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Spatial and temporal analysis by neurons in the representation of the central visual field in the cat's lateral suprasylvian visual cortex

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Abstract

We studied quantitatively the receptive-field properties of 74 units recorded from the representation of the central visual fields in the cat's lateral suprasylvian (LS) visual cortex. In agreement with previous workers, we found that LS receptive fields tended to be large and to lack discernible spatial structure. They resembled the complex receptive fields of areas 17 and 18 in their general organization. We examined the responses of these neurons to moving optimally oriented sinusoidal gratings that varied in spatial and temporal frequency of drift. Most LS neurons were selective for the spatial frequency of sinusoidal gratings; 7% responded to all spatial frequencies below a cutoff value. In agreement with previous reports, the optimal spatial frequencies for LS neurons covered a wider range than is seen in either area 17 or 18 alone (0.05–1 cycle/deg), but are certainly included in the range covered by both these afferent areas. Individual neurons in LS responded to a range of spatial frequencies broader than is typical for neurons in areas 17 and 18. The effect of varying the drift rate of otherwise optimal gratings was similar in LS to that reported for areas 17 and 18. Most neurons were optimally responsive to drift rates between 0.5 and 4 Hz, and resolved frequencies as high as 10–30 Hz. A few neurons had optima higher than 6 Hz and resolved frequencies in excess of 30 Hz. We conclude that the receptive fields of LS neurons reflect rather closely the properties of their afferents from areas 17 and 18. Apart from the increased incidence of directional selectivity in LS and the increase in receptive-field size seen there, we find no evidence for a significant reorganization of visual signals.

Keywords: Extrastriate cortex, Temporal selectivity, Spatial selectivity, Receptive fields

Introduction

The most prominent extrastriate visual areas in the cat's cerebral cortex occupy the banks of the suprasylvian sulcus (Palmer et al., 1978). These areas, unlike areas 17 and 18, receive significant functional input from intracortical projections (Razcowski & Rosenquist, 1983; Bullier et al., 1984; Symonds & Rosenquist, 1984*a*; Sherk, 1986). Lesions of primary visual cortex produce profound changes in the response properties of lateral suprasylvian (LS) neurons (Smith & Spear, 1979; Spear & Baumann, 1979; Spear et al., 1988). This, in combination with the laminar pattern of corticocortical connectivity (Bullier et al., 1984; Symonds & Rosenquist, 1984*b*), suggests that in the terms of Van Essen (1979), the LS areas may form part of the "second tier" of the cat's visual cortex; the areas of the "second tier" are dominated by their inputs from the areas of the "first tier" areas 17 and 18. In evaluating the role of LS, it is important to characterize the processing of visual information in this area in comparison to that seen in the "first tier." This paper is concerned with the differences in processing of spatial and temporal information between cells is LS and cells in areas 17 and 18.

The methods of frequency analysis have proved helpful in understanding the properties of neurons at many stages of the visual pathway (e.g. Enroth-Cugell & Robson, 1966; Maffei & Fiorentini, 1973; Shapley & Hochstein, 1975; Movshon et al., 1978*a*, *b*, *c*; DeValois et al., 1982). Applying these methods to LS provides a valuable means for the comparison of visual processing in LS with that in areas 17 and 18. In this study, we have restricted our analysis to neurons with centrally located visual fields in order to facilitate comparison with existing data from areas 17 and 18 (Movshon et al., 1978*a*, *b*, *c*). Our results show that LS neurons exhibit spatial and temporal properties like those of neurons in areas 17 and 18, with a range larger than that seen in either area alone (see also Morrone et al., 1986; Zumbroich & Blakemore, 1987; Blakemore & Zumbroich, 1987). Thus, to the degree that inputs from areas 17 and 18 influence the spatial and temporal properties of LS neurons, there is little or no elaboration of this processing in LS. The absence of spatial transformation in this area suggests that it is not in-

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volved in the processing of spatial information but rather is concerned with other visual dimensions, such as motion.

Some of these results have been briefly presented elsewhere (Gizzi et al., 1981).

Methods

Our general techniques of recording, stimulus presentation, and data collection have been described elsewhere (Gizzi et al., 1990); only methods peculiar to these experiments will be described in detail here. Adult cats weighing 2.5–4 kg were initially anesthetized with halothane and subsequently with barbiturates during surgery. Anesthesia was maintained during recording with a mixture of N_2O:O_2:CO_2 (typically 75:23:2). On the basis of continuously monitored EEG and autonomic signs, this anesthesia was supplemented when necessary with an infusion of sodium pentobarbital (1–2 mg/kg/h). The cats were paralyzed with gallamine triethiodide (Flaxedil) or pancuronium bromide (Pavulon) and ventilated artificially. Craniotomies were placed between Horsley–Clarke coordinates A4 and P2 from L12 to L14. Tungsten-in-glass microelectrodes were directed obliquely down the medial bank of the suprasylvian sulcus, toward the posterior representation of the *area centralis* in the area designated PMLS by Palmer et al. (1978). Mydriasis and cycloplegia were induced with topical atropine sulfate and neosynephrine and the corneas were protected with zero-power contact lenses containing 4-mm artificial pupils. Supplementary lenses provided refractive power for a screen 30–57 cm distant.

The receptive fields of single units were initially mapped by hand on a tangent screen using moving and flashing lines, edges, and spots. Units selected for quantitative study were stimulated through the eye more effective in driving the unit using a CRT and the other eye was covered. We used a PDP 11/34 computer to record average-response histograms and to create stimulus displays on the CRT. The stimuli had space- and time-averaged luminance constant for a particular experiment at a value between 25 and 50 cd/m^2. The screen subtended between 15 and 20 deg (depending on distance from the eye) and stimuli could be restricted electronically to a smaller rectangular region of arbitrary size; the surrounding region was uniformly illuminated at the prevailing mean luminance. In this way stimuli could be confined, when necessary, to the excitatory portion of the receptive field. We routinely looked for evidence of a strong inhibitory surround. Restricted stimuli were used only when stimulation of the surround dramatically reduced the responsiveness of the cell.

The optimal grating orientation and direction of motion were chosen by quantitative analysis described elsewhere (Gizzi et al., 1990); when a cell's response was bidirectional both directions were used for subsequent testing. We then studied the effect of variations in spatial and temporal frequency on the responses. The spatial frequency of a grating is the number of cycles of the modulating sinusoid that subtend 1 deg of visual angle. Its temporal frequency of drift is the number of cycles that pass a given point in 1 s. Thus, the angular speed of a grating's motion is given by the ratio of its temporal and spatial frequencies. The gratings were of moderately high contrast (0.25 or 0.5), calculated as the difference between the minimum and maximum luminance in the grating divided by twice the mean luminance). Typically 6–8 spatial frequencies and 4–6 temporal frequencies were used. In all experimental series, the stimuli were presented in several randomly ordered blocks.

At the end of the recording session, the cats were injected with fatal overdoses of sodium pentobarbital and perfused with saline followed by 10% formalin. Histological verification of electrode location was completed for most cells. Electrolytic lesions were located post mortem in 40 μm frozen sections stained for cell bodies with cresyl violet.

Results

Receptive fields

In all, 322 neurons were recorded in the cortex adjacent to the suprasylvian sulcus. One hundred and seven of these gave reliable responses to visual stimuli and were recorded with sufficient stability that they could be studied quantitatively. Because all of these units were also studied extensively for properties of orientation and direction selectivity (see Gizzi et al., 1990), a number were lost before spatial and temporal properties could be examined extensively. Seventy-four neurons were studied in detail with regard to spatial- and temporal-frequency tuning. All were histologically verified to lie within the medial bank of the suprasylvian sulcus or its fundus. The distribution of receptive-field eccentricities is shown in Fig. 1. All but eight had visual fields centered within 10 deg of the *area centralis*; the remainder had fields within the central 20 deg.

From hand maps, the cells were initially classified into the four types described by Spear and Baumann (1975). *Directional* units resemble complex cells in areas 17 and 18, having large, apparently uniform receptive fields and responding to moving lines or spots only when their direction is within a given range. Both unidirectional and bidirectional neurons exist within this class. Directional units usually prefer moving to stationary stimuli, but sometimes respond with a brisk ON–OFF discharge to flashed targets. *Motion-only* units respond to any moving stimulus, but without a preference for any direction of motion. *Stationary* units respond better to stationary flashing targets than to moving ones, although they may give some response to

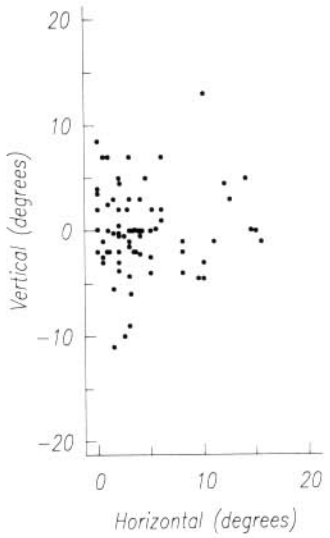

Fig. 1. The distribution of receptive-field eccentricities for 74 neurons recorded in LS. The values represent the horizontal and vertical distances from the area centralis to the center of the receptive field.

movement. They usually give ON–OFF responses to all flashed targets, and are not normally sensitive to stimulus orientation or direction. *Indefinite* units give visual responses but do not have mappable receptive fields or well-defined selectivity for any particular kind of stimulus. It should be noted that the receptive-field type as determined from hand maps did not always predict responsiveness to gratings. Roughly 10% of the neurons that responded briskly to moving bars or edges responded poorly to moving gratings. Conversely, a few units mapped as "indefinite" gave brisk and selective responses to gratings.

In agreement with previous studies, we found the receptive fields of LS neurons to be larger than those of area 17 neurons. In our hands, however, this difference was less marked than previously reported, probably because our sample was largely confined to the central 10 deg of the visual field, while other studies have included the middle and far periphery of the visual field (Khachvankian & Harutiunian-Kozek, 1981; Spear & Baumann, 1975; Zumbroich et al., 1986). On average, LS receptive fields were 2–4 times larger in linear dimension than those of neurons in area 17, ranging in width from 1–20 deg (mean 5.4 deg). LS receptive fields do not appear to be markedly larger than those in area 18 over the range of eccentricities we studied.

When stimulated with moving sinusoidal gratings, most LS neurons responded with an unmodulated elevation in firing rate. In units responding to low spatial frequencies, there was occasionally a response component that modulated in synchrony with the passage of the grating's bars across the receptive field, but in few cases was this response component larger than the unmodulated component. We noted no systematic differences in the peak spatial frequencies for the unmodulated or modulated components of individual cells' responses. The peak spatial frequency for each neuron was chosen by examining the greatest response amplitude, whether modulated or not. Chosen this way, the modulated response to the peak spatial frequency was greater than the unmodulated for only two of the 74 neurons we studied. Thus, the responses of LS neurons to gratings resemble those of complex cells in areas 17 and 18 (Maffei & Fiorentini, 1973; Movshon et al., 1978*b*,*c*). This result is similar to that reported by Zumbroich and Blakemore (1987) but differs from another report (Morrone et al., 1986) that found some cells in PMLS to have significant modulated response components.

Selectivity for spatial frequency

We determined the response to gratings of different spatial frequency that moved across the receptive field at the optimal drift rate. The gratings were optimally oriented and, when the unit was not directional, we measured spatial tuning curves for the two possible directions of motion; in these cases spatial tuning did not differ significantly in the two directions. As in areas 17 and 18, most LS neurons were selective for the spatial frequency of gratings, showing reduced responses to gratings whose frequency was either lower or higher than the optimum. Figure 2 shows the tuning characteristics of five LS neurons, plotting response magnitude (with spontaneous discharge subtracted) against spatial frequency. As discussed above, the response consisted predominantly of an elevation of the mean discharge rate, and we have simply plotted this mean elevation. Four of the neurons of Fig. 2 showed clear "band-pass" spatial-frequency tuning of the sort common in areas 17 and 18 (Movshon et al., 1978*c*). The fifth neuron (leftmost in Fig. 2) did not markedly decrease its response when the spatial frequency was reduced, and uniform fields flickering at the given temporal rate elicited strong responses. This "low-pass" tuning is rare in area 17, but characterizes about 10% of the units in area 18 (Movshon et al., 1978*c*). Five LS units of the 74 tested (7%) responded in this way. A further 22 units (30%) showed band-pass spatial-frequency selectivity but gave reliable responses to zero spatial frequency. The remaining 47 units (63%) did not respond to temporally modulated uniform fields. We did not systematically study the spatial-frequency tuning of this population with regard to the presence or absence of inhibitory surrounds. The four cells that required stimulation restricted to a small portion of the visual field all had band-pass spatial-frequency selectivity and were otherwise indistinguishable in terms of spatial tuning.

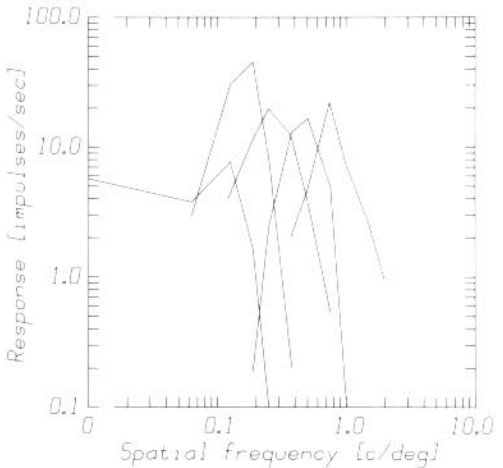

Fig. 2. Five examples of spatial-frequency tuning curves obtained from LS units using high-contrast drifting sinusoidal gratings of optimal orientation, direction, and drift rate. The response plotted is the mean firing rate elicited by the gratings minus the spontaneous firing rate.

We fit each spatial-frequency tuning curve with a function composed of the difference of two exponentials. This type of function was chosen for ease of comparison with data collected in areas 17 and 18 (Movshon et al., 1978*c*) and not because of any specific theory about the receptive-field structure of LS neurons. From these functions, we extracted information on the optimal spatial frequency and spatial-frequency bandwidth, which we took as the ratio between the highest and lowest frequencies that gave better than half-maximal response, expressed in octaves. Figure 3 shows the distributions of optimal frequency and tuning bandwidth. The optima (Fig. 3A) ranged from 0.05–0.94 cycle/deg, in rough agreement with other studies (Shelepin, 1983; DiStefano et al., 1985; Morrone et al., 1986; Zumbroich & Blakemore, 1987). This range is somewhat broader than seen for either area 17 or 18 (Movshon et al., 1978*c*), but fits within the range covered by both. The distribution rather evenly covers the range between 0.1 and 1 cycle/deg, with a broad mode near 0.3 cycle/deg and a logarithmic mean of 0.33 cycle/deg. These values fall between the mean optima for areas 17 and 18 over a comparable range of eccentricities. The distribution of spatial resolution, given as the spatial frequency at which the response fell to one-tenth of maximum, is shown in Fig. 3B. Spatial resolutions were generally in the range from 0.5–2.0 cycle/deg with a few reaching as high as 2.5 cycle/deg.

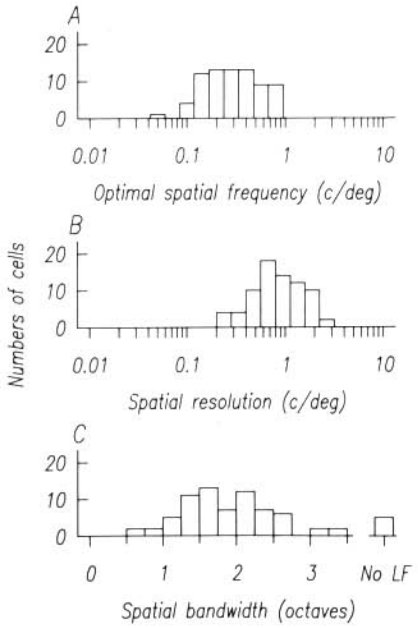

Fig. 3. Distributions of the spatial-frequency tuning properties for 74 units recorded in LS. A: The distribution of optimal spatial frequencies. B: The distribution of spatial resolution, defined as the frequency at which the cell's response fell to one-tenth optimum. C: The distribution of spatial-frequency bandwidths. Units in the "No LF" bin had responses to zero spatial frequency that were greater than half maximum, and therefore had no definable bandwidth.

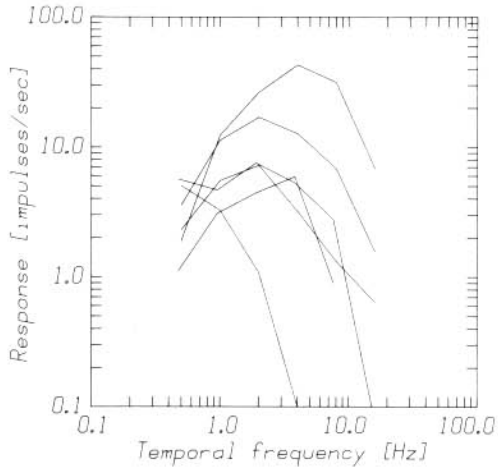

Fig. 4. Six examples of temporal-frequency tuning curves obtained from LS units using high-contrast drifting sinusoidal gratings of optimal orientation, direction, and spatial frequency.

The overall distribution again resembles a combination of the distributions seen for area 17, where resolution may be as high as 7 cycle/deg and area 18 where cells do not respond to spatial frequencies above 1.5 cycle/deg (Movshon et al., 1978*c*). The distribution of spatial-frequency tuning bandwidths is shown in Fig. 3C. The mode of this distribution is between 1.5 and 2 octaves, which is somewhat higher than the mode of 1.3 to 1.5 octaves reported for areas 17 and 18 (Movshon et al, 1978*c*). LS neurons having bandwidths less than 1 octave were rare, while these are not uncommon in areas 17 and 18. A more appropriate comparison might involve only complex cells, which provide the bulk of the input from areas 17 and 18 (Henry et al., 1978; Sherk, 1989), and whose receptive-field properties are similar to those of LS cells. Complex cells have wider spatial bandwidths than simple cells, and viewed in this way the difference between LS and areas 17 and 18 is much less.

Selectivity for temporal frequency

Many neurons in the lateral suprasylvian area respond to very high speeds of stimulus movement when tested with aperiodic spatial targets (Spear & Braumann, 1975; Camarda & Rizzolati, 1976). This perference might result either from an enhanced response to high temporal frequencies or from a preference for lower spatial frequencies. The speed of a moving grating is given (in deg/s) by the ratio of the drift rate (Hz) over the spatial frequency (cycle/deg). Clearly either an increase in the optimal temporal frequency or a decrease in the optimal spatial frequency will raise the optimal speed for a neuron. Figure 4 shows a representative sample of six temporal-frequency tuning curves for units in LS, measured with gratings of optimal orientation, direction, and spatial frequency. Optimal temporal frequencies, as shown in Fig. 5A, were distributed from below 0.5 Hz to over 6 Hz, with a modal value around 2 Hz. This is similar to previous reported values (Morrone et al., 1986; Zumbroich & Blakemore, 1987). The distribution of temporal resolution, defined as the frequency at which the response fell to one-tenth maximum, is shown in Fig. 5B. The temporal resolution limits for some neurons exceeded 40 Hz, but most fell between 10 and 30 Hz. Some neurons (like those yielding the lowest curves in Fig. 4) had low-pass temporal characteristics, while others were more band pass, responding poorly to low temporal frequencies. In general, the range of temporal tuning was similar to that seen in areas 17 and 18 (Movshon et al.,

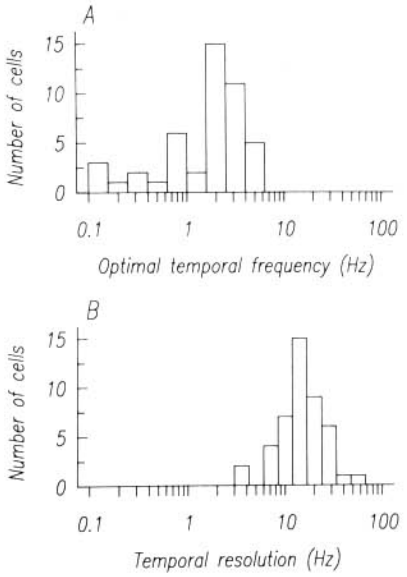

Fig. 5. Distributions of the temporal-frequency tuning properties of 46 units recorded from LS. A: The distribution of optimal temporal frequencies. B: The distribution of temporal resolution, defined as the one-tenth high cut.

1978*c*) and we have no evidence that higher temporal frequencies give enhanced responses in LS.

Since the temporal tuning curves for neurons in LS are not very different from those seen in primary visual cortex, the higher-velocity preferences appear to be a result of low spatial-frequency preference. Most units in areas 17, 18, and LS respond well to gratings moving at 4 HZ. A neuron in area 17 with a preferred spatial frequency of 1 cycle/deg and a preferred temporal frequency of 4 Hz would respond best to a speed of 4 deg/s. In LS the mean preferred spatial frequency was 0.33 cycle/deg. A neuron with this preferred spatial frequency and a preferred temporal frequency of 4 Hz would respond best to a speed of 12 deg/s. The optimal spatial frequencies for LS neurons were frequently as low as 0.1 cycle/deg and cutoff temporal frequencies were usually 10 Hz or greater; this is consistent with the finding that these units often respond to aperiodic targets at speeds in excess of 100 deg/s.

Discussion

Our results on the spatial selectivity of LS neurons are somewhat different from those previously reported by some investigators. The study by Zumbroich and Blakemore (1987) reported a considerable decline in spatial resolution in LS when compared with areas 17 and 18. The average optimal spatial frequency was 0.16 cycle/deg compared with 0.77 cycle/deg and 0.22 cycle/deg in areas 17 and 18, respectively (Movshon et al., 1978*c*). They also noted an average spatial bandwidth of 2.2 octaves compared with 1.5 octaves in areas 17 and 18. Other studies (DiStefano et al., 1985; Morrone et al., 1986) reported similar or slightly higher optima and acuities similar to those seen in area 18. Our results, in contrast, show the means to be intermediate to those of areas 17 and 18, and individual LS neurons to be similar to those in either area 17 or 18. The major difference in methods between these studies and our own was the range of eccentricities covered. Our population of neurons had receptive fields centered for the greatest part within 10 deg of the *area centralis* whereas the other studies have sampled a wide range of eccentricities. The study by Movshon et al. (1978*c*) of areas 17 and 18 was also almost completely confined to the central 10 deg of visual field. Therefore our population of LS neurons appears to be the most appropriate for comparison. We conclude that the spatial properties of LS neurons resemble those of their inputs from areas 17 and 18.

In terms of temporal properties, the population of neurons in LS also appeared to reflect the combined properties of areas 17 and 18. Movshon et al. (1978*c*) found units in area 17 to have temporal low-pass characteristics, diminishing their response at temporal frequencies above 2–4 Hz. Units in area 18 tended to diminish their response when the temporal frequency was moved either above or below some optimum (usually 2–8 Hz). The optima for units in LS ranged between 2 and 4 Hz and were sometimes as high as 6 Hz. We found units that exhibited either low-pass or band-pass characteristics; this variation might reflect the influence of areas 17 and 18, respectively.

Recent studies by Spear and his colleagues (see Spear, 1988) suggest that despite the density of projections from areas 17 and 18 to LS, these projections influence only the directionality of LS cells and their ability to respond to flashed stimuli. Spatial and temporal tuning appear to be unchanged after removal of contralateral or ipsilateral areas 17, 18, and 19. The spatial and temporal tuning of LS neurons has therefore been attributed to projections from the C layers of the lateral geniculate nucleus. Only Y cells could provide relevant input, as W cells respond to significantly lower spatial and temporal frequencies than cells in LS and no layers containing X cells project directly to LS. The distributions of spatial optima and resolutions we have found for LS are more similar to those of the X cells (Sherman, 1985), but there is clearly significant overlap with the distribution for Y cells. If, in fact, LS is relying on LGN, rather than areas 17 and 18 for its spatial properties, this would suggest that spatial processing is being carried out in LS in a fashion similar to that being carried out in primary visual cortex. The significance of such parallel and identical processing is unclear. If, alternatively, neurons in LS recieve much of their functional input from primary visual cortex, we see no evidence of further refinement of the spatial and temporal processing initiated in areas 17 and 18. The selectivity of LS neurons for spatial and temporal frequency (and orientation, Gizzi et al., 1990) is qualitatively and quantitatively very similar to that reported for neurons in areas 17 and 18. Our results suggest that the lateral suprasylvian area does not represent another major step in the hierarchy of spatial processing begun in striate cortex, since neurons in this area do not show any greater specificity for spatial and temporal stimulus parameters than is seen in areas 17 and 18. Rather, our results suggest that LS is primarily concerned with other features of the visual image, such as motion.

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