axis for the spot was parallel to preferred orientation (corresponding to motion along the long axis of the on-subregion) and hence orthogonal to the preferred axis for the bar, at all velocities tested, even at the velocity just above threshold for spot motion (Fig. 1C). Tuning for the spot was, however, sharper at high (Fig. 1E) than at low (Fig. 1C) velocity. Inspection of the peri-stimulus-time histograms shows that the long bar evoked no response when moving along the preferred axis for the spot (compare Fig. 1B with D) while, at the highest velocity tested, the spot evoked no response when moving along the preferred axis for the bar (compare Fig. 1B with E).

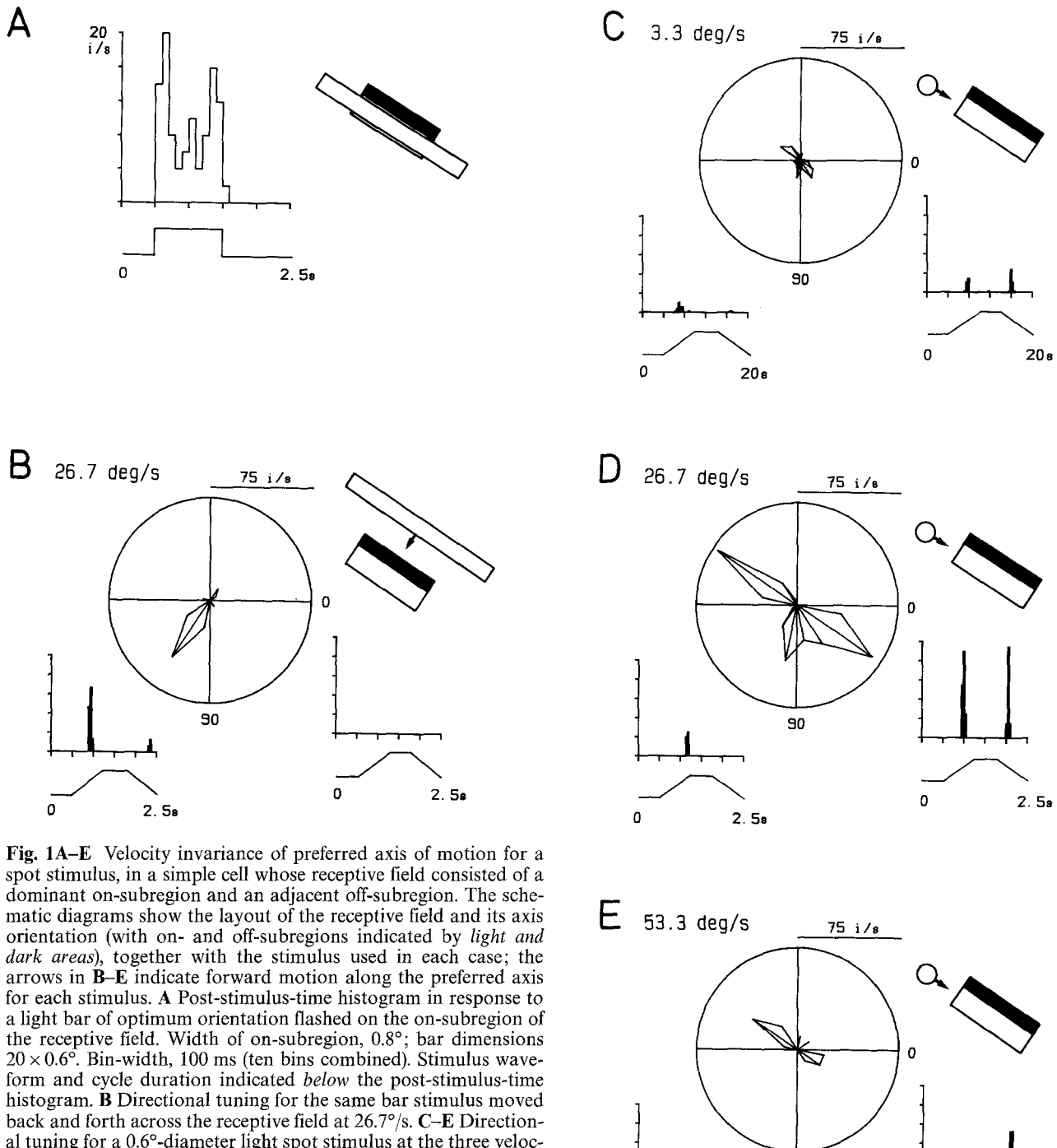

Fig. 1A–E Velocity invariance of preferred axis of motion for a spot stimulus, in a simple cell whose receptive field consisted of a dominant on-subregion and an adjacent off-subregion. The schematic diagrams show the layout of the receptive field and its axis orientation (with on- and off-subregions indicated by *light and dark areas*), together with the stimulus used in each case; the arrows in **B–E** indicate forward motion along the preferred axis for each stimulus. **A** Post-stimulus-time histogram in response to a light bar of optimum orientation flashed on the on-subregion of the receptive field. Width of on-subregion, 0.8°; bar dimensions $20 \times 0.6°$. Bin-width, 100 ms (ten bins combined). Stimulus waveform and cycle duration indicated *below* the post-stimulus-time histogram. **B** Directional tuning for the same bar stimulus moved back and forth across the receptive field at 26.7°/s. **C–E** Directional tuning for a 0.6°-diameter light spot stimulus at the three velocities indicated. In **B–E,** stimulus sweep was centred on the centre of the on-subregion; sweep amplitude 20°. Peri-stimulus-time histograms in response to motion along the preferred axis for the bar and along the preferred axis for the spot are placed at the appropriate vector angle around the perimeter of each polar diagram. Vertical calibration of each peri-stimulus-time histogram, 75 impulses/s. Bin-widths: **B, D** 40 ms; **C** 320 ms; **E** 20 ms; four bins combined in each case; stimulus waveform and cycle duration indicated *below* each peri-stimulus-time histogram. Zero spontaneous activity throughout. Note the velocity invariance of preferred axis of motion for the spot, which was parallel to preferred orientation and orthogonal to preferred axis of motion for the bar

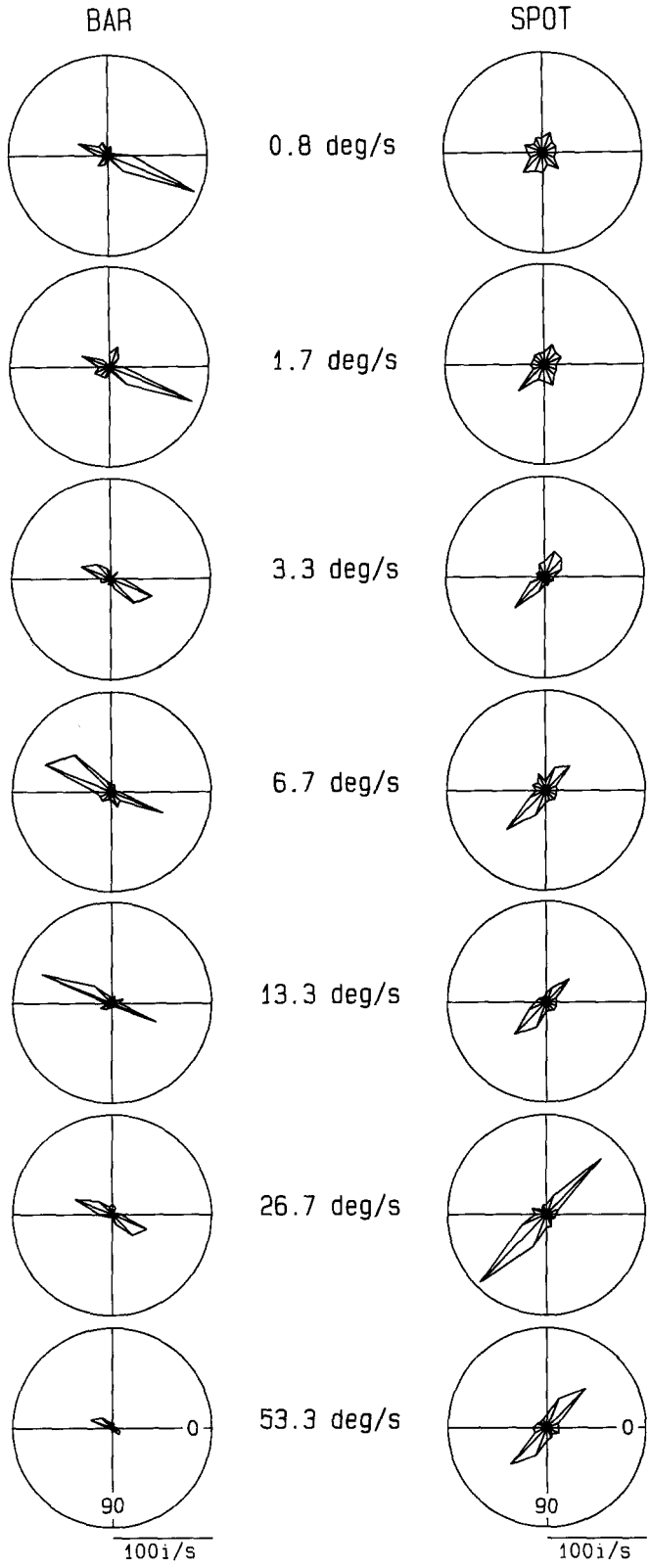

Fig. 2 Comparison of directional tuning of a simple cell for a light bar (20° × 0.4°) and a light spot (diameter 0.4°) (*left and right columns*, respectively), at the seven velocities indicated in the centre. Stimulus sweep was centred on the centre of the dominant on-subregion of the receptive field (width of on-subregion 0.6°). Note that the preferred axis of motion for bar and spot stimuli differed by 67.5° at all velocities tested, including that just above threshold for spot motion; also that both preferred and upper cut-off velocity were clearly higher for the spot than for the bar

Directional tuning comparisons for bar and spot motion over a greater number and wider range of velocities are shown for a different simple cell in Fig. 2. Although for the bar, direction preference (for one of two opposite directions of motion along the preferred axis) reversed as velocity was increased (Orban et al. 1981b), as in all other simple cells preferred axis of motion was velocity-invariant. The preferred axis for spot motion differed by 67.5° from that for bar motion at all velocities tested, even at the velocity which was just above threshold for the spot and optimal for the bar (0.8°/s). However, tuning for the spot became sharper as velocity was increased, due to an increase in response to spot motion along the preferred axis and a decrease in response to the spot moving along other axes, including the preferred axis for the bar. The tuning comparisons in Fig. 2 were chosen for illustration because they show that the radical difference in the preferred axes of motion for bar and spot stimuli could be maintained over a wide range of velocities. The high upper cut-off velocity for the bar was atypical; most of our striate simple cells showed velocity low-pass functions for bar motion (Orban et al. 1981a). However, even in the cell illustrated in Fig. 2, it is clear that both preferred and upper cut-off velocity were higher for the spot than for the bar. This difference in velocity tuning for bar and spot motion was a consistent feature of the present results.

The radical difference in preferred axis of motion for bar and spot stimuli illustrated in Figs. 1 and 2 was seen in all simple cells which responded to spot motion (20/23). Eighteen cells showed orthogonal preferred axes for bar and spot motion (Fig. 1); in two cells the observed difference in axis preference was 67.5° (Fig. 2). Three cells showed no response to spot motion at any velocity. Their preferred axis of motion for the shortest bar which evoked a consistent response was the same as that for a long bar.

Discussion

The principal aim of the present study was to test the hypothesis that in simple cells of cat striate cortex the preferred axis of motion for a single spot stimulus is velocity dependent. It had been suggested (G.A. Orban, personal communication) that, in striate simple cells, the preferred axes for motion of a long bar and a spot might be similar at low velocities, but orthogonal at high velocities when spot motion along the long axis of the receptive field causes greater temporal summation than motion along the axis orthogonal to it. We found, on the contrary, that in those simple cells which responded to spot motion, the preferred axis for the spot was approximately orthogonal to that for a long bar and parallel to preferred orientation at all velocities tested, even at velocities just above the threshold for spot motion.

Superficially, the approximately orthogonal preferred axes for motion of an oriented bar and a single spot, together with the velocity invariance of axis prefer-

ence for each stimulus, would seem to suggest the existence of separate orientation and directional/motion mechanisms in striate simple cells. A dissociation of orientation and directional/motion mechanisms has been postulated previously for complex cells on the basis of their radically different preferred axes of motion for a long bar and a field of visual texture or a single spot stimulus (Hammond 1978; Hammond and Reck 1980; Hammond and Smith 1983; Crook 1990, 1991). However, it has been pointed out (Movshon et al. 1980, 1985; Nakayama 1985; Gizzi et al. 1990) that axis selectivity in response to motion of texture or single spot stimuli cannot *a priori* be attributed to directional/motion mechanisms. Both types of stimulus contain components at all orientations, and the velocity of each component decreases with the angle between its orientation and the overall direction of motion. Movshon et al. (1980) have suggested that the difference in the preferred axes of motion for bar and texture stimuli, which is typically most pronounced above the optimum velocity for bar motion, can be explained by assuming that a cell's response to texture merely reflects its sensitivity to the vectorial component of texture velocity along the preferred axis for a moving bar, the vector of velocity along this axis being lower than the velocity of texture motion to either side. In principle, a similar explanation could account for the radically dissimilar preferred axes of motion for bar and single spot stimuli. This hypothesis implies that preferred axis of motion is always orthogonal to preferred orientation. As far as complex cells are concerned, there are grounds for rejecting it. There are aspects of complex-cell tuning for texture motion which the hypothesis does not predict. In particular, many complex cells show radically different preferred axes for bar and texture motion well below the preferred velocity for either stimulus (Hammond and Smith 1983; Crook 1990). Additionally, some two-thirds of complex cells show both broader and more asymmetrical orientation tuning for a moving bar than for a stationary flash-presented bar, with broader tuning for bar motion on the flank closest to the preferred direction of motion for a single spot stimulus (Crook 1991). The broader, more asymmetrical tuning for a moving bar presumably reflects stimulation of the directional mechanism caused by bar *motion*. This implies that in many complex cells preferred axis of motion is not orthogonal to preferred orientation. The results from the present study indicate that the same is true for striate simple cells. Had the preferred axis for spot motion simply reflected sensitivity to components oriented orthogonal to the preferred axis of motion for a bar, one would have expected axis preference for the spot to be velocity dependent. A cell would have shown similar preferred axes for bar and spot stimuli at some (low) velocity when the speed of those components of the spot oriented orthogonal to the preferred axis for the bar matched the cell's preferred velocity, with the preferred axis for spot motion shifting progressively further away from that for bar motion as velocity was increased. Approximately orthogonal preferred axes of motion for bar and spot stimuli would have been seen only at high velocities when only components oriented almost parallel to the axis of spot motion would have moved slowly enough to be effective. We found, on the contrary, that in most simple cells preferred axis for spot motion was approximately orthogonal to that for bar motion at velocities just above threshold for the spot and remained so over a wide range of velocities in the face of a marked increase in response to spot motion. We conclude that both simple and complex cells respond to motion of a spot *per se* and not just to its oriented components, and that in most simple cells preferred axis for spot motion is genuinely approximately orthogonal to that for motion of a long bar.

That most simple cells show approximately orthogonal preferred axes of motion for bar and spot stimuli is probably a straightforward consequence of the marked elongation of simple-cell receptive field subregions. Since most simple cells respond weakly to a flash-presented spot, the vigorous responses to spot motion would seem to be due predominantly to temporal mechanisms operating along the long axis of the receptive field. Directional responses to spot motion along the preferred axis and the change in directionality with velocity (Figs. 1, 2) might then reflect the balance of facilitation and inhibition along the length of each receptive field subregion, much as the facilitatory and inhibitory interactions contributing to simple-cell direction selectivity for bar motion can occur within each on- or off-zone (Goodwin et al. 1975; Emerson and Gerstein 1977; Ganz and Felder 1984).

Wörgötter and Holt (1991) have developed a spatio-temporal filter model of simple-cell receptive fields incorporating intracortical feedforward facilitation along the long axis of each subregion which can account for the axial preference and tuning and velocity sensitivity for spot motion observed in the present study. The model predicts that the preferred axis for spot motion is orthogonal to that for motion of a long bar at all velocities above threshold. We found this to be the case in 18 of the 20 simple cells which responded to spot motion. The difference in preferred axis of motion for bar and spot stimuli of 67.5° seen in the remaining two cells (see Fig. 2) may be explained by considering the detailed two-dimensional receptive field structure in simple cells. The individual subregions of simple-cell receptive fields can be irregular in shape, and of different length and/or displaced relative to each other along an axis parallel to their long dimensions (Jones and Palmer 1987). These factors, coupled with the rather coarse "grain" of our tuning curves (22.5°), may account for observed differences in preferred axes of motion for bar and spot stimuli of less than 90°. Two further aspects of the present results which were predicted by the model of Wörgötter and Holt (1991) are the higher preferred and upper cut-off velocity for spot motion compared with bar motion and the sharper axial tuning for spot motion at high than at low velocity.

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