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Selectivity for Orientation and Direction of Motion of Single Neurons in Cat Striate and Extrastriate Visual Cortex

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SUMMARY AND CONCLUSIONS

1. We consider the consequences of the orientation selectivity shown by most cortical neurons for the nature of the signals they can convey about the direction of stimulus movement. On theoretical grounds we distinguish *component direction selectivity*, in which cells are selective for the direction of movement of oriented components of a complex stimulus, from *pattern direction selectivity*, or selectivity for the overall direction of movement of a pattern irrespective of the directions of its components. We employed a novel test using grating and plaid targets to distinguish these forms of direction selectivity.

2. We studied the responses of 280 cells from the striate cortex and 107 cells from the lateral suprasylvian cortex (LS) to single sinusoidal gratings to determine their orientation preference and directional selectivity. We tested 73 of these with sinusoidal plaids, composed of two sinusoidal gratings at different orientations, to study the organization of the directional mechanisms within the receptive field.

3. When tested with single gratings, the *directional tuning* of 277 oriented cells in area 17 had a mean half width of 20.6°, a mode near 13°, and a range of 3.8–58°. Simple cells were slightly more narrowly tuned than complex cells. The selectivity of LS neurons for the direction of moving gratings is not markedly different from that of neurons in area 17. The mean direction half width was 20.7°.

4. We evaluated the *directional selectivity* of these neurons by comparing responses to stimuli moved in the optimal direction with those elicited by a stimulus moving in the opposite direction. In area 17 about two-thirds of the neurons responded less than half as well to the non-preferred direction as to the preferred direction; two-fifths of the units responded less than one-fifth as well. Complex cells showed a somewhat greater tendency to directional bias than simple cells. LS neurons tended to have stronger directional asymmetries in their response to moving gratings: 83% of LS neurons showed a significant directional asymmetry.

5. Neurons in both areas responded independently to each component of the plaid. Thus cells giving single-lobed directional-tuning curves to gratings showed bilobed plaid tuning curves, with each lobe corresponding to movement in an effective direction by one of the two component gratings within the plaid. The two best directions for the plaids were those at which one or other single grating would have produced an optimal response when presented alone. For simple cells the size of the lobes depended on the relative spatial phase of the component gratings, but this was not the case for complex cells.

6. Although the shape of tuning curves for plaids could be well predicted from responses to gratings, the plaid responses of cells in area 17 were on average one-third smaller than expected. This probably reflects inhibitory processes acting in the orientation domain. This effect was much less pronounced in LS.

7. We tested a few LS neurons for their sensitivity to the orientation of stationary gratings whose contrast was modulated in time. All showed a definite selectivity for the orientation of these targets, which closely matched the same neurons' selectivity for the orientation of moving gratings.

8. We conclude that cells in both area 17 and LS show response patterns to two-dimensional stimuli that are linked to the orientation of the stimulus' spatial components and not to the direction of motion of the whole stimulus pattern. Thus directional selectivity in these neurons appears to be secondary to orientational selectivity.

INTRODUCTION

The responses of most visual cortical neurons are influenced by the direction of motion of visual targets. These neurons are typically selective for stimulus orientation, and, because extended oriented targets can only move in a direction orthogonal to their orientation, they respond preferentially to certain directions of motion of oriented stimuli. In addition, most cortical neurons respond reliably better to motion in one direction than to its opposite. Because neurons in some cortical areas that are direction selective seem also to be orientation selective, it is interesting to consider the effects of this orientation selectivity on the way these neurons can signal visual motion. If simple line or grating stimuli are used, only two directions of motion (orthogonal to the pattern's orientation) are possible, and a direction-selective neuron could signal which of these two directions was present. When more complex patterns containing many orientations are used, however, it is less obvious how these neurons will respond. It is necessary to consider information about the motion of contours or spatial components of more than one orientation to discriminate the true motion of complex patterns (Adelson and Movshon 1982; Marr and Ullman 1981; Movshon et al. 1985; Wallach 1935). In striate cortex, neurons have been modeled as quasilinear spatiotemporal filters (DeValois et al. 1982; Movshon et al. 1978a–c) that should, in effect, be "blind" to all orientations outside their response range, and their responses should not be affected by them. Yet, the addition to a moving grating of a second, very different in orientation, can dramatically alter the direction in which a pattern is seen to move (Adelson and Movshon 1982; Movshon et al. 1985; Wallach 1935). We became interested in the question of whether the direction selectivity of orientation-selective neurons in general and striate neurons in particular is merely a selectivity for the direction of motion of the oriented constituents of a pattern or whether these neurons have a more complex organization than has been thought and can correctly signal the motion of whole patterns.

We formalize this question by defining two possible kinds of direction selectivity that a visual neuron might exhibit. *Component direction selectivity* represents a selectivity for the direction of motion of particular oriented components of a pattern without regard to the overall motion of the pattern that contains them. *Pattern direction selectivity* represents a selectivity for the direction of motion of simple or complex patterns that is independent of the orientation of particular components of moving patterns. Component direction selectivity should be shown by neurons that are truly orientation selective but that also respond preferentially to one of the two directions of motion possible for properly oriented stimuli. Pattern direction selectivity should be shown by neurons that are primarily sensitive to directional motion and that do not have a particular orientation preference. Although most workers agree that most striate neurons are orientation selective and would thus be expected to be component direction selective, some have described a group of neurons of the complex type as being "pure direction selective" (Bishop et al. 1980; Blakemore and Van Sluyters 1975; Cynader et al. 1976; Palmer and Rosenquist 1974); these might plausibly be expected to be pattern direction selective.

There has been disagreement in the literature concerning the status of direction selectivity as a fundamental property in the receptive fields in LS neurons as well as the presence or absence of orientation selectivity. Most neurons in LS have large, direction-selective receptive fields whose general organization resembles that of complex cells in areas 17 and 18. Wright (1969) and Hubel and Wiesel (1969) studied the selectivity of LS neurons with the use of moving line stimuli and claimed that these neurons, like their afferents from areas 17 and 18, are selective for stimulus orientation. On the other hand, Spear and Baumann (1975) argue that LS neurons are not truly orientation selective because they respond with roughly the same vigor and directional specificity to moving spots as they do to moving lines. Because they found few neurons that responded well to stationary flashing stimuli, they could not generally test for orientation selectivity by using stimuli that do not move. More recent studies (Blakemore and Zumbroich 1987; Morrone et al. 1986; Zumbroich and Blakemore 1987) have found that those cells in LS that do respond to stationary phase-reversing sine-wave gratings do so in an orientation-selective manner, but a large proportion remain that cannot be tested in this fashion. The disagreement suggests that a well-defined test for orientation selectivity using moving stimuli (to which nearly all LS cells would respond) should be devised.

Tests of direction and orientation selectivity

To provide a clear test for these two kinds of directional selectivity, it is necessary to use stimuli that dissociate the orientations of the constituents of patterns from the direction in which they move. Previous attempts to make this kind of distinction have relied primarily on establishing the presence of orientation selectivity as determined either by the response to stationary flashed line or grating stimuli or by comparison of the response to motion of spots with that to lines or extended edges. If orientation selectivity cannot be demonstrated in a particular neuron, it is by default considered to be pure direction selective or (in our terms) pattern direction selective (Barlow and Pettigrew 1971; Cynader et al. 1976; Palmer and Rosenquist 1974; Spear and Baumann 1975; Zeki 1974). These criteria for orientation and direction selectivity are problematic.

Establishing orientation selectivity with flashing stimuli requires that a neuron respond reliably to these stimuli; many neurons in the striate and extrastriate visual cortex respond weakly if at all to flashed stimuli. On the other hand, comparing responses with spots and lines is also unsatisfactory. First, the test assumes that a spot of light is a stimulus without orientation and that any selectivity for direction of motion must therefore be attributable to directionally selective mechanisms. A spot, however, does not contain *no* orientations but rather contains *all* orientations. This is not merely a semantic point because it means that a spot is orientationally isotropic only so long as it is stationary. When it is moved, the oriented components that it contains are moved differentially: those oriented orthogonally to the movement are moved most rapidly, whereas those parallel to the movement are *not moved at all*. Thus a moving spot is, in fact, an orientationally biased stimulus and should elicit selective responses from any orientationally selective neuron, even if the neuron is not directionally selective. Indeed, the presence of inhibition in the orientation domain (Blakemore and Tobin 1972; Creutzfeldt et al. 1974) might even make an orientationally selective neuron *more* selective for the direction of spot motion than for bar motion. Moreover, there is no consensus in the literature concerning either the relative size and contrast of the bar and line stimuli to use for this test or the magnitude of the difference in response or selectivity needed to establish a cell as "orientation selective." This lack of agreement reflects the lack of a theoretical basis for the spot/line test.

A NEW TEST OF DIRECTION SELECTIVITY. The test we used to distinguish between the two types of direction selectivity relies on the difference in a cell's response to moving grating and plaid stimuli. Sine-wave plaids are composed of two gratings that differ only in orientation. A single grating, like a single line, always moves in a direction orthogonal to its orientation. A plaid, however, may be moved in such a way that the overall direction of movement bisects the angle separating the orientation of its component gratings. The insets in Fig. 1 show a single grating (*top*) and a 90° plaid (*bottom*). In the plaid, each component grating's orientation is 45° from the direction of motion; the single grating, of course, is oriented 90° from its direction of motion. A pattern-direction-selective neuron should show the same directional preference for gratings and for sine-wave plaids. A component-direction-selective neuron, however, should respond not to the direction of overall pattern motion, but to the direction of motion of each of the oriented component gratings within the pattern. When the plaid is oriented so that one of the gratings falls within such a neuron's orientation tuning curve, the other would be "invisible" to the neuron and should therefore not affect its response. This test, then, does not require that the neuron respond to stationary patterns, and it has the further advantage that the stimuli to be compared are identi-

cal in luminance, spatial extent, and physical contrast. It is not applicable to neurons that fail to respond to gratings, but there are few visually responsive neurons in the visual cortex that do not give reasonable responses to gratings.

Predictions for the responses of component- and pattern-direction-selective neurons are easy to generate. The polar diagrams in Fig. 1 illustrate the responses of a hypothetical component-direction-selective neuron to the inset gratings and plaids. In each plot the direction of motion of the stimulus is indicated by the angle, and the response of the cell to that direction by the distance of the point from the origin. This "neuron" responded best to gratings moving directly rightward; it was direction selective and failed to respond to motion in the back direction; the direction-tuning curve for a single grating has therefore a single peak corresponding to the best direction of motion. Because the neuron should respond to each grating in the plaid in this same manner, the predicted direction-tuning curve to a plaid is the sum of the responses to the two components presented separately. The bottom polar plot in Fig. 1 shows this prediction. Because direction of motion is the angular coordinate of the polar plot, the peaks corresponding to the two component gratings are each displaced 45° from the peak response to a single grating. The predicted tuning curve for the plaid is thus a bilobed curve whose peaks straddle the single peak derived from the single grating experiment. The prediction for pattern direction selectivity is equally simple: the neuron's tuning curves for gratings and plaids should be similar because their directions of motion are the same. The predicted tuning curve is thus simply the curve derived from the single grating experiment (shown in the top polar plot). The two predictions for the different types of direction selectivity are radically different, and the actual response of a neuron can be compared with each.

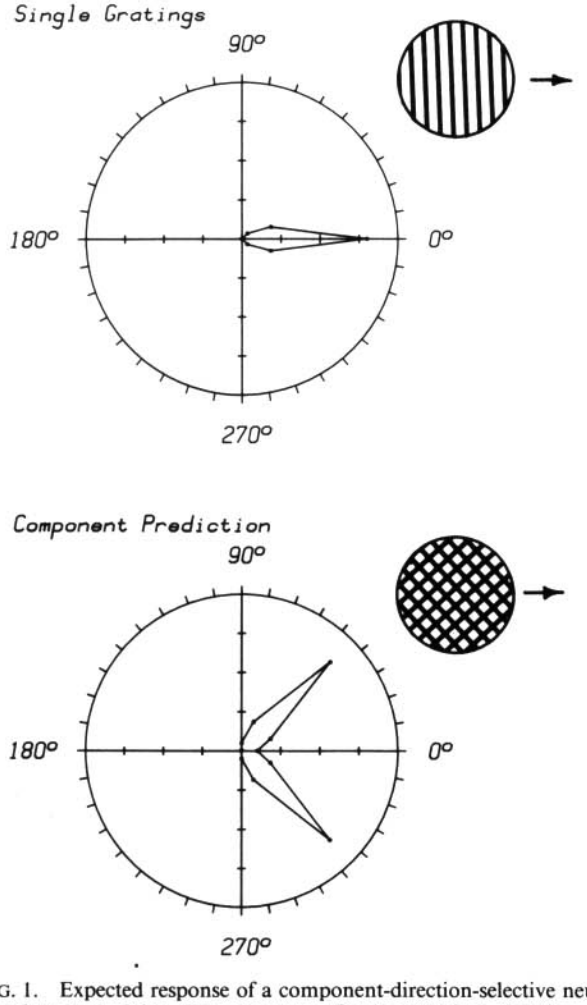

FIG. 1. Expected response of a component-direction-selective neuron to gratings and plaids. *Top*: response of a hypothetical direction- and orientation-selective neuron to single grating targets (*inset*). The polar diagram shows response as a function of the direction of target motion; this particular neuron prefers vertical gratings moving rightward. *Bottom*: the expected response of the same neuron to plaids produced by superimposing 2 moving gratings. While each grating alone moves perpendicular to its orientation, the composite plaid moves in a direction exactly between those of the 2 gratings. In the case of the 90° plaid shown in the inset, the direction of motion is 45° from the orientation of each of the gratings. The cell would not respond to rightward motion of a plaid, but rather to those plaids in which the component gratings were oriented optimally. This response is simply the sum of the responses to the 2 component gratings.

We have applied the test outlined above to neurons in the cat's striate and lateral suprasylvian cortex (LS) and find that almost all of them are component direction selective, even when they fail conventional tests of orientation selectivity. This suggests that descriptions of striate cortical neurons in terms of quasilinear spatial, orientational, and temporal filtering provide a good approximation to their actual behavior. Furthermore, our results from LS unambiguously demonstrate that these neurons, like their afferents from area 17, are component direction selective. LS neurons are, in general, insensitive to the true direction of motion of complex patterns, and we observed no clear case of pattern direction selectivity in this population. This also means that LS neurons are genuinely orientation selective because their response to direction of motion is clearly secondary to the determination of orientation. Portions of this work have been briefly described elsewhere (Gizzi et al. 1981; Movshon et al. 1985; Movshon et al. 1980).

METHODS

Surgical preparation and maintenance

Adult cats (2.5–4 kg) were anesthetized with halothane. After venous cannulation, surgery was carried out under intravenous pentobarbital sodium or sodium thiopental anesthesia. Anesthesia was maintained during recording by artificial ventilation with a mixture of N_2O, O_2, and CO_2 (typically 49:49:2), combined with an infusion of pentobarbital sodium (1–2 $mg \cdot kg^{-1} \cdot h^{-1}$). In some cases the gas ratios were 75:23:2, and the additional barbiturate anesthetic was only given when electroencephalogram (EEG) or autonomic signs indicated its necessity. Infusion of gallamine triethiodide (Flaxedil, 10–20 $mg \cdot kg^{-1} \cdot h^{-1}$) or pancuronium bromide (Pavulon, 0.15 $mg \cdot kg^{-1} \cdot h^{-1}$), together with bilateral cervical sympathectomy, served to minimize eye movements. These infusates were given in 5% lactated dextrose Ringer solution at a rate of 5.4 ml/h. Rectal temperature was maintained near 37.5° with a thermostatically controlled heating pad. The end-expiratory P_{CO2} was continuously monitored and held between 4 and 4.5% by manipulation of the respiratory volume or the proportion of CO_2 in the inspired gas mixture. EEG and electrocardiogram (EKG) were continuously monitored to verify

the adequacy of anesthesia and the soundness of the animal's physiological condition.

Recording

Tungsten-in-glass microelectrodes (Levick 1972) were advanced hydraulically into the striate cortex through a small craniotomy and durotomy centered near the midline between Horsley-Clarke coordinates P3 and P7. Penetrations were angled to proceed down the medial bank of the lateral gyrus. Most units had receptive fields within 5° of the area centralis, and all were within 15°. For the LS recordings craniotomies were placed between Horsley-Clarke coordinates A4 and P2 from L12 to L14, and the electrode tracks were directed obliquely down the medial bank of the suprasylvian sulcus, toward the representation of the central visual fields in the area designated posterior medial lateral suprasylvian (PMLS) by Palmer and his colleagues (1978). With the electrode in place, the brain was covered with agar gel to minimize pulsation and preserve the condition of the cortex.

Histology

In most experiments, electrolytic lesions were placed at points along the track by passing DC current (1–2 μA, 1–4 s, tip negative) through the electrode. At the end of the recording session, the animal was killed with an overdose of barbiturate and perfused through the heart with Ringer solution followed by 10% formol-saline. Blocks of cortex were cut in the plane of the electrode tracks, frozen sectioned at 40 μm, and stained with cresyl violet. In those cases in which we did not obtain histological verification that the recordings were made from area 17, the position of the recording electrode, relatively high preferred spatial frequency and small size of the receptive fields, and consistent drift of receptive fields into the contralateral hemifield convinced us that our recordings were from area 17. All electrode tracks in the lateral suprasylvian gyrus were reconstructed histologically and cells were assigned to areas PMLS or posterior lateral lateral suprasylvian (PLLS) (Palmer et al. 1978).

Physiological optics

Topical atropine sulfate and neosynephrine hydrochloride produced mydriasis and cycloplegia, and the corneas were protected with zero-power contact lenses containing 4 mm artificial pupils. Supplementary lenses chosen by direct ophthalmoscopy were used to make the retinas conjugate with a screen 57 cm distant. The locations of the visual axes were determined by projecting an image of the fundus onto the plotting screen (Fernald and Chase 1971).

Visual stimulation

The receptive fields of each unit were first mapped by hand with the use of stationary and moving bars, edges, and spots rear-projected onto the tangent screen. In area 17, neurons were classified as simple or complex on the basis of the spatial arrangement of "on" and "off" regions and the presence of spatial summation within each region (Hubel and Wiesel 1962). We found that the spatial relationship between the regions of the receptive field that gave excitatory responses to moving light-dark borders was useful in classifying as simple those few cells of this type that could not be reliably excited by stationary targets (Henry 1977). These classifications were later confirmed by the degree to which the units modulated their firing rate in synchrony with the passing bars of moving sinusoidal gratings (Maffei and Fiorentini 1973; Movshon et al. 1978a, 1978b). We distinguished "special" from "standard" complex neurons by the former's relatively large receptive fields, high spontaneous firing rate, and brisk responsiveness to spots and lines whose size was small compared to the receptive field. The receptive fields of LS units were initially mapped by hand on a tangent screen by the use of moving and flashing lines, edges and spots, and classified into the four types described by Spear and Baumann (1975): *directional* (both unidirectional and bidirectional), *motion only* (no preference for direction), *stationary*, and *indefinite*. All area 17 units and the majority of LS units had receptive fields centered within 10° of the area centralis.

After a unit was selected for quantitative study, the eye less effective in driving the unit was occluded, and the receptive field in the other eye was reflected onto the face of a display oscilloscope (Tektronix 608 or Hewlett-Packard 1332A) subtending 10° at the cat's eye. A PDP 11 computer generated grating and plaid stimuli on this CRT by luminance modulating a uniform raster whose mean luminance was near 40 cd/m^2, regardless of the presence or absence of a stimulus. The orientation of grating stimuli could be changed between frames (8-ms duration), and plaid stimuli were generated by displaying two gratings of differing orientation on alternate frames. The spatial frequency, temporal frequency of drift, orientation and direction of motion, spatial extent, and contrast of the patterns were under direct computer control. All neurons were tested with gratings of optimal spatial and temporal frequency and moderately high contrast (0.25–0.5). For single gratings, we used the conventional definition of contrast (the difference between the maximum and minimum luminance in the pattern divided by twice the mean); when plaid stimuli were used, we constructed them by adding two gratings each of whose contrasts was the same as the contrast of the single gratings used to test the neuron; as a result, the physical contrast of plaid stimuli was double that of grating stimuli, but the "contrast per component" of all stimuli was identical. The screen subtended between 10 and 20° and stimuli could be restricted electronically to a smaller rectangular region of arbitrary size; in this case the surrounding region was uniformly illuminated at the prevailing mean luminance. In this way stimuli could be confined to the excitatory portion of the receptive field. This was necessary for ~10% of the units studied, whose receptive fields contained inhibitory surrounds that markedly attenuated responses to extended stimuli. In these cases we used the largest area of stimulation that did not produce a decrement in the cell's response.

Data collection and analysis

The computer was also used to collect average response histograms and perform on-line analysis. Each experiment consisted of several blocks of trials (usually 5). Within each block, all stimuli were presented for the same amount of time (between 2.5 and 10 s); the order of presentation was randomized to reduce the effect of response variability. In all experiments, a uniform raster of the standard mean luminance was included as a blank stimulus to provide a measure of the unit's spontaneous firing rate.

Spatial frequency and drift rate were optimized either by manually adjusted contrast sensitivities or by extracting optima from spatial and temporal frequency tuning experiments. Using these optima, we measured the unit's directional tuning. Typically, 24 or 32 directions covering a 360° range were presented. Direction tuning for plaids and gratings were compared to classify the cells as component or pattern direction selective. Plaids composed of gratings separated by either 90 or 135° were used, and some experiments were repeated using two different relative phases for the component gratings. Direction-tuning experiments for these and for single gratings of the same spatial frequency as the components of the plaids were interleaved, so that all the direction-tuning curves to be compared were collected simultaneously.

RESULTS

We studied 280 units recorded from the striate cortex. Three of these were unselective for the orientation or direction of motion of gratings. For the remainder we extracted tuning curves for the direction of moving gratings. In the LS we examined the receptive fields of 322 neurons recorded in the cortex adjacent to the suprasylvian sulcus. Of these, 107 gave sufficiently reliable responses and were recorded with sufficient stability to warrant quantitative study. Ninety-five of these neurons were histologically verified to be within PMLS as defined by Palmer et al. (1978). Five neurons were recorded in the adjacent area PLLS, and seven could not definitely be assigned to either area. The properties of these 12 neurons did not differ systematically from those of the rest of our sample. Some of our penetrations passed through area 7 near the lip of the suprasylvian sulcus, but we did not encounter any visually responsive neurons in this area. We used the receptive-field types of Spear and Baumann (1975) for our initial categorization of LS neurons. Among visually responsive neurons we found the following proportions of their types: directional, 72%; indefinite, 18%; stationary, 6%; and motion only, 4%.

Directional selectivity for moving gratings

The direction tuning of all cells was measured with drifting sinusoidal gratings of the optimal spatial frequency and drift rate. Figure 2 shows four examples of tuning curves obtained in this way for striate neurons. Figure 4*A* shows the distribution of direction half widths for 129 simple cells, and Fig. 4*B* for 148 complex cells. In agreement with previous reports (Henry et al. 1974; Ikeda and Wright 1975; Rose and Blakemore 1974), we found that simple cells were, on average, somewhat more narrowly tuned for direction than complex cells. We established the tuning half width by fitting the main lobe of each tuning curve with a function consisting of two half Gaussians centered on the optimal direction (2 half widths are used to account for any asymmetry); the half width of this function is the magnitude of the change in direction needed to reduce the response by half, and the mean half width of the two sides is given. The mean half width for simple cells was $17.2 \pm 9.7°$ (SD), whereas that for complex cells was $23.6 \pm 11.3°$ (SD). The modal values for both cell types were near 13°, but complex cells with rather broad tuning were much more numerous than similarly unselective simple cells.

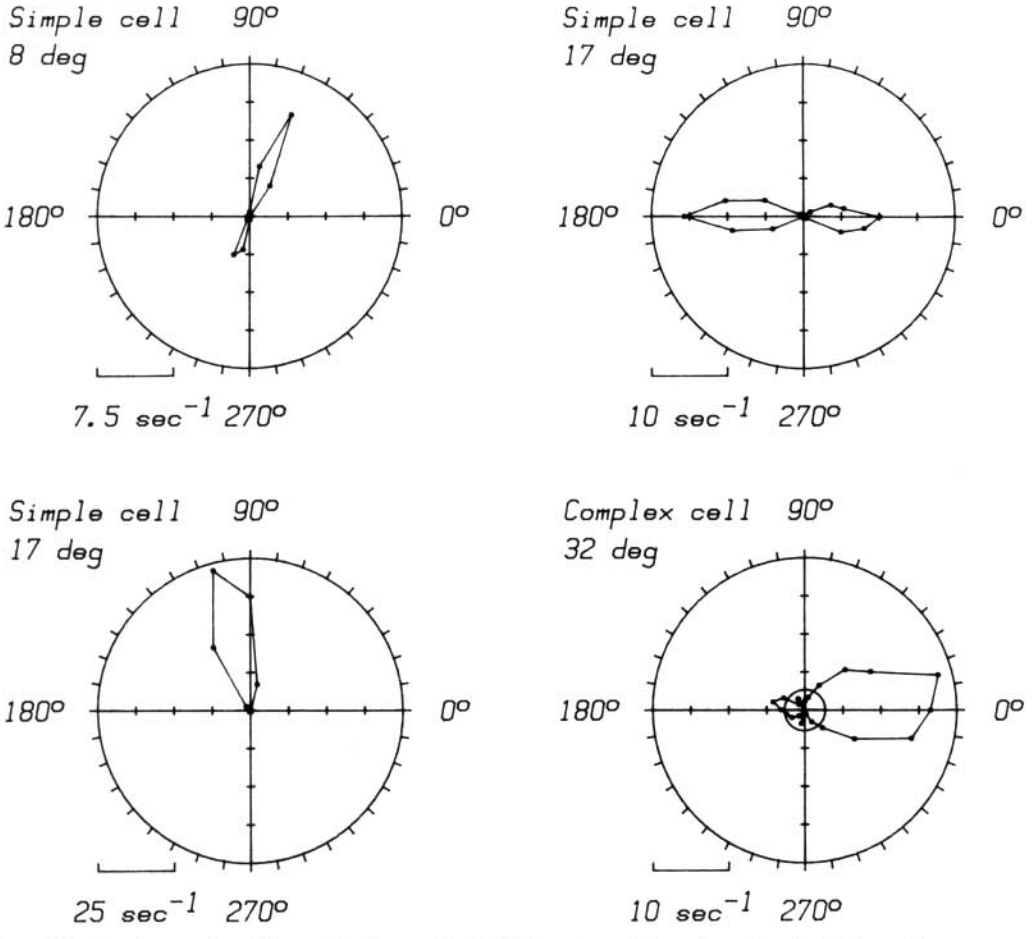

FIG. 2. Polar plots of the direction tuning of 4 area 17 cells tested with drifting sinusoidal gratings of optimal orientation and spatial frequency. The angular coordinate represents the direction of movement of the grating, orthogonal to its orientation. The radial coordinate represents mean firing rate. Maintained activity, if present, is indicated by a circle centered on the origin. The angle above each plot is the *half width*, the amount of direction change from optimal needed to halve the neuron's response.

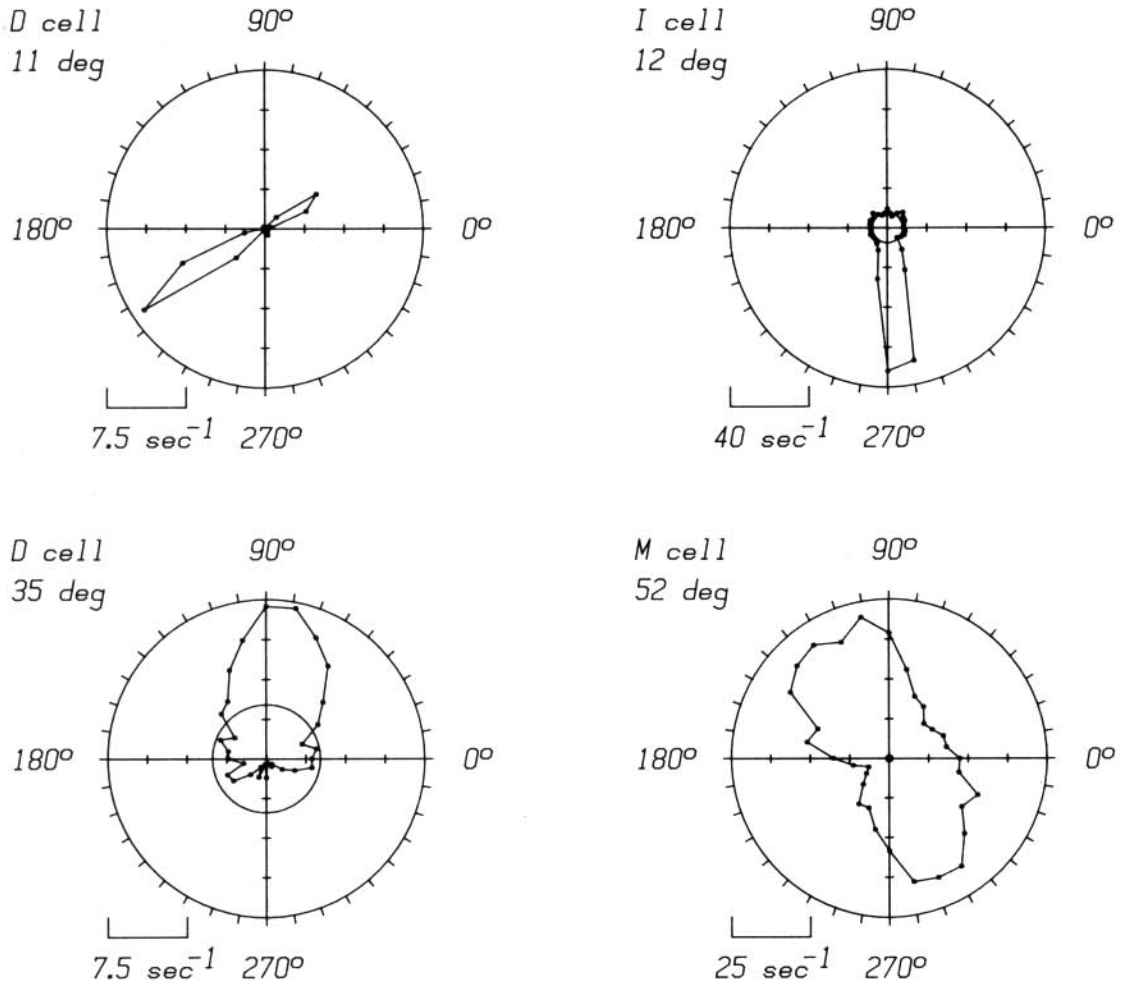

FIG. 3. Four examples of directional tuning curves for LS units, measured with drifting sinusoidal gratings of optimal spatial and temporal frequency. The 2 left-hand plots were from units mapped as directional (D); the top right plot is from a unit mapped as indefinite (I); the bottom right plot is from a unit mapped as motion only (M).

Figure 3 shows polar diagrams of the selectivity of four LS neurons for the direction of motion of sinusoidal gratings. For each neuron the receptive-field type (D, directional; M, motion only; I, indefinite) and tuning half width are inset next to the plot. It is apparent that the degree of selectivity varied markedly among LS neurons. The *top two neurons* of Fig. 3, for example, were more selective than most area 17 neurons, whereas the *bottom right neuron* of Fig. 3 responded well to any direction of motion. Notice also that the difference in response between the two directions of movement of an optimal grating could vary. The *top left unit* of Fig. 3 gave respectable (albeit unequal) responses in both directions, whereas the *top right unit* gave no response whatever in one direction. The *bottom left unit* was inhibited below its spontaneous rate by optimally oriented gratings moving in the inappropriate direction, and the *bottom right unit* responded equally well to motion in either direction of an optimally oriented grating. We did not notice reliable accessory peaks near 90° from optimal (cf. Zumbroich and Blakemore 1987). The half widths for these neurons ranged from 5 to 68° with a mean of 20.7° and a mode near 13°. This is in agreement with previous reports (Blakemore and Zumbroich 1987; Morrone et al. 1986; Zumbroich and Blakemore 1987). The distribution of half widths is shown in Fig. 4*C*. The overall distributions for LS and area 17 are indistinguishable.

It is clear from the examples in Figs. 2 and 3 that both striate and LS neurons varied considerably in the asymmetry of their response to the two possible directions of movement of an optimally oriented grating. We calculated an index of this asymmetry by subtracting the spontaneous firing rate from the response to both the preferred and nonpreferred directions at the optimal orientation and then taking the ratio of the response to the nonpreferred direction over the response to the preferred direction. The fraction is then subtracted from 1. Thus a unit with no preference will give equal responses in both directions and will have a directionality index of 0. A completely directional unit will have an index near 1, and a unit that is inhibited by movement in the nonpreferred direction will have a value >1. Figure 5 plots the distribution of this index for 245 striate neurons and 107 LS neurons. Figure 5, *A* and *B*, shows the distributions separately for 114 simple and 131 complex units; Fig. 5*C* shows the distribution for the LS units. We consider a neuron *direction selective* when the direction index exceeds 0.8, *directionally biased*

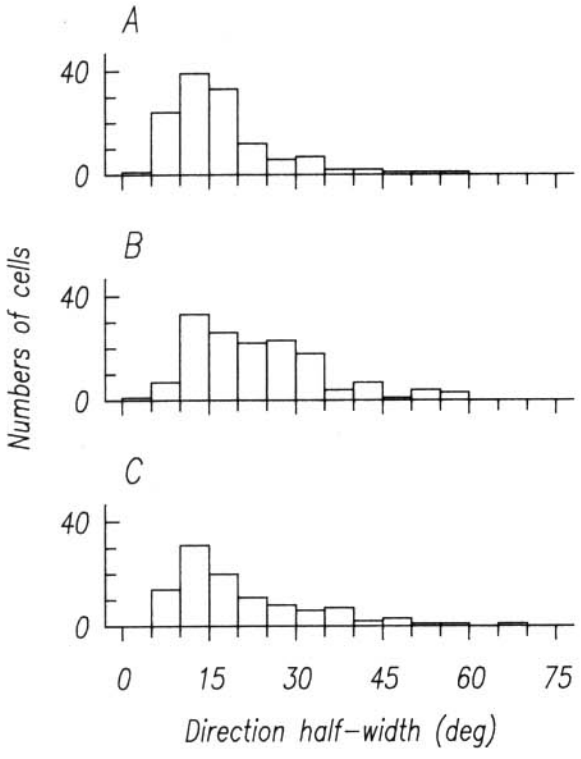

FIG. 4. Directional tuning. *A*: distribution of half widths for 129 simple cells. *B*: distribution for 148 complex cells. *C*: distribution for 107 LS cells.

when it falls between 0.5 and 0.8, and *nondirectional* when it is <0.5. Overall, in area 17, 166 units (64%) were either biased or selective for direction, and 97 (40%) were direction selective. Complex cells were slightly more directional than simple cells. Of the complex units, nearly one-half (64/131, 49%) were direction selective, whereas only 29% (33/114) of simple cells fell in this group. Overall, 90 of 131 complex units (69%), but only 66 of 114 simple units (58%), were selective or biased for direction. As has been previously reported (Camarda and Rizzolati 1976; Hubel and Wiesel 1969; Spear and Baumann 1975; Zumbroich and Blakemore 1987) most LS neurons show significant directional asymmetries. Eighty-nine of the LS neurons (83%) had directionality indices >0.5, and 35 (33%) had indices >1 (meaning that they were inhibited by stimuli moving in the inappropriate direction). Our results thus confirm previous reports that directional asymmetry is a prominent characteristic of LS receptive fields.

For complex cells in area 17, there was a weak positive correlation between the direction half width and the directionality index ($r = 0.145$, $n = 131$, $t = 1.66$, df = 129, $P = 0.048$). This may be because of the linked tendency for special complex cells to be less tightly tuned for direction and more strongly asymmetric in their responses than standard complex cells (Gilbert 1977).

Comparison of direction selectivity for gratings and plaids

Figure 6 shows the response of a special complex unit in area 17 to gratings and plaids moving in various directions. Shown in the figure are the tuning curves for gratings and for 90° plaids. The tuning for gratings was rather broad (a half width of 24°), and the cell responded to only one direction at the optimal orientation. The tuning curve for plaids had two lobes, each centered on a direction near 45° from the optimum for single gratings. When the plaid was moving in the direction optimal for gratings, the response of the unit was quite small. The component-direction-selective prediction is shown in dashed lines, and although the amplitude of the actual response differed from that of the prediction, the shapes of the two curves are very similar. All neurons whose responses we measured to gratings and plaids showed the same pattern of response: when a cell had a single-lobed tuning curve for gratings, the tuning curve for plaids was bilobed.

The results of three experiments performed on a directional unit recorded in PMLS are summarized in Fig. 7. Each experiment compared the directional tuning of the unit for gratings and plaids; the three experiments differ only in the angles chosen for the plaids, which were 45, 90, and 135°. Each column of the figure shows the result of one experiment. For each, the top plot shows the direction tuning for a single grating, which is also the "pattern" prediction for the plaid tuning. The middle plots show the "component" prediction derived from the single grating data. The bottom plots show the observed direction tuning for plaids. The figure shows that the results fit the component prediction well for all three experiments. The pattern prediction is unsatisfactory for all three angles.

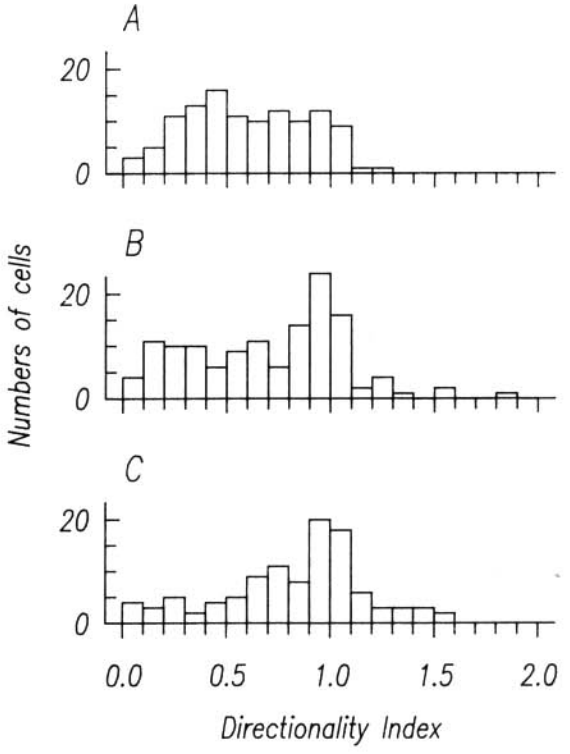

FIG. 5. Directional selectivity of striate neurons, represented by distributions of the "directionality index", given by $DI = 1 - (R_{np}/R_p)$ where R_{np} is response (above base line) in the nonpreferred direction, and R_p is response (above base line) in the preferred direction. Neurons whose directionality index exceeded 1 were inhibited by stimuli moving in the inappropriate direction. *A*: distribution for 116 simple cells. *B*: distribution for 129 complex cells. *C*: distribution for 107 LS cells.

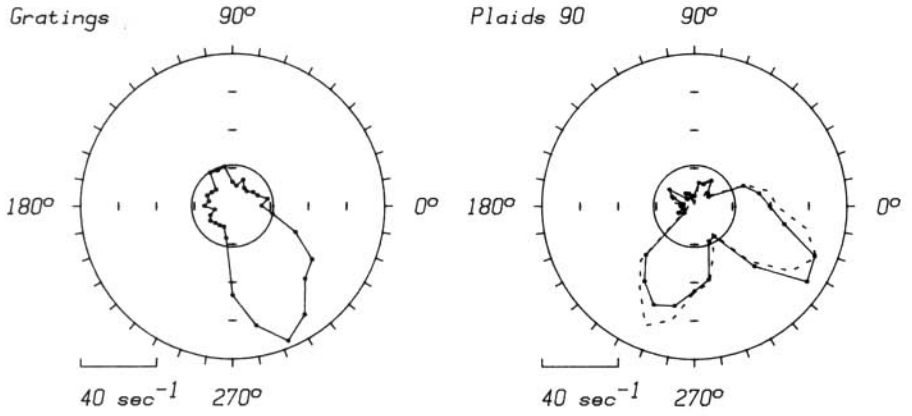

FIG. 6. Direction-tuning curves for a complex cell measured with gratings (*left*) and plaids (*right*). The component-direction-selective response prediction (see Fig. 1) is shown on the right in dashed lines.

To compare the goodness of fit of the component and pattern predictions, we correlated the observed response of the neuron to plaids with each prediction. Because the two predictions are not entirely uncorrelated themselves, we computed a partial correlation of the form

$$R_p = r_p - r_c r_{pc}/\sqrt{(1 - r_p)(1 - r_c)}$$

where R_p is the partial correlation coefficient for the pattern prediction, r_c is the simple correlation of the data with the component prediction, r_p is the sample correlation of the data with the pattern prediction, and r_{pc} is the intercorrelation of the two predictions. A similar partial correlation for the component prediction (R_c) is calculated by exchanging r_c and r_p (Crow et al. 1960). For the unit shown in Fig. 6, the component-prediction correlation coefficient was 0.966, and the pattern correlation coefficient was 0.079. For the neuron whose data are shown in Fig. 7, the values of the pattern correlation were 0.584 (45°), −0.103 (90°), and −0.186 (135°); the values of the component correlation were 0.989, 0.935, and 0.995, respectively. All of the component correlation coefficients significantly exceed zero; only the pattern correlation coefficient for the 45° test significantly exceeded zero, but this value was significantly less than the component correlation coefficient for the same angle. Behavior of this sort characterized almost all the LS neurons we studied in this way. In a number of cases, we repeated the experiment at a higher spatial frequency, so that the periodicity of the "blobs" within the plaid pattern matched the optimal spatial frequency for the neuron. In no case was the character of the result changed by this manipulation.

Partial correlations were computed for all the cells tested. The two correlations define a point in the space schematically shown in Fig. 8*A*. The abscissa plots the component-prediction correlations, and the ordinate the pattern-prediction correlations. The space contains three regions of interest, which are marked off by solid lines. The region marked "Component" contains those data for which the component correlation significantly exceeds either zero or the value of the pattern correlation. The region marked "Pattern" analogously contains data for which the pattern correlation is dominant. The region marked "Unclassed" contains those data for which either the two correlations do not differ from one another or from zero. We adopted a criterion probability of 0.1 to define these regions (Crow et al. 1960); we justify the laxness of the criterion by the fact that this is not a true test for statistical significance but a convenient way to reduce data. Clearly, neurons for whose data the component prediction provides the better description will fall in the Component zone, and neurons for whose data the pattern prediction provides the better correlation will fall in the Pattern zone. Neurons may fall in the Unclassed region either because their data are too variable to permit satisfactory analysis or because the two predictions are too similar to be disentangled by the partial correlation computation.

We compared directional tuning for gratings and plaids for 33 cells recorded in area 17 (17 complex and 14 simple) and for 40 neurons recorded in LS (38 directional, 2 indefinite). Because there were no evident differences among cells that depended on their receptive-field type (or indeed on any other identified feature), we have combined the data collected within each area. Using the format defined in Fig. 8*A*, we show the scatter plot for the area 17 cells in Fig. 8*B*. Figure 8*C* shows similarly presented data for the LS neurons. When more than one experiment was run on a particular neuron (e.g., Fig. 7), we used the values from the experiment that yielded the highest single correlation value. The plots include cells tested with 90° plaids and cells tested with 135° plaids. In area 17 all cells showed correlations that were better for the component prediction than for the pattern prediction. Two area 17 neurons, both unusually broadly tuned for direction, fell in the unclassed region; the remaining 31 units were clearly component direction selective, as were all 35 units in *monkey V1* that we subjected to the same test (Gizzi et al. 1983).

It is evident from Fig. 8*C* that most LS neurons could be unambiguously assigned to the component class. Only two met (barely) our criteria for pattern direction selectivity. Thus neurons in LS are not, in general, capable of signaling the true direction of motion of complex patterns; the most important selectivity evident in their responses is not for direction of motion but for stimulus orientation.

Orientation selectivity for stationary targets

Because component direction selectivity can only reflect the presence of orientation selectivity, we decided to reexamine the responsiveness of LS neurons to stationary, flashed targets. In agreement with Spear and Baumann (1975), we found that the vast majority of neurons in LS preferred moving stimuli. A significant proportion of units,

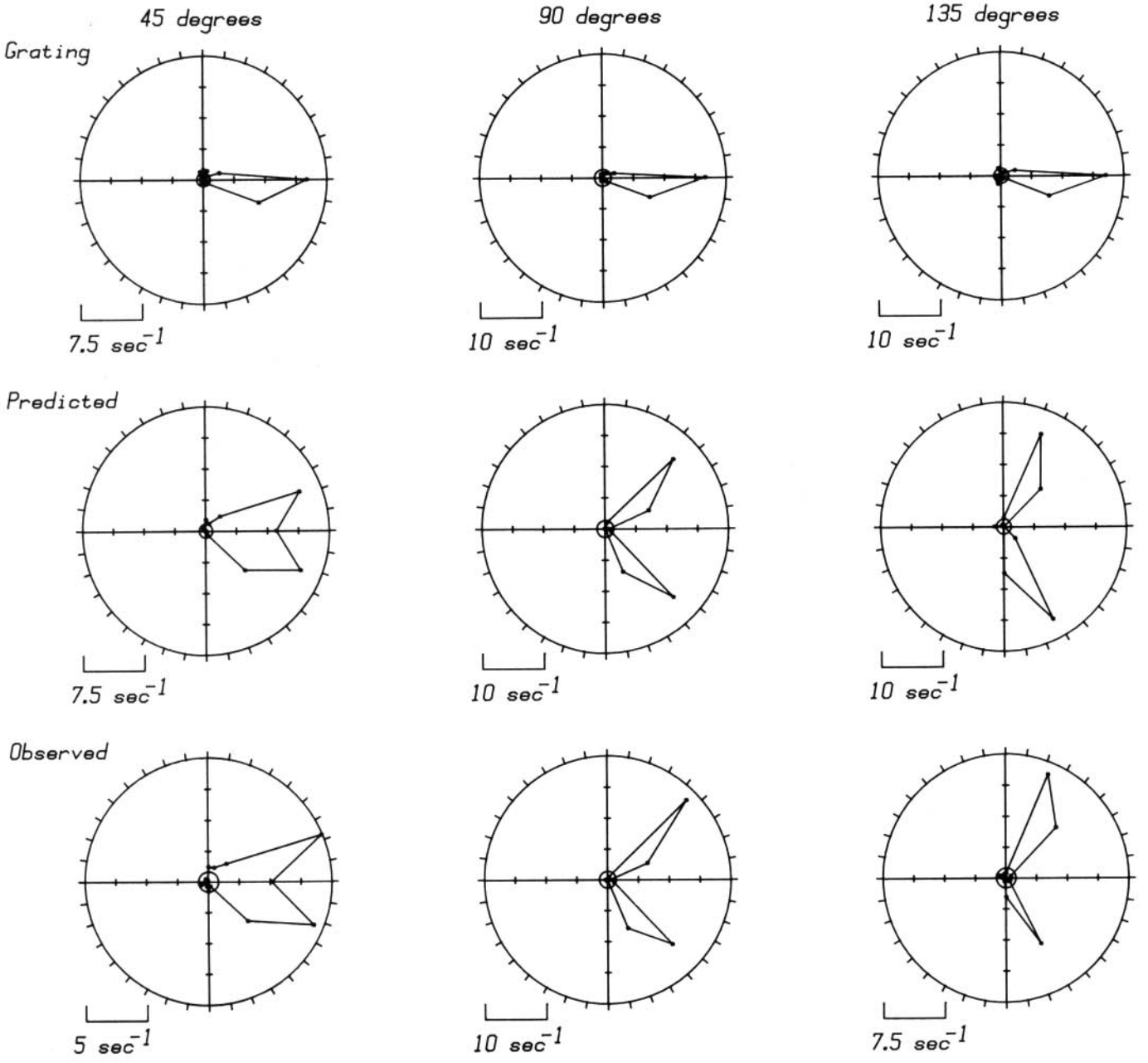

FIG. 7. Results of 3 separate grating/plaid experiments performed on a single LS unit. Each column shows the results of an experiment, and the value at the top of the column gives the angle between the gratings composing the plaid. The top row of plots shows the unit's responses to single gratings moving in different directions. The middle row of plots shows the predicted response to plaids on the assumption that the unit was component direction selective (i.e., orientation selective). The bottom row of plots shows the unit's observed responses to plaids.

even in the directional class, did, however, respond reliably to stationary, flashed targets. We tested five units with both stationary and moving gratings of several orientations. Unlike some previous investigators using flashed bars or lines (Camarda and Rizzolati 1976; Spear and Baumann 1975), we found that all of these units responded in an orientation-selective manner. Similar results have also been reported by Blakemore and Zumbroich (1987).

Figure 9 shows the direction-tuning curve for one of these units (*A*), together with its orientation-tuning curves for flashed gratings (*B*). The contrast of the stationary gratings was sinusoidally modulated in time at 2 Hz, which was also the drift rate of the moving gratings. Stationary and moving gratings had identical spatial frequencies and contrasts. For this neuron, the primary response to moving gratings was an elevation of the mean discharge rate. The response to stationary modulating gratings was a mixture of an elevation of the mean and a response at the second harmonic of the stimulus frequency. The 180° orientation axis plots only one-half the range of possible directions of motion for moving gratings; therefore motion in one direction is plotted with circles, and motion in the opposite

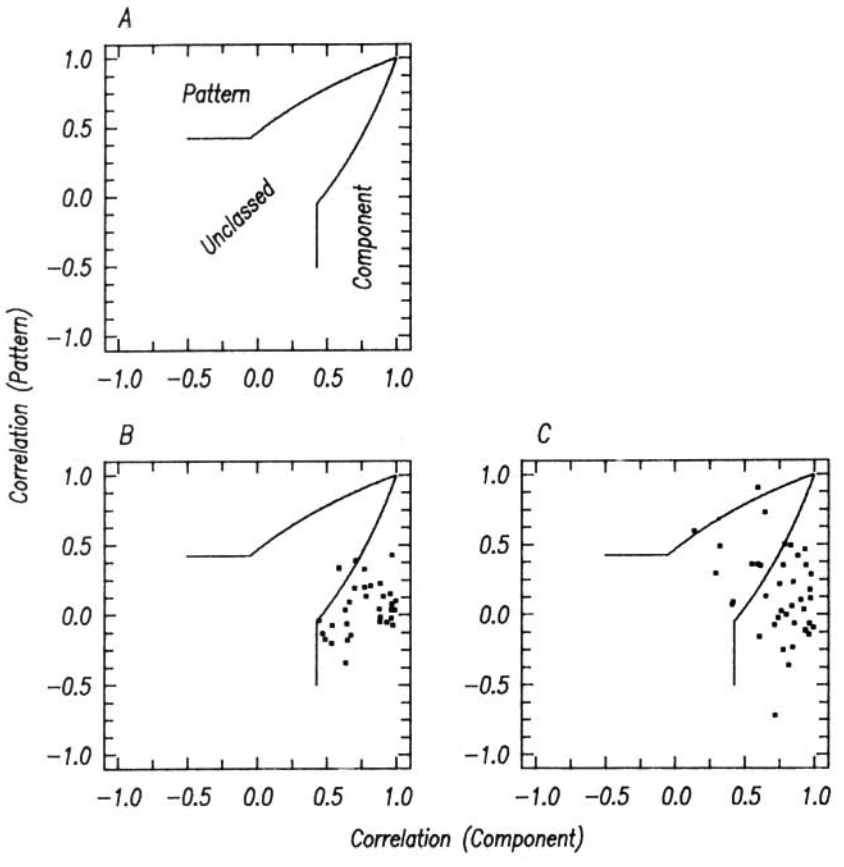

FIG. 8. *A*: diagram outlining the space in which scatter plots of directional correlation values are plotted. The region of the space marked "Component" contains those neurons for which the component correlation significantly exceeded either zero or the pattern correlation coefficient, whichever was greater. The region marked "Pattern" conversely contains cells whose pattern correlation coefficients were dominant. The region marked "Unclassed" contains those neurons whose correlation values did not differ significantly from zero, or from one another (this format for representing these data was introduced in Fig. 11 of Movshon et al. 1985). *B*: diagram in the format of *A* showing the distribution of values for 33 V1 neurons. *C*: distribution of values for 40 LS neurons. *C* is a corrected representation of data previously published in Movshon et al. (1985), Fig. 11*C*.

direction is plotted with triangles. We collected eight different tuning curves for stationary gratings, with the use of spatial phases 22.5° apart, to ensure that any selectivity we observed was not artefactually due to some selectivity for spatial phase or position. In one orientation a bright bar might fall across the field, whereas in another a dark bar might fall across the field. If the neuron preferred light over dark bars, then the orientation-tuning curve would reflect this preference rather than a true sensitivity to orientation. Figure 9*B* shows the tuning curves for the same neuron when the gratings were presented in eight different phases. None of the tuning curves for any of the neurons tested showed any dependence on phase. Blakemore and Zumbroich (1987) found a similar insensitivity to phase among orientation-selective neurons in LS. This type of response is characteristic of complex cells in area 17 (Movshon et al. 1978b) and further emphasizes the general similarity in receptive-field organization between LS neurons and complex cells.

EFFECTS OF SPATIAL PHASE ON RESPONSES TO PLAIDS. As mentioned above, the sample from area 17 includes both simple and complex cells. Simple cells, having discrete on and off regions and small receptive fields, may respond differently to plaids depending on their position relative to the receptive-field regions. For instance, if a plaid is oriented so that one of its component gratings represents an optimal stimulus for that cell, the second grating may be positioned so that every time a bar of one sign in the optimal grating passes over a region of the field, a bar of oppo-

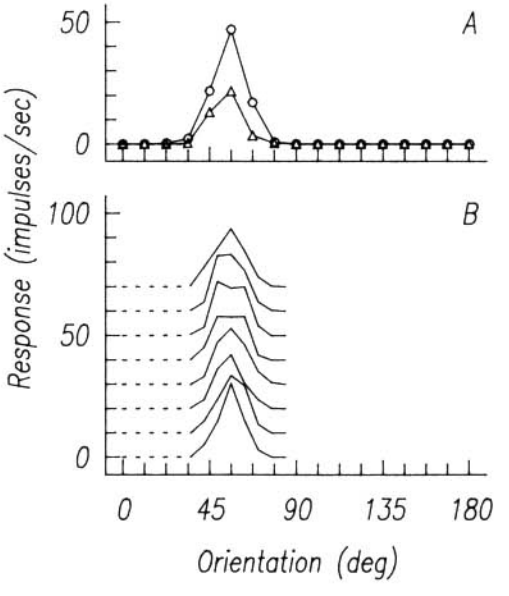

FIG. 9. Results of an experiment on the orientation selectivity of a directionally selective LS unit. *A*: response of the unit to high-contrast drifting gratings of the optimal spatial frequency and drift rate; circles plot the response in the "forward" direction, and triangles plot the response in the "back" direction. *B*: response of the unit to stationary gratings, of identical spatial frequency and contrast to those used in *A*, whose contrast was modulated sinusoidally in time at the same rate as the drift rate used in *A* (2 Hz). The 8 curves plot responses for different spatial phases, separated by 22.5°. Each curve is vertically offset from its neighbors by 10 impulses/s for clarity, and the dashed lines indicate the true zero response for each curve.

site sign in the second grating passes over the same region. The resulting effect is that there is no luminance change in the area corresponding to that particular region. Because the two gratings move at the same temporal frequency, the cancellation will occur at the same place each cycle. Shifting the phase of the second grating by 90° has the effect of substituting a high-contrast region wherever there was previously a region of low contrast. Where there was previously cancellation, there will now be addition, and the cell should respond much more vigorously to the second case than to the first. There should be no such problem for complex cells because they are, in general, insensitive to variations in spatial phase (Movshon et al. 1978b). To test this we tested 24 cells, 10 simple and 14 complex, by running two plaid direction-tuning experiments differing only in the relative phase of one of the components. As usual, these two experiments were interleaved with a single grating experiment for the purpose of generating predictions. Figure 10 shows the results of two such experiments, one performed on a simple cell and the other on a complex cell.

The simple cell gave drastically different responses to the plaids when the phase was changed. At the optimal phase the two lobes appeared exactly where predicted. At a 90° relative phase shift, however, one lobe of the tuning curve was completely absent. The component-prediction correlation changed from 0.697 for the first case to 0.096 for the second. The pattern-prediction correlation, however, remained very low for both phases, changing from 0.189 to 0.242. This change in response was typical for simple cells; one or both lobes of the tuning curve were often atten-

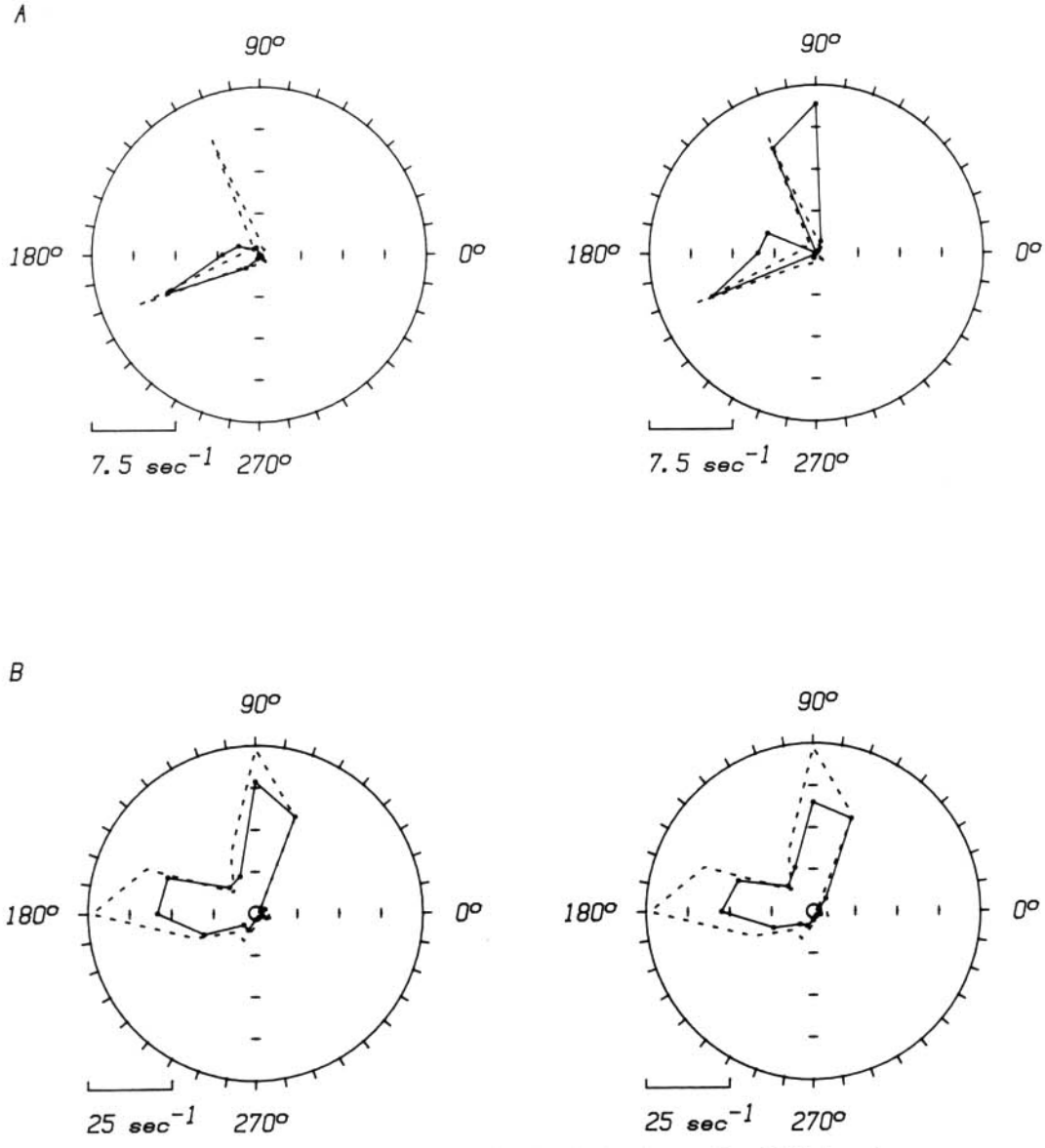

FIG. 10. Directional tuning for plaid targets of 2 spatial phases for a simple cell (*A*) and a complex cell (*B*). Actual curves are shown in solid lines and component predictions (derived from the single-grating tuning curves, not shown) are plotted as dashed lines. For each cell the tuning curves were measured for plaids whose relative phase was optimal, and for plaids at a relative phase 90° from optimum. The complex cell gave nearly identical responses at both relative phases, whereas the simple cell showed a dependence on the relative phases of the 2 component gratings.

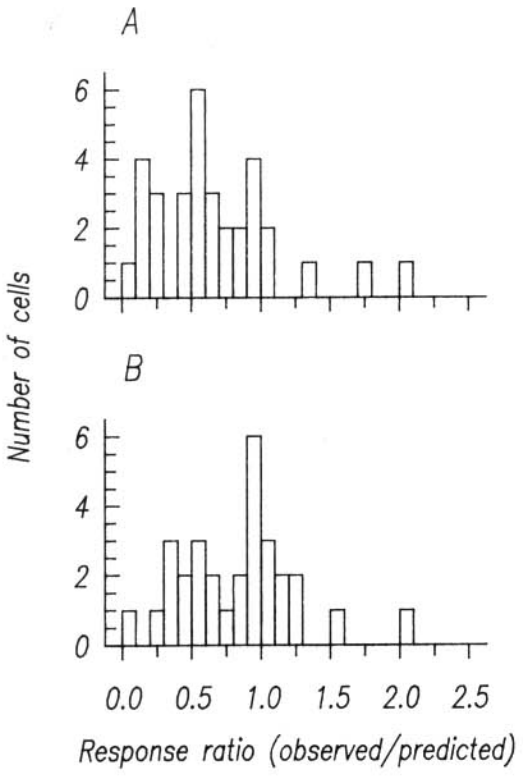

FIG. 11. The distribution of ratios of the observed peak response to plaids to the peak response predicted from the model of component direction selectivity. A ratio <1 indicates suppression, and a ratio >1 facilitation. *A*: distribution for area 17. *B*: distribution for LS.

uated, changing the component correlation, but the pattern correlation never improved.

In marked contrast to the variability of the simple cell response, those of the complex cell of Fig. 10*B* showed little dependence on phase. The response at both phases was very much the same, and the component prediction correlation changed from 0.966 to 0.962. It was characteristic of complex cells that a change in phase never significantly altered the value of either correlation coefficient.

INHIBITION IN THE ORIENTATION DOMAIN. There is evidence that striate neurons are inhibited by stimuli at nonoptimal orientations (Blakemore and Tobin 1972; Burr et al. 1981; Creutzfeldt et al. 1974). Evidence of inhibition can be seen by examining the response magnitude of cells to plaids. Our prediction for the component-direction-selective response does not take inhibition into account, and deviations in the observed response magnitude from the prediction are most likely because of inhibition of the response to one grating by the presence of the other. As a measure of this, we computed the predicted peak response to plaids (with spontaneous activity subtracted) and compared this to the actual peak response. Figure 11*A* is a histogram for area 17 of the ratios of the actual response magnitude to the predicted magnitude. The majority of cells showed some sign of inhibition, and the mean ratio was 0.67. We should stress that, despite this reduction in response *magnitude*, the *shape* of the tuning curves usually conformed closely to the component model (Fig. 1). A similar histogram for cells recorded in LS is shown in Fig. 11*B*. It is clear that the reduction in response magnitude (the mean is 0.83) is less pronounced in LS, indicating that inhibition in the orientation domain is not so prominent a feature of LS responses.

DISCUSSION

Component direction selectivity in area 17

We consider two hypotheses about the response mechanisms of striate cells that determine their preferences for orientation and direction of motion. The first is that their selectivity for direction arises only after orientation selectivity is established and is thus simply a selectivity for one of two possible directions orthogonal to the optimal orientation. The second is that the cells are truly selective for direction and will respond to any pattern moving in a given direction regardless of the orientation of its components. Our results show that both simple- and complex-cell response patterns are tightly linked to the orientation of the *components* of stimuli and not necessarily to the direction of movement of the stimulus as a whole. Directional tuning for plaids typically shows two peaks separated by the angle that separates the components of the plaids. The responses are well approximated by a simple linear sum of the responses to the components of the plaid measured separately. Simple cells show a dependence on the relative phase of the component gratings; this is consistent with the linear summation they show for one-dimensional stimuli (Movshon et al. 1978a). Complex cells, consistent with their nonlinearity of spatial summation and independence of phase (Movshon et al. 1978b), respond similarly to plaids at any relative phase. The mechanisms that produce tuning for the direction of single gratings, then, appear to be secondary to the mechanisms producing orientation selectivity. Direction preferences for one-dimensional targets are always perpendicular to the cell's orientation preference and are not determined by a separate "motion mechanism" (cf. Bishop et al. 1980; Hammond 1978; Hammond and Reck 1980).

Component direction selectivity in LS

The results of this study refute earlier claims that neurons in the lateral suprasylvian area are not orientation selective. Our experiments using grating and plaid stimuli unambiguously demonstrate that the vast majority of LS units respond to the oriented components within a pattern and are insensitive to the overall motion of the pattern. It is important to note that this conclusion is not based on any substantial conflict concerning the observed behavior of LS neurons. In general we agree with previous reports that LS neurons are no more selective for the direction of motion of lines than they are for large spots and that many LS neurons cannot easily be shown to be orientation selective with flashing line stimuli. These data have been used to support the claim that LS neurons are not orientation selective, but we simply consider them inadequate to demonstrate the orientation selectivity that our more sophisticated analyses reveal.

Tests of orientation selectivity have failed to disentangle orientation and direction either because they involve only

one-dimensional stimuli or because no consistent method has been devised for making the parameters of the one- and two-dimensional stimuli commensurate. Tests involving single lines cannot possibly distinguish orientation and direction because any motion parallel to a line's orientation is invisible and only motion orthogonal to the orientation can be detected. Thus lines of greater length than the receptive field can move only orthogonal to their orientation. Stationary, flashed lines can be used to assess the presence of orientation selectivity, but the failure of such a test does not always lead to an unambiguous interpretation. This is especially a problem in LS, where neurons that respond to flashed stimuli often also respond to full-field flicker. The solution to this problem is to use stimuli whose mean luminance matches that of the background, thereby eliminating the problem of the full-field response. All the neurons we tested in this way gave orientation-selective responses to stationary gratings.

The plaid and grating stimuli have identical spatial extent and physical contrast. The orientation and direction of motion can be separately manipulated. And a major advantage is that a large proportion of cells will give adequate responses to these stimuli; in general, any cell that responds to gratings will respond to the plaid pattern. From the response to a moving plaid, one can infer sensitivity to orientation, direction, or both. The neurons recorded in LS clearly responded to the orientation and not to the direction of the pattern. This insensitivity to "pure" direction indicates that the tuning for single gratings reflects a mechanism of orientation and not direction selectivity.

Invariant response characteristics

In considering the function of a visual neuron, it is useful to enquire after the visual stimulus qualities for which selectivity is *invariant* under parametric manipulation of stimulus conditions. It seems reasonable to argue that the stimulus qualities selected in an invariant fashion are those that a neuron's output may be said to "code." In the striate cortex, selectivity has been demonstrated for a wide variety of stimulus variables including orientation, spatial frequency, speed, binocular disparity, and direction of motion (Hubel and Wiesel 1962; Maffei and Fiorentini 1973; Movshon 1975; Orban et al. 1987; Pettigrew et al. 1987). Of these variables it appears that orientation and spatial frequency are the best candidates for invariant qualities. Orientation selectivity does not depend on the spatial frequency or bar width of a stimulus pattern, or on the direction in which the pattern moves (Campbell et al. 1968; DeValois et al. 1982; Henry et al. 1974; Movshon 1979); the dependence of orientation selectivity on stimulus length (Henry et al. 1974) can be neatly explained by the broadening of the distribution of orientational energy produced by shortening a line. Spatial frequency selectivity does not depend on the orientation or drift rate of the test grating (DeValois et al. 1982; Movshon 1979; Tolhurst and Movshon 1975). Indeed, we are aware of no instance in which the selectivity of striate cortical neurons for these parameters has been shown to depend on other stimulus factors; our results suggest that in this respect the receptive fields of LS neurons are similar to those in striate cortex.

Cortical neurons do not, however, appear to have invariant selectivity for parameters related to stimulus motion. Speed selectivity, for example, varies inversely with the spatial frequency of a test grating (Tolhurst and Movshon 1975). The present results show, for neurons both in area 17 and in LS, that directional selectivity depends on the spatial composition and speed of motion of the test pattern: a neuron's optimal direction for one kind of test pattern can be quite different from its optimum for another. Thus, despite the fact that compelling signs of selective sensitivity to moving targets are evident, it does not appear that these cells can be usefully thought of as "coding" the motion of objects.

It is important to appreciate that this is not because of arbitrary limitations in the construction of visual cortical receptive fields. A neuron that shows appropriate invariance in its tuning for direction must, *of necessity*, sacrifice its invariant selectivity for orientation: to show identical direction preferences for gratings and plaids, for example, the neuron's orientational selectivity would need to be modified by signals concerning the direction of motion. The fact that this behavior is not seen in area 17 confirms that this area's main responsibility is for analysis of the spatial configuration of visual patterns and suggests that the analysis of their motion must proceed, in part, in other areas of the cerebral cortex. We have previously reported that such analysis is evident in area MT in the macaque monkey's extrastriate cortex (Movshon et al. 1985), and, in view of the similarities between monkey MT and cat LS, it is surprising that our results from LS show no sign of the necessary transformation of visual motion signals. Nevertheless, there are reasons to believe that the function of LS is at least partly related to visual motion processing.

The function of LS

What distinguishes the lateral suprasylvian area from other cortical areas is the large proportion of direction-selective units. By direction selective, we mean here a preference for one of two possible directions of motion for a stimulus held at the optimal orientation. Estimates of the proportion of direction-selective neurons in areas 17 and 18 vary somewhat. From quantitative studies the best estimate of the proportion of direction-selective cells (those whose direction index exceed 0.8) is about one-quarter in area 17 and slightly higher in area 18 (Orban et al. 1981). Perhaps another one-third of neurons in these areas are directionally biased (having indices between 0.5 and 0.8). In LS, more than one-half the neurons in our sample were directionally selective, and 85% were selective or biased. There is evidence that the area 17 cells projecting to LS are complex cells in the superficial layers (Henry et al. 1978; Symonds and Rosenquist 1984a,b), and these neurons may be direction selective even less often than the area 17 population as a whole (Henry 1977). Thus we find, in agreement with others (e.g., Spear and Baumann 1975), a clear enhancement of direction selectivity in LS.

Lest we conclude that LS is the "motion area" of the cat's cerebral cortex, however, a brief comparison with data on area MT of the macaque is instructive. MT is a visual area in the macaque superior temporal sulcus which re-

ceives strong inputs from V1 and V2. MT, like LS, contains neurons that are predominantly direction selective (Maunsell and Van Essen 1983; Van Essen et al. 1981; Zeki 1974). We have examined the properties of neurons in macaque MT by the use of methods similar to the ones described in this paper, however, and our results in MT are strikingly different from those in LS (Movshon et al. 1985). In MT, pattern-direction-selective neurons comprise about one-quarter of the population, and the neurons are generally much more broadly tuned for spatial frequency and orientation than in macaque V1. Moreover, the increase in receptive-field size between V1 and MT in the macaque is many times greater than the increase between V1 and LS in the cat. Our evidence and recent lesion studies of MTs role in the generation of pursuit eye movements (Dürsteler and Wurtz 1988; Dürsteler et al. 1987; Komatsu and Wurtz 1988; Newsome et al. 1985; Newsome et al. 1988) and in perceptual decisions about motion (Newsome et al. 1989; Newsome and Paré 1988) strongly implicate MT in the analysis of visual motion by the macaque's cerebral cortex. The ability of MT to signal the direction of motion of coherent patterns is precisely the quality that makes it useful in the generation of smooth eye movements. The differences between MT and LS suggest, although the latter may be responding differentially to direction of motion, it does not handle motion processing in the same manner as MT and that there might exist another area that represents a subsequent stage of motion processing in the cat's cerebral cortex that fulfills a more nearly similar function to that of MT in this species.

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