

## TEMPORAL AND SPATIAL RESPONSE CHARACTERISTICS OF THE CAT SUPERIOR COLLICULUS

ROBERT B. PINTER\* and LAURENCE R. HARRIS\*\*

*Department of Psychology, Dalhousie University, Halifax, Nova Scotia (Canada)*

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### SUMMARY

We have examined the responses of 72 cells of the cat superior colliculus to drifting gratings of sinusoidal luminance profile as a function of spatial frequency, velocity and contrast. Of 72 cells, 66 responded to gratings either by change in mean firing rate only (58/72) or in a temporally modulated pattern in addition to the change in mean firing rate (8/72). The remaining 6 showed no change in discharge rate in response to any of the gratings tested. Many cells (24/72) were inhibited or excited by particular combinations of spatial *and* temporal frequencies. Some (8/72) demonstrated selective inhibition or excitation to a particular temporal frequency independent of spatial frequency and velocity and could therefore be said to be tuned specifically to *temporal* frequency. No cells were tuned *only* to a constant spatial frequency or a constant velocity. (24/72) cells displayed maximum inhibition or excitation only at a particular combination of spatial and temporal frequencies. Some cells (8/72) demonstrated a temporal modulation synchronous with the drifting grating in addition to an elevated mean discharge rate. The change in discharge rates evoked by gratings are generally less than those evoked by presentation of moving small slits or spots of light. Collicular cells often demonstrate a center-surround organization in their response to gratings. The center and surround often differ in their spatial frequency and velocity preferences. Compared to cortical and retinal ganglion cells, individual collicular cells are extremely non-linear. On a cell population basis, however, a linear Fourier analysis on grating response predicts the collicular cells' preference for movement of small objects.

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\* Address for reprints: Departments of Electrical Engineering and Zoology, University of Washington, FT-10, Seattle 98195, Wash., U.S.A.

\*\* Present address: Department of Psychology, University of Durham, Durham, U.K.

## INTRODUCTION

Many cells in the superior colliculus of the cat are responsive to visual stimuli and respond well to slits and spots of light moving through their visual receptive fields (for reviews see refs. 6, 20, 28 and 30). The cat's superior colliculus has also been implicated in the generation of eye movements (e.g. ref. 12) and head movements<sup>11</sup>. One of the colliculus' primary functions may be to connect visual responses to moving objects with the generation of eye and head orienting movements towards these objects. These functions demand not only a response to the object of the orienting response, but also the ability to take into account the movement of the external world during the eye or head movement. For this reason, and also because not all objects worthy of orienting responses are small, we have examined the responses of collicular cells to extended visual stimuli.

An extended visual stimulus which has been much employed in visual neurophysiology is a grating of sinusoidal luminance profile. This stimulus has as its basis the theorems of Fourier, which state that any two-dimensional scene can be represented by an appropriate combination of these gratings<sup>7,10</sup>. Therefore, the sinusoidal grating is an elementary component of a visual scene by linear super-position *whether or not* the visual cell observing the scene is linear. In a preliminary study of responses of cat superior colliculus cells to drifting gratings of sinusoidal luminance profile, Bisti and Sireteanu<sup>1</sup> determined that the responses of 65% of the units they tested depended on the spatial frequency of the grating. The effects of grating velocity were unreported<sup>1</sup>.

This paper reports the responses of single cells in the superior colliculus to drifting gratings of sinusoidal luminance profile over a range of spatial frequencies, velocities, and contrasts. Many cells are inhibited or excited by a particular *combination* of spatial frequency and velocity. Varying the velocity profoundly modifies the spatial frequency tuning of most cells. Other cells demonstrate selective inhibition or excitation to a particular *temporal* frequency independent of spatial frequency and velocity. Only a small fraction of the cells we recorded that were responsive to other visual stimuli did not respond to gratings. The majority of cells responded to gratings only by changes of mean spike firing rate and were therefore non-linear.

## METHODS

### *Surgical preparations*

Eight cats weighing approximately 3 kg each were prepared for neurophysiological recording using the standard procedures of Cynader and co-workers<sup>4,5</sup>. Anesthesia was induced by intravenous sodium pentathol (2.5%) and anesthesia was maintained during recording by inhaled nitrous oxide (N<sub>2</sub>O/O<sub>2</sub>: 70%/30%). Eye movements were abolished by continuous infusion of a mixture of gallamine methiodide (Flaxedil, 5.0 mg/kg/h) and D-tubocurarine (0.5 mg/kg/h in 5% lactated dextrose). Body temperature was maintained at 38 °C by a heating pad and anal probe. Expired CO<sub>2</sub> was monitored continuously with a carbon dioxide gas analyzer (Beckman) and maintained between 4 and 5% by adjusting the stroke volume of a respiration pump.

The pupils were dilated by atropine and the nictitating membranes retracted by neosynephrine, both applied topically. Contact lenses with 4 mm artificial pupils were used and supplementary spectacle lenses were chosen by ophthalmoscopy and streak retinoscopy to bring the display oscilloscope into accurate focus on the retina. The position of the areae centrales were plotted on the oscilloscope screen by reverse ophthalmoscopy. Use of 3% saline with the contact lenses helped prevent clouding of the cornea.

Single units were recorded from the superior colliculus with glass-coated platinum-iridium microelectrodes. A craniotomy was performed centered over the left superior colliculus of each animal and a small slit in the dura was made through which an electrode was maneuvered to the colliculus below. After each animal had been recorded for 3 days, electrolytic lesions were made at the end of an electrode track for later histological verification of the recording site and the animal sacrificed by an overdose of Nembutal.

#### *Data collection, stimulus delivery and control*

Only visually responsive cells with visual receptive fields within 5–10° of the area centralis were examined monocularly. These receptive fields were first plotted by a hand-held projector. The electrode tip was positioned according to standard stereotaxic coordinates for the cat superior colliculus. We always correlated the measured approach to the colliculus with the appearance of hippocampal ‘galloping’ units and then the silent subarachnoid space. Then the characteristic summed multiple action potentials (visual) signaled electrode arrival at the surface of the colliculus. The cat’s left colliculus was used in this study. Cell depth was recorded by an electronic stepping motor microdrive from the level of the first appearance of the summed multiple action potentials.

The cells’ action potentials were converted to pulses by a Schmitt trigger and transmitted to a PDP 11/34 digital computer. This computer also generated the visual stimuli on the face of a high resolution display monitor (Tektronix 606). The display subtended  $32 \times 40^\circ$  of visual angle and had a mean luminance of 6 cd/sq.m (P31 green phosphor).

The display was generated as follows. A digitized sinusoidal waveform was stored in the computer, and read out through a digital-analogue converter to provide sinusoidal Z-axis screen modulation. The X-axis modulation (to scan the sinusoid across the screen) was provided by a ramp waveform synchronized to the sinusoidal Z-axis modulation. The Y-axis modulation (to spread the luminance of an X-axis point uniformly up and down the screen) was provided by a 2.5 MHz burst from a waveform generator (Wavetek) synchronized to the data-ready pulse of the PDP 11/34. The drift velocity of the sinusoidal grating was determined by a program loop stepping through new initial points of the sinusoidal readout for each subsequent sweep of the X-axis ramp. For every spatial frequency and velocity the initial phase of the grating was constant on the oscilloscope screen. The contrast of the grating was determined by another computer controlled voltage multiplied with the sinusoidal Z-axis signal. The frame rate was approximately 100 Hz.

The visual stimulus (presented monocularly, to the cats' right eye) was thus a drifting grating of sinusoidal luminance profile whose spatial frequency, velocity of drift and contrast, could be varied under computer control in a randomized order. Cell responses were accumulated into histograms synchronized with the stimulus presentation both in time and parameter space. The stimulus display was centered on the visual receptive field of each cell and adjusted to match the preferred direction of movement of the cell. Cardboard masks were used to restrict the stimulus either to the receptive field center or to the surround (see Fig. 4). When the center of the receptive field was stimulated alone, the grating size along the bars was slightly less than the size of the receptive field which had been accurately measured by slow movements of a hand operated variable aperture (down to  $0.1^\circ$ ) projector. In the case of surround only stimulation, the mask was extended, in the direction of the bars, into the measured center of the receptive field by a small amount. This was done to avoid contamination of center response by surround, and vice versa. However, for center only stimulation there was unavoidable stimulation of a part of the surround by the grating since we chose to not truncate our gratings in the direction of drift, so that in all cases the grating was truncated by the receptive field center rather than a mask edge (see Appendix).

Each presentation of the drifting grating began with a 500 msec ramp-increase in contrast from zero to the final value to reduce possible responses to abrupt changes in contrast. These kinds of responses were never observed for the ramp-increase. The ramp was followed by a 5 sec recording period during which grating spatial frequency, contrast, speed and direction of drift and extent remained constant.

#### *Data analysis and presentation*

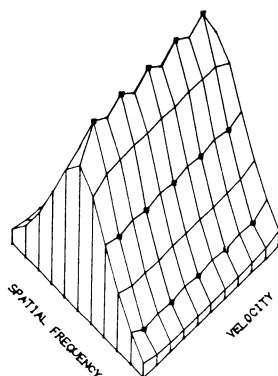
The time of occurrence of every spike with respect to stimulus onset was recorded within 1 msec by the computer. This allowed analysis of spike counts as a function of stimulus parameters of any desired combination, and the construction of post-stimulus time histograms (PST). This was accomplished by the program 'POST' designed and programmed by Dr. Robert M. Douglas. Files were transferred to another program 'GRID' (also by Dr. Robert M. Douglas) for computer construction of the three-dimensional graphs. This program used a Laplacian interpolation technique.

In this study we determined that collicular cells do not respond well to sinusoidal temporally modulated ('counterphased') sinusoidal luminance gratings, but that they do respond somewhat to square-wave temporally modulated sinusoidal luminance gratings. (see Results below.) The ranges of parameters for this response were used initially to determine ranges of parameters for one-dimensional moving sinusoidal luminance gratings as reported below. Larger parameter ranges were not possible given cells' recording longevity (30–90 min).

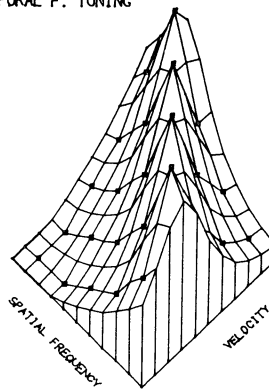
We looked at both spatial frequency and velocity tuning characteristics of the visual responses of collicular cells. Temporal frequency is defined as the product of these two parameters: temporal frequency (Hz or cycles/sec) = spatial frequency (cycles/deg.)  $\times$  velocity (deg./sec); degrees are of visual angle subtended at the eye.

The 3-dimensional plots of this paper show spatial frequency on a logarithmic X-axis, velocity on a logarithmic Y-axis, and cell response on the Z-axis. There the  $-45^\circ$  line (in the X,Y plane) represents constant temporal frequency. The response of a cell preferring a temporal frequency independent of spatial frequency and velocity appears as a diagonal ridge such as that of the hypothetical plot 'temporal frequency tuning' in Fig. 1. This is distinct from other hypothetical types of tuning, for example spatial frequency tuning ('spatial frequency tuning') in which a cell prefers a given spatial frequency independent of velocity and temporal frequency: velocity tuning in which a cell prefers a specific velocity independent of spatial and temporal frequency, or the situation in which a cell prefers a specific spatial and temporal frequency and velocity. Fig. 1 shows these 4 possible tuning types for a cell's response to a grating. Note that if only spatial frequency were varied and velocity kept constant, three of these cases would give the impression of some spatial frequency tuning even though only the plot

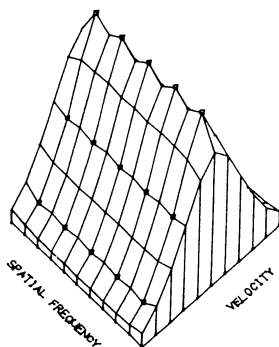
SPATIAL F. TUNING



TEMPORAL F. TUNING



VELOCITY TUNING



TUNING

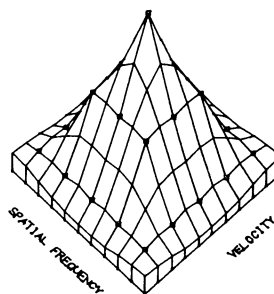


Fig. 1. These 4 plots represent hypothetical response characteristics demonstrating either spatial frequency tuning (top left), temporal frequency tuning (top right), velocity tuning (bottom left) or simple tuning (bottom right). Spatial frequency and velocity are plotted on logarithmic scales, and the hypothetical response is plotted on a linear arbitrary scale of average spikes/sec over the stimulus presentation period.

labeled 'spatial frequency tuning' could properly be said to have a single-valued spatial frequency selectivity. The same misleading impression can be achieved for temporal frequency tuning if not all the relevant stimulus parameters are varied.

## RESULTS

Seventy-two visually responsive cells of the superior colliculus were investigated using drifting spatial gratings of sinusoidal luminance profile at spatial frequencies, velocities and contrasts chosen in an interleaved random sequence from a predetermined set. The axis of drift of the grating through the cell's receptive field was determined by the cell's preferred direction of spot movement. The response characteristics of our sample are summarized in Table I. Visually responsive cells in the superior colliculus were carefully distinguished from retinal fibers. Most collicular cells were binocularly activated and exhibited direction selectivity (see Table I) (all grating stimuli are monocular).

Few units fell neatly into the theoretical categories delineated in Fig. 1. Only 'temporal frequency tuning' and 'tuning' categories were found (see Table 1). In the following figures, responses of several representative collicular units are presented. Determining whether a cell responded or not to gratings was decided by examining its activity (relative to spontaneous level) during presentation of all spatial frequencies and speeds of drift of a grating as a function of direction and contrast. Only 6 of the 72

TABLE I

*Responsiveness to gratings of collicular cells*

	<i>Number/number tested</i>	<i>% of number tested for this parameter</i>
<i>General</i>		
Cells with no response to gratings	6/72	8 %
Cells with response that increased with contrast	52/65	80 %
Cells with directional selectivity	47/58	81 %
Cells with temporal spike rate modulation	8/66	12 %
<i>Spatial-temporal tuning</i>		
Cells with tuning to one combination of spatial frequency and velocity	24/66	36 %
Cells tuned to a particular temporal frequency	8/66	12 %
Cells tuned to low spatial frequency and high velocity	7/66	11 %
<i>Centre-surround organization</i>		
Cells with surround inhibiting centre response	9/12	75 %
Cells responding well to full-field (32 × 40°) gratings	18/72	25 %

cells studied were completely unresponsive to the gratings we presented, even though these 6 cells responded well to slits or spots of light moved across their visual receptive fields.

### *Variation of responses with contrast*

The response of a typical cell to gratings drifted across its visual receptive field is shown in Fig. 2. The contrast is specified for each plot of the figure. There is a peak of response for each contrast at 0.1 cycles/deg. and 32 deg./sec, suggesting that this combination is optimal for this cell over the range studied. Note that even if the spatial frequency is kept constant at the optimal value, the response declines steeply with change of velocity. The response at optimal spatial frequency and velocity increases

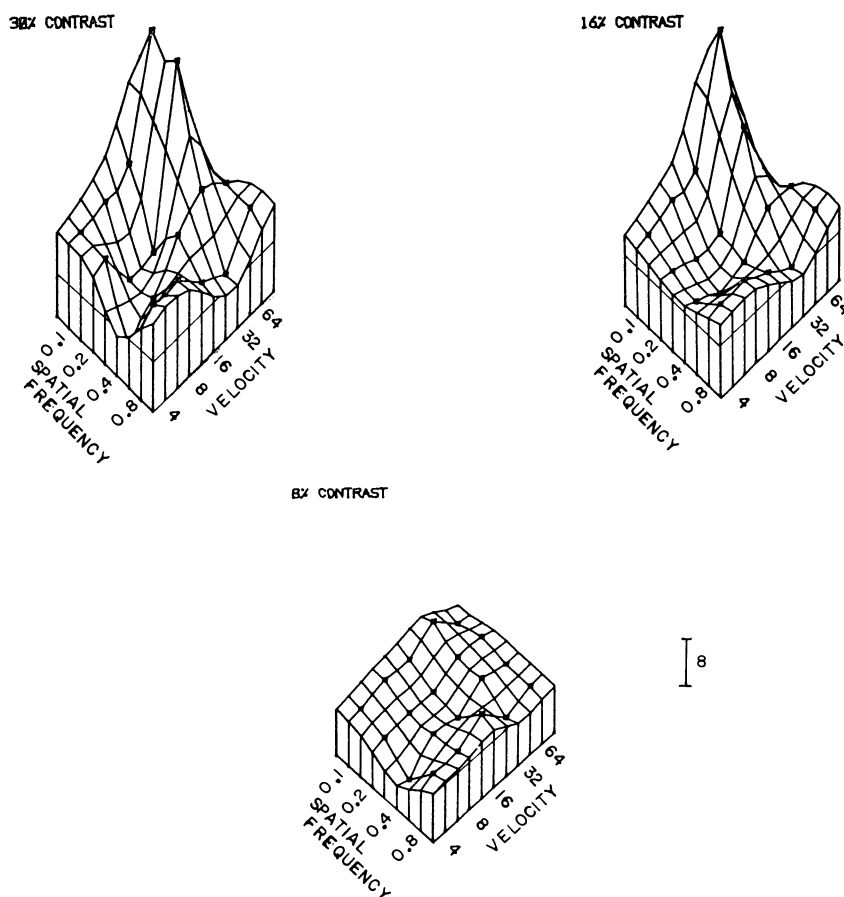


Fig. 2. These 3 plots of identical scales and angle of view, show the response of a collicular cell for three values of contrasts: 30%, 16% and 8%. The response is the average spike rate over the recording period during which the grating drifted at a given contrast, spatial frequency and velocity. The spontaneous spike rate was 8 spikes/sec and is indicated by the horizontal line on the face of each plot. The peak rate for 30% contrast was 33 spikes/sec and occurred for a stimulus of 0.2 cycles/deg. and 32 deg./sec. The receptive field of this cell was large and included a substantial portion of the grating which subtended  $32 \times 40^\circ$  centered on the center of the cell's receptive field. Calibration bar in spikes/sec/presentation.

with contrast. Since the preference for one spatial frequency exists for only a small range of velocities it could be said equally well that this cell prefers temporal modulation at approximately 3.2 Hz at a spatial frequency of 0.1 cycle/deg. This selectivity for low spatial frequency and high velocity was a characteristic of 7 of the 72 cells. These are also of the simple 'tuning' category of Fig. 1.

### *Temporal frequency selectivity*

While the cell of Fig. 3 demonstrates an excitatory response at low spatial frequencies and velocities, most notable is the inhibition which appears as a valley in

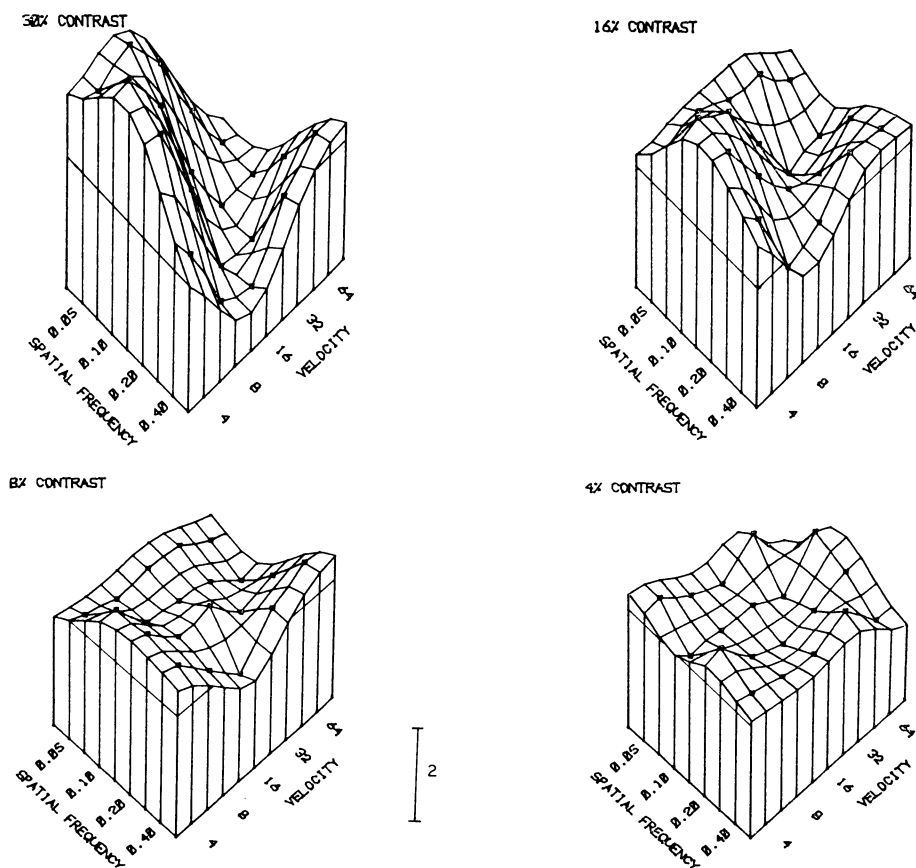


Fig. 3. These 4 plots show the response of a cell to gratings of (interleaved) contrasts 30%, 16%, 8% and 4%. Note the trough of response at a constant temporal frequency of 5 Hz which appears as a *diagonal* on this plot (cf. Fig. 1). All plots in all figures are shown from the same viewing angle, but vertical scales of the figures vary; plots within a figure are on identical scales. An indication of the relative scales can be obtained from the spontaneous rate. This is indicated by the horizontal line around the face of the plots. In this figure the spontaneous rate was 2.6 spikes/sec. The response (for this and subsequent figures) is the average spike rate over the 5 sec recording period per repetition (10 repetitions of each stimulus). Its peak value was 5.4 spikes/sec and occurred at the highest contrast at 0.1 cycles/deg. and 4 deg./sec. The contrast, spatial frequency and velocity were randomly interleaved under computer control. The visual receptive field was approximately circular with a diameter 10°. The grating display subtended  $32 \times 40^\circ$  and was centered on the receptive field. This cell showed temporal modulation at the temporal frequency of the grating (see also Fig. 9). Calibration bar in spikes/sec/presentation.



this plot. This valley represents an inhibition of response at a temporal frequency of 5 Hz *independent* of spatial frequency and velocity over the range studied. As contrast is increased the amount of both excitation and inhibition increase. This cell was selectivity tuned (by inhibition) to stimuli of temporal frequency of 5 Hz. A further temporal-frequency tuned response (of opposite polarity) can be observed at 0.4 Hz. Units with temporal-frequency tuned properties resembling those of this cell were not uncommon; 8 of the 72 cells studied displayed inhibition or excitation at a particular temporal frequency, independent of stimulus spatial frequency and velocity.

### *Directionality*

Many cells of the cat's superior colliculus respond best to stimulus movement in a particular direction<sup>28</sup>. Often there is inhibition in the opposite (null) direction<sup>6</sup>. In this study the responses in the preferred and null directions were compared in 47 directionally selective cells.

The response of a cell with obvious directionality is illustrated in Fig. 4 (top two plots). For stimulation of the center only, this cell strongly prefers movement to the cat's right. However, not all directional cells displayed such obvious selectivity.

### *The contribution of the surround*

The response of collicular cells to full field stimulation (surround and center simultaneously by the same stimulus) was compared to that evoked by stimulation of either the receptive field center or surround alone. The grating could be partially masked with masks which were always orthogonal to the bars of the stimulus grating. The grating always subtended 40° (full width of the screen) along the direction of drift to avoid any edge effects produced by the stimulus (see Appendix and inserts on Fig. 4).

Fig. 4 shows a typical strongly directionally selective cell whose response to gratings is primarily excitatory. The directional specificity is preserved when stimulation is restricted to either the center or the surround. However, stimulation of the surround alone evokes a weaker response than stimulation of the center but of similar spatial frequency and velocity preference. Stimulation of the full field (both the center and surround) produces a response very much weaker than stimulation confined to the center. This suggests inhibition of the center response by the surround. A similar pattern of response is shown for another cell in Fig. 5. This cell is not directionally selective for a stimulus that falls only on the center of its receptive field. It is, however, directional in its response to stimulation of the surround alone or for full field stimulation.

A further example of interaction between center and surround is shown in the cell whose responses are illustrated in Fig. 6. This cell demonstrates strong non-directional tuning (category 'tuning' of Fig. 1), peaking at 0.1 cycles/deg. and 8 deg./sec (0.8 Hz) for stimulation of the center only. This response is, however, abolished by extending the grating into the surround region (full field, Fig. 6). There is no strongly tuned response when the surround is stimulated alone, but the surround is a potent inhibitor of the center.

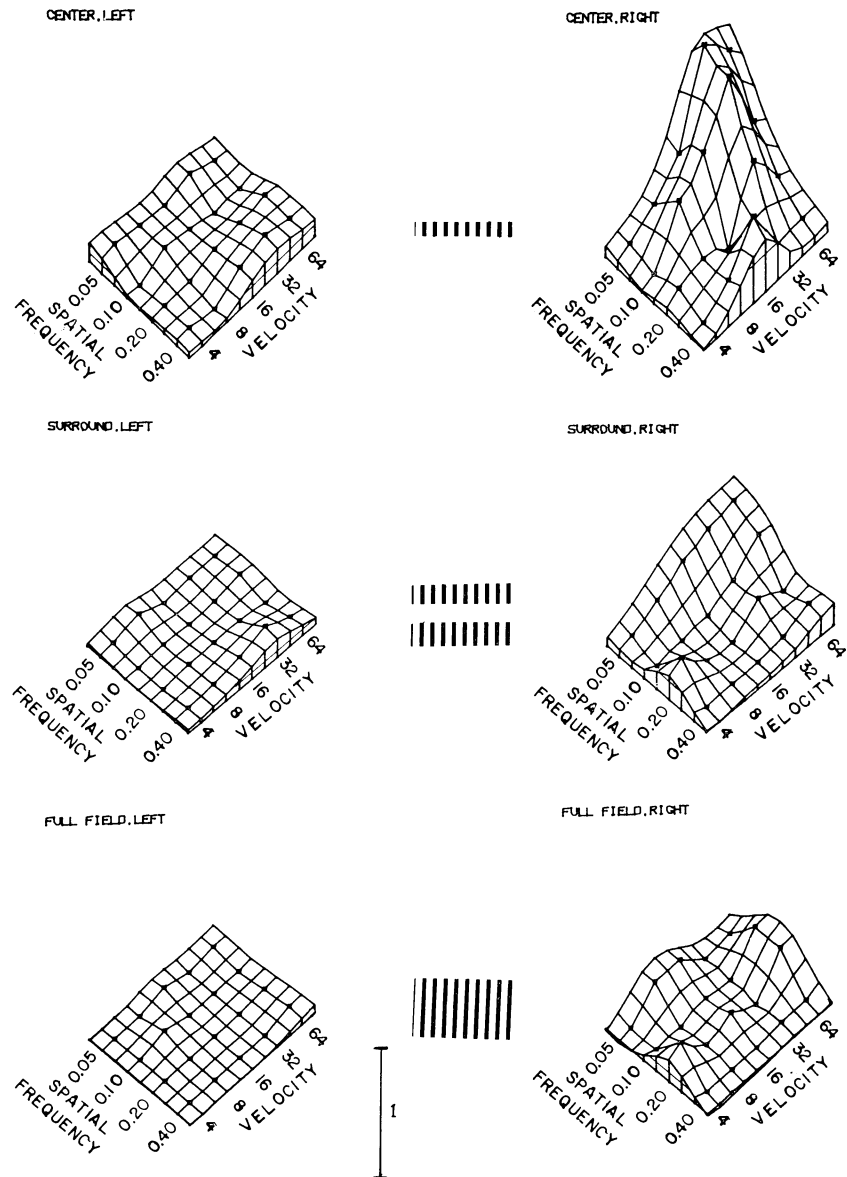


Fig. 4. A comparison of the properties of the central and peripheral parts of the visual receptive field of a collicular cell. The center only stimulation (top two plots) used a grating display  $4 \times 40^\circ$  centered on the receptive field (the longer dimension being the direction of drift, see inset and Appendix). The receptive field was about  $5^\circ$  across. For surround only stimulation (middle two plots) a  $6 \times 40^\circ$  mask (of approximately the average luminance of the grating) was centered on the receptive field resulting in two  $13 \times 40^\circ$  displays above and below the mask. For full field stimulation, the mask was removed resulting in a grating display of  $32 \times 40^\circ$  centered on the receptive field. The peak spike rate was obtained for center stimulation, rightward drift at 0.05 cycles/deg. and 32 deg./sec and is 1.4 spikes/sec. Note the low spontaneous discharge rate of this cell. In this and Figs. 5 and 6 the spontaneous discharge rate varied for center-surround stimulus configuration changes, but control spontaneous levels for center only stimulation were checked and found constant. Other conditions as for Fig. 3. Insets: configuration of grating. Calibration bar in spikes/sec/presentation.

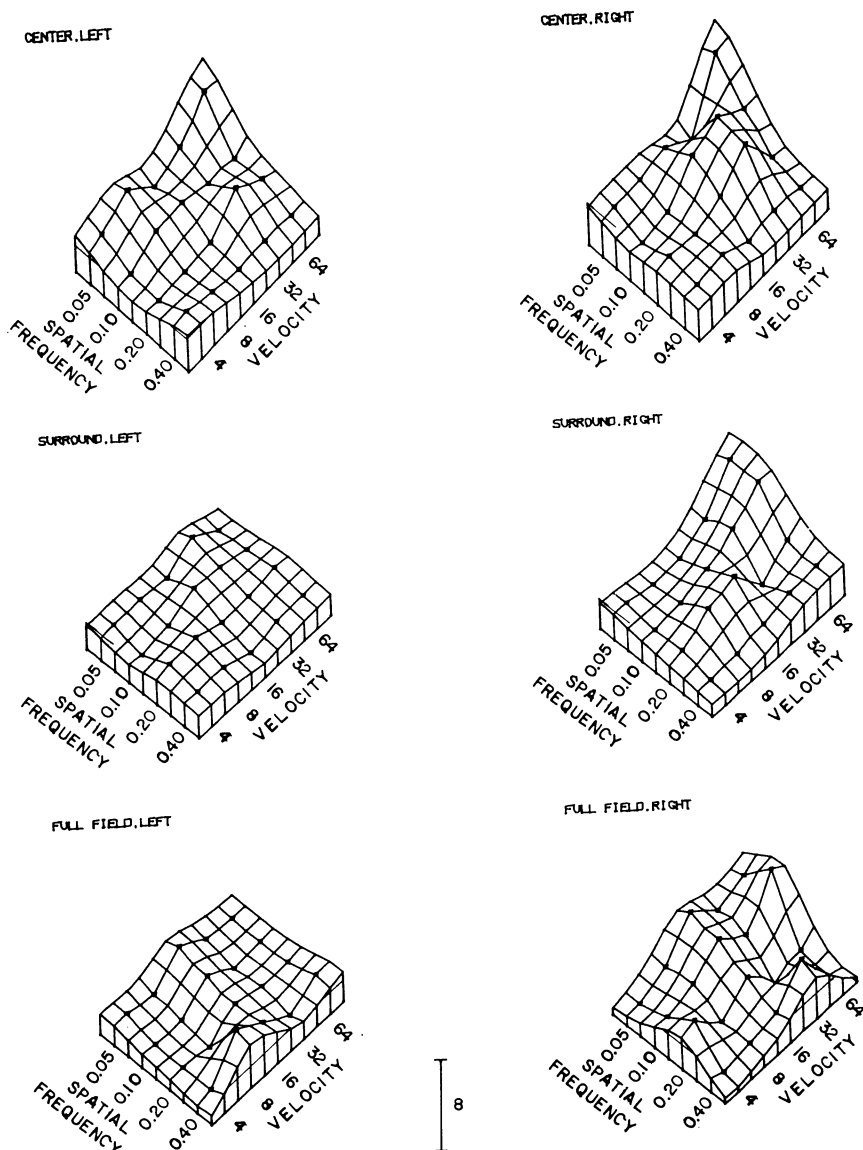


Fig. 5. An example of a cell that was directionally selective only if the surround was stimulated. The receptive field size was approximately  $6^\circ$ , and the center only stimulation (top two plots) used a grating display of  $6 \times 40^\circ$  centered on the receptive field (the longer dimension is along the direction of the drift). For surround only stimulation (middle two plots) a  $6^\circ$  mask (of approximately the average luminance of the grating) was centered on the receptive field. For stimulation of the full field, the mask was removed. The peak spike rate was found for center stimulation, rightward drift, at 0.05 cycles/deg., 64 deg./sec, and is 8.3 spikes/sec. Format as in Fig. 3. Calibration bar in spikes/sec/presentation.

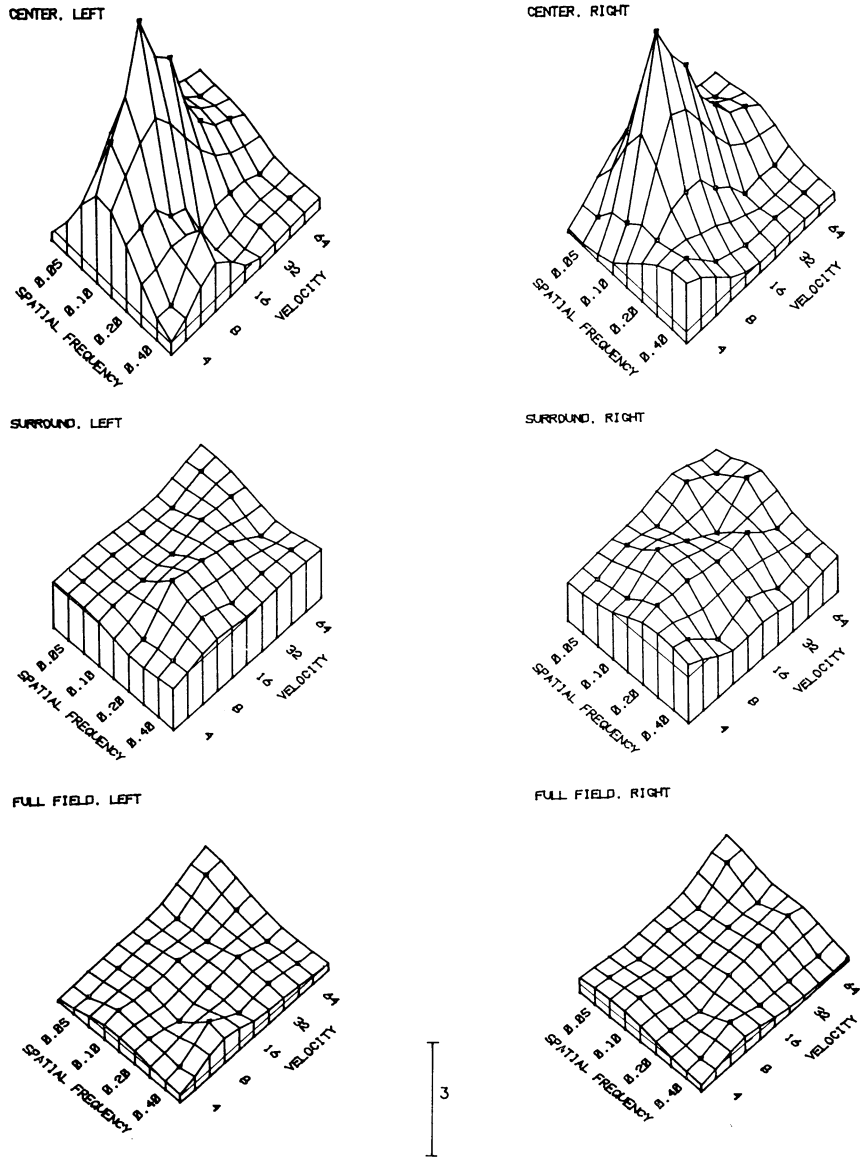


Fig. 6. A further example of the interactions between center and surround of collicular cells. The receptive field size was approximately  $2^\circ$  and center only stimulation (top two plots) used a grating display of  $1.6 \times 40^\circ$ . For surround only stimulation (middle two plots) a  $5.2^\circ$  mask of the same average luminance of the grating was centered on the receptive field, resulting in a flanking grating in the surround. For stimulation of the full field, the mask was removed. The peak spike rate was found for center only stimulation at 0.1 cycles/deg. and 8 deg./sec, leftward motion and was 7.3 spikes/sec. Spontaneous levels (obtained for interleaved stationary gratings) are indicated by the horizontal lines on the faces of each plot. Format as for Fig. 3.

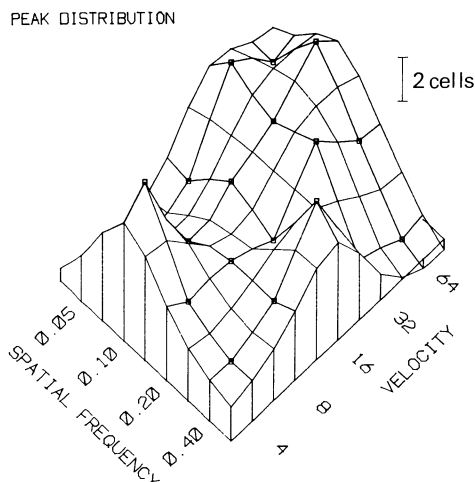


Fig. 7. The distribution of preferred spatial frequencies and velocities (those yielding peak responses), for 60 cells with measurable peak responses. The Z-axis represents the number of cells for each combination of spatial frequency and velocity and center only stimulation. The vertical calibration bar shows the height corresponding to 2 cells.

#### *Preferred tuning characteristics*

While only 24 of the 72 cells studied here demonstrated a distinct single peak or null response as a function of spatial frequency and velocity (e.g. Fig. 6, center response), 60 cells had a response topography such that a 'best combination' of stimulus parameters could be defined. The best combination of spatial frequency and velocity (center only stimulation) for the number of cells (Z-axis) is plotted in Fig. 7 on the same axes used in the previous plots. Clearly, most cells preferred lower spatial frequencies (0.05–0.1 cycles/deg.) but higher velocities (64 deg./sec).

#### *Temporal characteristics of responses*

The descriptions discussed above of responses to gratings are based only on changes in mean spike rate. The maximum spike rates obtained over a five second recording period for each cell are shown in Fig. 8, as a frequency distribution.

Most cells of this study responded to gratings by a continuous elevation or diminution of the spike rate. However, 8 cells of the 72 studied showed in addition a distinct temporal modulation of spike rate synchronous with the temporal frequency of the drifting grating. The amplitude of the modulation of response at any one temporal frequency was always dependent on the spatial frequency of the stimulus. An example of this is shown in Fig. 9, for a temporal frequency of 0.8 cycles/sec. This is taken from the cell illustrated in Fig. 3 (see inset of Fig. 9). As spatial frequency is increased from 0.05 (Fig. 9A) to 0.2 (Fig. 9C) cycles/deg. at a constant temporal frequency of 0.8 cycles/sec, the modulation clearly decreases. For this cell, modulation also occurred at 0.2 and 0.4 cycles/sec, but not at temporal frequencies above 0.8 cycles/sec. For all other cells, synchronous temporal modulation, when present, was found only below 1.6 Hz.

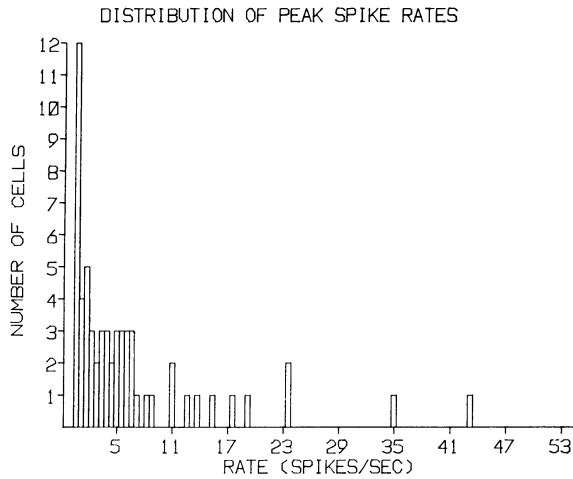


Fig. 8. The peak responses of collicular cells to gratings. The number of cells is plotted against the peak spike rate obtained as an average over the 5 sec recording period. The peak responses of the 60 cells of Fig. 7 are plotted here.

#### *Responses to counterphased (temporally modulated) gratings*

In this study we initially measured response of collicular cells to temporally modulated stationary (counterphased) gratings of sinusoidal spatial luminance profile. For sinusoidal temporal modulation of the gratings (of spatial frequency 0.2–3.2 cycles/deg.) no consistently measurable response could be obtained for any temporal frequencies in the range of 0.2–5 Hz (see Discussion). However, for square wave temporal modulation of these gratings (of spatial frequencies 0.2 to 3.2 cycles/deg.) in the range of temporal modulation 0.2–1.0 Hz, response of some cells was a sharp transient change in spike rate following a shift of luminance (of any given cycle). This response did not in most cases depend on the spatial phase of the grating, but did depend on spatial frequency, falling from maxima at 0.2 cycles/deg. to the noise level at 0.8–1.6 cycles/deg. This response also depended on contrast, falling to the noise level at 2 to 1 % contrast. These data allowed a preliminary selection of ranges of parameters for drifting gratings, but the predominance of non-linear response and variety of cell response types and recording longevity prevented accurate predictions of response to counterphased gratings from drifting grating results (see Discussion).

#### *Spatial frequency and velocity preferences as a function of receptive field diameter and recorded depth of cell*

To examine distribution of spatial frequency and velocity preferences in the colliculus with respect to measured receptive field size and recorded depth of cell, plots are shown in Fig. 10. The decrease of preferred spatial frequency (increase of preferred spatial wavelength) with increase of receptive field size is shown in Fig. 10A, while the less steep decrease of preferred spatial frequency with increased depth is shown in Fig. 10B. These functions for preferred velocity are shown in Fig. 10C, D,

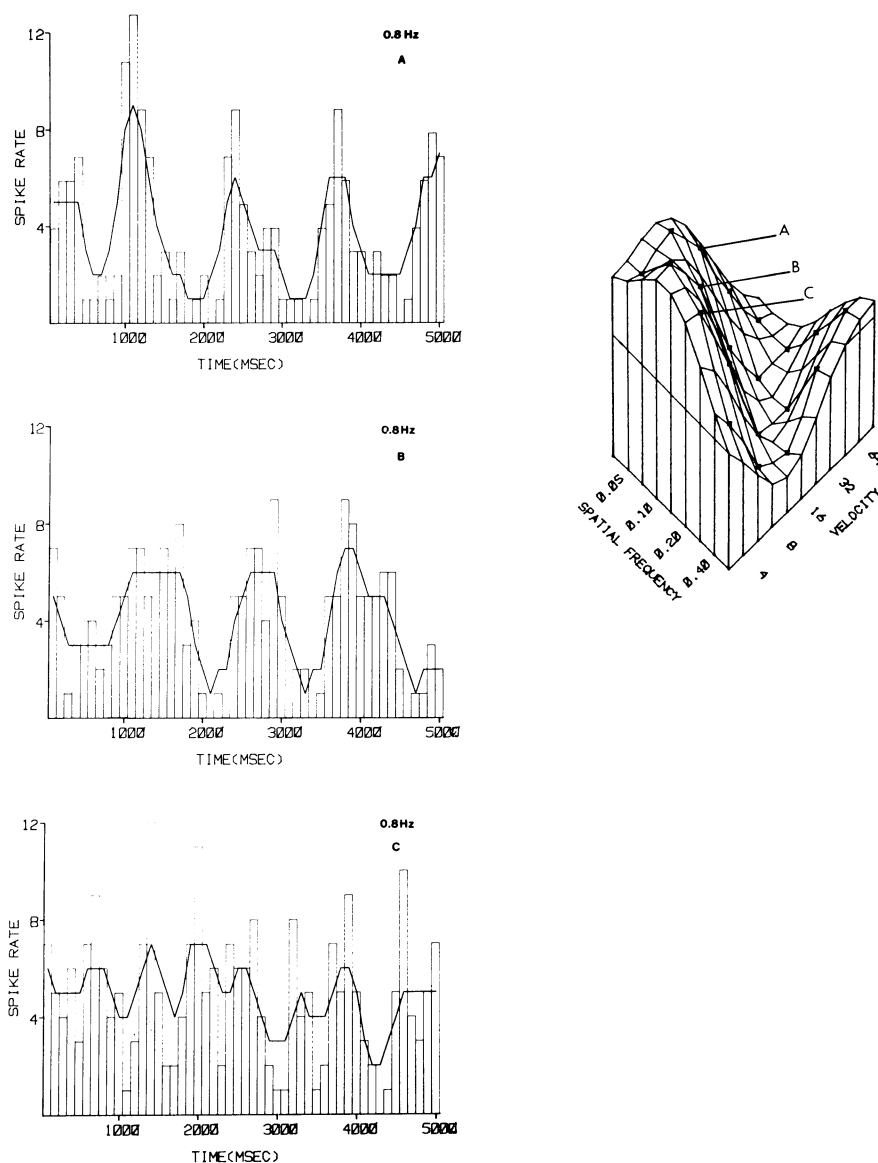


Fig. 9. Some collicular cells exhibit a modulation in their response to drifting gratings. An example of this is shown in these peri-stimulus time histograms. Through the histograms are plotted continuous curves which represent smoothed versions of the histograms. The temporal frequency of the grating is 0.8 Hz for each case (A, B and C). Spatial frequency increases and velocity decreases in the order A, B, C. (Spatial frequencies 0.05, 0.1 and 0.2 cycles/deg., respectively; and corresponding velocities 16, 8 and 4 deg./sec.) The modulation of the spike train shown in these histograms is in addition to an elevation of the mean rate (see inset). 100 msec binwidth; 10 sweeps; spike rate in spikes/sec/sweep. The inset is from Fig. 3 and shows the points from which the histograms are obtained.

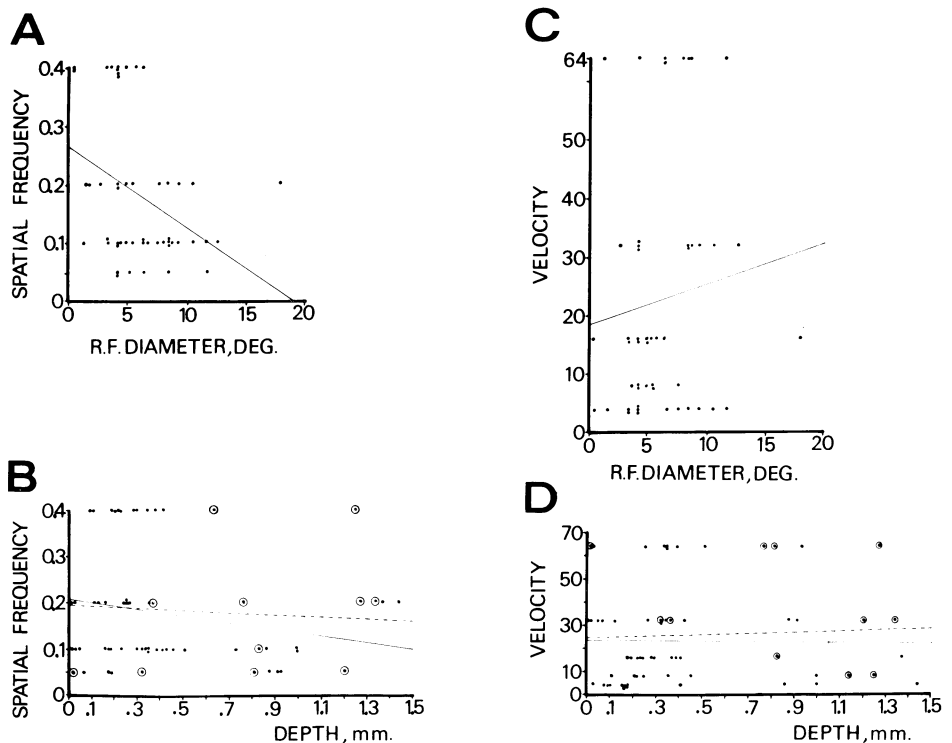


Fig. 10. Plots of spatial frequency and velocity preferences (of Fig. 7) as functions of receptive field diameter and recorded depth of the cell from the collicular surface (see Methods). Solid regression lines plotted for A ( $r = 0.344$ ), B ( $r = 0.19$ ), C ( $r = 0.122$ ) and D ( $r = 0.013$ ), where  $r$  is the correlation coefficient. The abscissae in A and C do not extend to all receptive field sizes; there are no cells of diameters between 20 and 35°, and there are 11 cells of diameter of receptive field larger than 35°, which could not be plotted precisely. These 11 cells are shown in the recorded depth plots B, D as circled points. Inclusion of them for regression lines (dashed) in B, D give  $r = 0.087$  and  $r = 0.053$ , respectively.

and are less steep (for the given ranges of ordinate) than the functions for preferred spatial frequency. Temporal frequencies showed no systematic trend to dependence on receptive field size or depth, although the 8/66 (see Table I) cells tuned to a *particular* temporal frequency were all but one (0.858 mm) found within 0.4 mm of the collicular surface, and had receptive field diameters less than 9.3°. Cells having temporal modulation (8/66, Table I) were not found below 0.830 mm of the collicular surface, but had receptive field diameters distributed over the entire range found. The cells sharply tuned to low spatial frequencies and high velocities (0.05 cycles/deg., 32–64 deg./sec, the 7/66 of Table I) were distributed toward larger receptive fields and greater depth. Cells responding well to full-field gratings (18/72 of Table I) had large receptive fields and were distributed toward greater depth. Overall, cells of larger receptive fields were found at greater depth.



## DISCUSSION

### *Selectivity of collicular cells to spatial frequency, velocity, and temporal frequency*

Many visually responsive cells in the cat's superior colliculus respond differentially as a function of the spatial frequency of the stimulus. The range of preferred spatial frequencies that we found (see Fig. 7) is similar to the range of preferred spatial frequencies found by Bisti and Sireteanu<sup>1</sup>. We have shown how a selectivity for velocity interacts with the spatial frequency selectivity of collicular cells and complicates the interpretation of tuning curves to either variable alone. The ranges of preferred velocities to gratings (shown in Fig. 7) are close to the optimal velocities found by Dreher and Hoffman<sup>6</sup> using a small spot stimulus. They found 3 classes with velocities less than 15 deg./sec, velocities of 30–60 deg./sec, and velocities above 100 deg./sec. Our ranges of preferred velocities fall into their first two classes. However, we did not test velocities above 64 deg./sec. We also confirmed Dreher and Hoffman's report<sup>6</sup> that cells preferring higher velocities also had larger receptive fields. The velocity and spatial frequency preferences depend, often dramatically, on the direction of grating drift. This is similar to the observation of Mandl<sup>18</sup> who found that collicular cells' velocity preference often depended on the direction of movement of a spot.

The temporal frequencies of drifting gratings preferred by collicular cells were invariably below 8 Hz (Fig. 7). This range includes the range of maximum temporal modulation that could be followed by a modulated spike train, approximately 1.6 Hz.

### *Temporal characteristics of the spike train in response to gratings*

The change in spike rates (averaged over the 5 sec recording period) in response even to the optimal combination of spatial frequency and velocity (Fig. 8) was always far lower than the response to moving slits and spots evoked by the hand operated projector. Fig. 8 shows that highest mean firing rate we saw in response to a grating was 44/sec, and this only for one cell. The response to a spot was often up to 100/sec. These latter rates were similar to those found by other investigators<sup>6,20,28,30</sup>.

It may be that the difference in spike rate between responses to gratings and small objects (spots and slits) plays an important role in collicular units' ability to distinguish among specific spatial and temporal frequencies of an extended image, i.e. a drifting grating, and movement of small targets. The high spike rate of the response elicited by slits and spots has a duration far smaller than the elevated rate caused by the passage of a drifting grating, since, for the preferred velocity ranges of collicular cells the small target moves through the cell's receptive field in at most approximately one second. Response to drifting gratings lasted at least 5 sec.

### *Interaction of center and surround*

We often found inhibition of a response to gratings by extending the grating into the surround of the visual receptive field (Table I). The response to stimuli in the surround only was always far smaller than the response to stimuli in the center alone. In some cases (e.g. Fig. 4) the surround response resembled the response of the center alone, but at a lower spike rate.

There are two aspects of the interaction between the centre and surround of collicular cells seen by Mandl<sup>18</sup> which are confirmed and extended in the present study. Firstly, Mandl found the directional sensitivity to change markedly as different areas of the visual receptive field were stimulated. Secondly, selectively masking the center or the surround of a cell's visual receptive field changed the velocity preference of the cell for a moving edge. In our study, Figs. 4 and 5 show typical changes in directional selectivity for stimulation of different areas of the visual receptive fields. Further, most of our cells altered their velocity preferences depending on whether the center or surround were stimulated.

*Relationship of collicular cells' responses to responses of visual cells in other structures*

The direct retinal projection from the retina of the cat to the superior colliculus consists only of the Y- and W-type retinal ganglion cells<sup>8,15</sup>. However, there is potentially an indirect projection of all retinal ganglion cell types and their transformations via the cortex, since visual cortical areas 17, 18 and 19 and the lateral suprasylvian gyrus project to the superior colliculus<sup>9,13,16,19,31</sup>.

The property of some collicular cells in this study most closely resembling that of retinal Y-cells is their non-linear rectification<sup>14</sup>. The response of retinal Y-cells to drifting gratings is often only a sustained elevation of spike rate above spontaneous level since the non-linear subunits of the Y-cell are not synchronously stimulated by a drifting grating<sup>14</sup>. The appearance of temporal modulation in response of some of our collicular cells to drifting gratings is also consistent with Y-cell properties, whether it occurs synchronously with the temporal frequency of the grating (Fig. 9) or in one case rectified, at twice the temporal frequency of the grating (cf. refs. 32 and 33, for such Y-cell rectification properties). The range of preferred velocities we found was also consistent with those for retinal Y-cells<sup>2</sup>, and for phasic retinal W-cells<sup>29</sup>, but we did not test above 64 deg./sec or below 2 deg./sec. Hochstein and Shapley<sup>14</sup> argue that retinal Y-cells respond to much higher spatial frequencies (to 2 cycles/deg. and beyond) by sustained elevation of spike rate rather than by modulation of the spike train. We, however, did not look at such high spatial frequencies.

The majority of collicular cells in our study (Fig. 7) showed a preference for spatial frequencies well below those transmitted by either X- or Y-cells (range 2–8 cycles/deg.<sup>3,14,32</sup>) and below those available in visual cortical cells of area 17 and 18 (range 2–4 cycles/deg.<sup>23</sup>). It is probable that the superior colliculus in some cases acts as a spatial frequency filter centered on low frequencies; this is consistent with its role in orienting responses to small targets, since the major spatial frequency components locating a small target are below the low spatial frequency ranges for the X-, Y- and cortical cells given above<sup>10</sup>.

*Predictions from drifting grating responses*

The responses of all collicular cells in this study were non-linear because different spatial and temporal frequencies always evoked changes in *mean* firing rate. This change in mean firing rate does not reproduce the frequency of stimulation presented to the cell and is therefore non-linear since linearity requires that a cell's

response contain only the input frequencies. For approximately 8 % of the cells (cells with temporal modulation) the response contained a linear component summed with the stronger non-linear components. The non-linearities of collicular cells are stronger than for retinal ganglion<sup>32,33</sup> or simple and complex striate cortical cells<sup>21,22</sup>. To make direct mathematical predictions of individual cell response to stimuli other than gratings was beyond the scope of this study, requiring techniques such as Volterra/Wiener kernels or sums of sinusoids<sup>32,33</sup>. We used single frequencies which of course is a beginning in analysis of response to multiple frequencies.

Even though the individual collicular cells' responses are non-linear and response categories so varied, there are two predictions one can make from Fig. 7 on a cell population basis. First, the grating velocity ranges preferred by collicular cells correspond to those for small moving objects<sup>6</sup> (Discussion above). Second, the spatial frequency preference distribution for the lower spatial frequencies and higher velocities (left back corner Fig. 7) predicts the preference for movement of small objects, since the major spatial frequency components specifying or composing a small object are the low range here. Specifically, by approximating to the low spatial frequency — high velocity range dominant peak (left back corner Fig. 7, 0.05–0.2 cycles/deg., 32–64 deg./sec) a sinc function (with first zero at 0.4 cycles/deg.) and Fourier inverting that function the predicted preferred spot size is 2.5°. This corresponds approximately to the average preferred spot size given our average receptive field size of approximately 6° diameter, and the ratio of receptive field size to preferred spot size from other studies<sup>28</sup>. Therefore, even though individual collicular cells are non-linear, their average preference for spatial frequencies of drifting gratings predicts their average preference for size of small spots and slits, on the basis of the above calculation. Fig. 10A also conforms to Fourier predictions on a population basis, in that cells with larger receptive fields prefer lower spatial frequencies.

The counterphased grating results have aspects which are qualitatively predicted from drifting grating results, especially their range of response to spatial frequency. However, when the temporal modulation waveform of the counterphased grating is sinusoidal, there is no measurable response probably because this grating is composed of two gratings drifting in opposite directions. (Observation of a counter-phase grating, attending to one direction or the other, will confirm this, and also that  $\cos[2\pi(f_x x + f_t t)] + \cos[2\pi(f_x x - f_t t)] = 2\cos(2\pi f_x x)\cos(2\pi f_t t)$ , where  $f_x$  and  $f_t$  are the spatial and temporal frequencies, respectively, and the stationary temporally modulated (counterphased) grating is represented by the right-hand term.) Thus, the null direction grating component will inhibit response to the preferred direction grating component in a counterphased grating, for directional collicular cells (as most of those tested with counterphased gratings were). However, when the temporal modulation of the counterphased grating is square wave (corresponding to the two direction component gratings jumping instantaneously in opposite directions), narrow transient responses of collicular cells at the jump or transition may be a result of the non-simultaneous inhibition by the null direction grating on the preferred direction grating response. The jump velocity of the grating is extremely large, well beyond the range of our drifting gratings, which prevents any attempt at predictions based on drifting sinusoidal gratings.

Prediction of very general kinds of non-linearity mediating collicular cell responses can be made on the basis of predominance of sustained increase or decrease in mean firing rate. A process of summation in the colliculus which is linear could sum non-linear subunit responses, but non-linear summation could integrate both non-linear and linear subunit responses. The fundamental non-linear subunit response may be similar to Y retinal ganglion cells, and include them. Their fundamental non-linearity is rectification<sup>14,33</sup>, which may arise from threshold mechanisms and low spike firing rates. Non-linear lateral inhibition having variable coefficients of cell coupling may account for non-linear summation. The tuning of the collicular cell response in spatial frequency and velocity will be determined by receptive fields and temporal response of subunits, by their spatial distribution (as predicted for the case of retinal cells by Kelly<sup>17</sup>) and by the nature of the summation process. Models of collicular cell response will require detailed neuroanatomy<sup>16</sup>, detailed information on properties of retinal ganglion cells as determined by Hochstein and Shapley<sup>14</sup> and Victor and Shapley<sup>32,33</sup> and properties of cortical visual cells as determined by Movshon, Thompson and Tolhurst<sup>21-23</sup>. Here it is of great interest that low rather than high spatial frequency responses were deficient in collicular cell responses of decorticate animals in Bisti and Sireteanu's study<sup>1</sup>.

We have shown quantitatively in this study that many previously determined receptive field and velocity sensitivity properties of collicular cells extend to response to drifting sinusoidal gratings. That the sustained elevation or diminution of spike rate in these responses is numerically less than the short bursts in response to small moving objects may be an aspect of collicular mechanisms distinguishing large background from small target stimuli. If individual collicular cells were linear their responses to gratings could be predicted to be numerically in the neighborhood of those found here. How the spatial frequency spectrum components combine to give collicular cells great sensitivity to small moving objects is a non-linear problem awaiting study.

The experiments reported here are a beginning in an attempt to determine whether collicular cells demonstrate properties allowing an image-based discrimination between small moving objects and a large moving background. In a simpler nervous system, the locust descending contralateral movement detector (DCMD), a basis for this discrimination on the stimulus spatial frequency has been reported<sup>26,27</sup>. Thus, experiments requiring two independent stimuli, e.g. a small target and a moving grating (having complementary spatial frequency spectra), are the next step in determination of discrimination properties of collicular cells.

## APPENDIX

### *Truncation of the extent of gratings and the effects of edges*

In studies of visual cells having surround-inhibitory receptive fields, it is tempting to truncate moving gratings such that they do not extend into the inhibitory surround. It is possible to truncate the grating by a mask orthogonal to the bars of the grating, i.e. to shorten the bars, without introducing significant artifacts. However, truncating the grating by producing fewer bars with a mask parallel to the bars

produces unwanted artifactual spatial and temporal frequency components<sup>10,24</sup> which are both above and below the original frequency of the bars of the gratings. The spatial frequency spectrum of such artifacts can be computed by a convolution of the mask spatial frequency spectrum with the spectrum of the grating (assuming an infinite extent of grating)<sup>10</sup> or by the method used by Palka<sup>24</sup>. It is easily demonstrated that there is a smearing out of the desired frequency spectrum of the grating, extending to zero frequency, and that there is a strong temporal modulation at the frequency of passage of the bars at the edge of the mask (as the bars pass under the mask). Therefore such truncation of rectangular drifting gratings must be avoided as much as possible, or extensive deconvolution and other window analysis will be required for each cell measured.

One method of avoiding edge effects on grating stimulation is to use a grating having circular symmetry<sup>26,27</sup> where the bars resemble the spokes of a wheel. These, however, must be made to very high precision and place some constraints on the kind of receptive field on which they are used<sup>25</sup>.

To reduce problems of truncated gratings in this study the grating was always 40° in extent along the direction of drift. This allows a one-dimensional spatial frequency analysis of the cells' response along the direction of drift, but with a small, unavoidable contamination of 'center only' response with some response due to stimulation of part of the surround. That this contamination was not major is seen in Figs. 4, 5 and 6 and data from other cells. The surround only response shows effects in the combined full field stimulation far different than the center only response. Further, given the receptive field size and spatial frequency range of significance for collicular cells, to truncate the grating to the receptive field center size would result in very little coherence or spectral purity of the grating. The effect of edge windows and spectral purity (or multi-frequency inputs) was beyond the scope of our study because of the variety, non-linearity and recording longevity of collicular cells.

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