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SPATIAL-FREQUENCY CHARACTERISTICS OF NEURONES OF AREA 18 IN THE CAT: DEPENDENCE ON THE VELOCITY OF THE VISUAL STIMULUS

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SUMMARY

1. The spatial and temporal response properties of neurones of areas 17 and 18 were studied in single units (165) of anaesthetized and paralysed cats. The visual stimuli were drifting or alternating gratings.

2. We confirmed and extended the observation by Tolhurst & Movshon (1975) showing that the spatial-frequency characteristics of neurones of area 17 are largely independent of the temporal parameters of drifting or alternating gratings.

3. The spatial-frequency tuning curves of neurones of area 18 shift along the spatial-frequency axis when the velocity or the temporal frequency of the drifting grating are changed. The effect of an increase either of velocity or temporal frequency is to shift the cell spatial-frequency tuning curve down the spatial-frequency scale, keeping relatively constant the strength and band width of the response.

4. The spatial-frequency tuning curves of neurones of area 18 do not show this temporal-frequency-dependent phenomenon when the stimuli are gratings alternated in phase. In this case neurones of areas 17 and 18 show a similar behaviour.

5. The response properties of neurones of area 18 are compared with recent psychophysical results obtained in similar experimental conditions. The hypothesis is advanced that both areas 17 and 18 are devoted to the processing of spatial information. Area 17 would be responsible for the processing of patterns in stationary or quasi-stationary situations while area 18 would be responsible for that of patterns moving at high velocities.

INTRODUCTION

The perceptual effects of the interactions between spatial and temporal characteristics of a visual scene are often very striking (see for instance Sekuler, Pantle & Levinson, 1978; Campbell & Maffei, 1979). An example of these interactions relevant to the problem faced in this paper is the enhancement observed both in man and animals of the detectability of gratings of low spatial frequencies by movement or temporal modulation of the visual stimulus (Tolhurst, 1973; Kulikowski & Tolhurst, 1973; Blake & Camisa, 1977). Several years ago Tolhurst & Movshon (1975) investigated whether these interactions take place in neurones of the cat striate

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cortex. They found that the spatial-frequency tuning curves of striate neurones remain relatively unaffected by changes of the temporal modulation frequency of the stimulus. Accordingly they concluded that neurones in area 17 were not the neural substrate underlying the effects of temporal modulation on grating sensitivity. More recently Movshon, Thompson & Tolhurst (1978) have observed that neurones of area 18 have different response characteristics to the spatio-temporal properties of the stimulus with respect to neurones of area 17. They found that neurones of area 18 are very sensitive to low spatial frequencies and relatively insensitive to low temporal frequencies. They concluded that neurones of area 17 might be responsible for pattern analysis and neurones of area 18 for the analysis of movement.

The results reported in this paper allow us to extend their conclusion and to advance a new hypothesis which tends to unify the function of cortical areas 17 and 18. Both areas would be involved (or they would be also involved) in the processing of patterns. Area 17 would process patterns in stationary or quasi-stationary situations while area 18 would process patterns moving at high velocities.

We have found that neurones of area 18 shift their spatial-frequency tuning curves along the spatial-frequency axis on changing the velocity of the drifting grating. The higher the velocity of the visual stimulus the lower the spatial frequencies to which they become tuned in their response.

METHODS

Experiments were performed on twenty-five adult cats.

Anaesthesia was induced with Althesin (alfaxalone 0·18%, Glaxo) 1·5 ml kg^{-1}. A small opening in the skull was made over area 17 and/or 18 and at the end of the surgical procedure all the operated areas were infiltrated with local anaesthetic (Novocaine). After removal of the dura the animal was paralysed with intravenous injection of Pavulon (pancuronium bromide 0·2%, N.V. Organon) 0·2–0·3 ml kg^{-1} h^{-1} and artificially ventilated. During the recording session anaesthesia was maintained with a continuous injection of Althesin 0·3 ml kg^{-1} h^{-1}.

P_{CO_2} (3·8–4·2%), electrocardiogram (e.c.g.) and electroencephalogram (e.e.g.) were monitored throughout the experiment and the body temperature was maintained at 38 °C.

Pupils were dilated with atropine sulphate (1%) and contact lenses with artificial pupils of 3 mm diamenter were applied. The refraction of the cat's eyes was determined by means of retinoscopy and corrected with suitable spectacle lenses placed in front of the eye. At the beginning of the experiment the position of the papillae and of the area centralis was determined using the technique described by Fernald & Chase (1971).

A micropipette filled with either NaCl (3 M) or pontamine in sodium acetate (0·5 M) was inserted either perpendicularly to the cortex (area 17) or obliquely in the posterolateral sulcus (area 17–area 18) and a solution of agar–agar in saline was used to prevent drying of the cortex.

All the penetrations performed with a micropipette filled with pontamine were marked at the end of the recording session (for details see Berardi, Bisti, Cattaneo, Fiorentini & Maffei, 1982).

Visual stimuli were generated by a computer on the face of a display oscilloscope subtending at the cat eye 22 × 25 deg at a distance of 57 cm or 31 × 35 deg at a distance of 40 cm (area 18 experiments). The mean luminance was 7 cd m^{-2}. Stimuli used were sinusoidal gratings of various spatial frequencies and contrast. Contrast was defined as:

$$(L_{max} - L_{min})/(L_{max} + L_{min}),$$

where L_{max} and L_{min} are the maximum and the minimum luminance, respectively. Three types of temporal modulation were used: continuous lateral drift, sinusoidal modulation of the contrast and phase reversal of a stationary grating.

The experimental procedures were the following: (1) location of the receptive field in visual space and centring of the oscilloscope display on the centre of the receptive field; (2) a preliminary

estimate of the optimum orientation and direction of movement; (3) occlusion of the non-dominant eye; (4) determination of spatial-frequency tuning curves at various velocities (and temporal frequencies) of the drifting grating at fixed contrast 2–3 times threshold; (5) determination of spatial-frequency tuning curves at various temporal frequencies of contrast modulation of the grating; (6) determination of temporal-frequency tuning curves at various spatial frequencies both for drifting and alternating gratings; (7) determination of the preferred direction of motion at various temporal frequencies of the drifting grating.

Single-neurone responses were averaged on-line over 50–200 successive stimulus periods by means of a computer (PDP 11/03). Each averaged response was Fourier analysed off-line.

The cells were classified on the basis of their response to drifting gratings. Cells which responded to a drifting grating with a modulation of their discharge were classified as simple (simple-like in area 18). For these cells the peak-to-trough response amplitude was measured. Results did not change when the first-harmonic component of the response was considered. Several cells of area 18 showed both a modulation and an increase of the mean firing rate. For these cells both variables, amplitude of response and average discharge, were measured and similar results obtained.

Complex cells are considered those which responded to a drifting grating with an increase of their discharge, without any modulation. For these cells average discharge is reported. The spontaneous firing of the cells is indicated in the Figures with an arrow on the ordinate axis. For the purpose of this paper, however, an accurate classification of neurones of area 18 is not a crucial point since every neurone we have tested behaved in a similar way.

The number of recorded cells was eighty-eight in area 17 and seventy-seven in area 18. Of these, sixty-eight in area 17 and thirty-three in area 18 were fully analysed. The receptive fields of the cells were all located within 10 deg of the area centralis.

RESULTS

Spatio-temporal properties of neurones of area 17

Several years ago Tolhurst & Movshon (1975) reported that the general form of the spatial-frequency tuning curves of simple and complex cells of area 17 was little affected by changing the temporal frequency of the drifting grating. Their experiments were performed at threshold values of contrast (contrast-sensitivity curves). We have extended their results for suprathreshold values of contrast and for different modalities of stimulus presentation. An example of the results is illustrated in Fig. 1 for three simple and three complex cells. Fig. 1*A* and *B* shows the results obtained when the stimuli were gratings of fixed contrast and various spatial frequencies drifting at a constant temporal frequency (the number of cycles of the grating which pass any point of the screen in a given time is kept constant). The various curves were obtained at different temporal frequencies (numbers near each curve in the Figure). The spatial tuning curves remain rather similar. The responsiveness of the cell, however, can decrease when the temporal frequency of the stimulus is increased.

The spatial-frequency tuning curves of cells of area 17 are also largely constant when tested with other modalities of stimulus presentation. Fig. 1*C* and *D* shows the effects of varying stimulus velocity on the spatial-frequency tuning curve. The various curves were obtained at different velocities (numbers in the Figure). Fig. 1*E* and *F* shows the results obtained when the stimulus was a stationary grating, the contrast of which was sinusoidally modulated in time at various temporal frequencies. The results remain qualitatively the same for the three sets of experiments, namely when the temporal properties of the stimulus are changed the spatial tuning curves of striate neurones remain largely invariant showing only a shift along the amplitude axis.

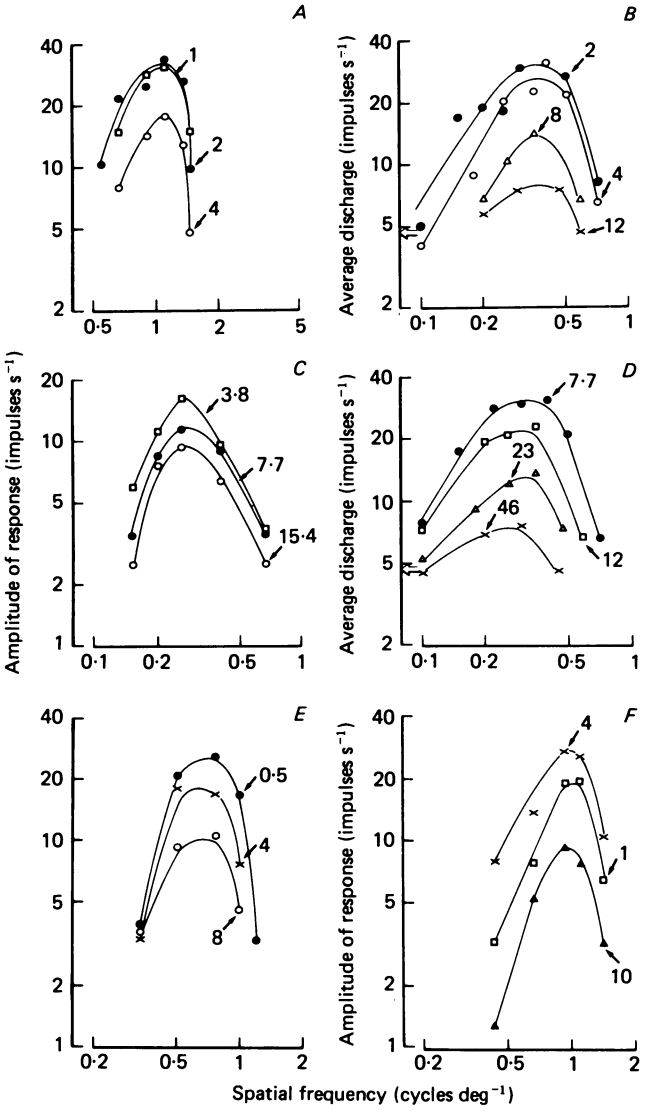

Fig. 1. Spatial-frequency tuning curves for three simple and three complex cells of area 17 for drifting and alternating gratings. When the stimulus was a drifting grating, amplitude of modulation (peak-to-trough) for simple cells and average discharge for complex cells were reported as a function of spatial frequency. *A* and *B*, stimulus: grating drifting at constant temporal frequency. Temporal frequency: □, 1 Hz; ●, 2 Hz; ○, 4 Hz; △, 8 Hz; ×, 12 Hz. Contrast 0·1 (*A*), 0·25 (*B*). *C* and *D*, stimulus: grating drifting at constant velocity. Velocity: □, 3·8 deg s^{-1}; ●, 7·7 deg s^{-1}; □, 12 deg s^{-1}; ○, 15·4 deg s^{-1}; △, 23 deg s^{-1}; ×, 46 deg s^{-1}. Contrast 0·1 (*C*), 0·25 (*D*). *E* and *F*, the contrast of the grating was sinusoidally modulated in time at constant temporal frequency. For simple cells amplitude of modulation and for complex cells amplitude of the second-harmonic component were reported as a function of spatial frequency. Temporal frequency: ●, 0·5 Hz; □, 1 Hz; ×, 4 Hz; ○, 8 Hz; ▲, 10 Hz. Contrast 0·1 (*E*), 0·1 (*F*). Mean luminance in all cases 7 cd m^{-2}. In *B* and *D* the arrows on the ordinate axis indicate the spontaneous firing rate of the cells.

Spatio-temporal properties of neurones of area 18

Neurones of area 18, when tested in the same experimental conditions as those of area 17 show completely different properties. Contrary to neurones of area 17 their spatial-frequency tuning curves are changed dramatically when the temporal characteristics of the drifting grating are changed.

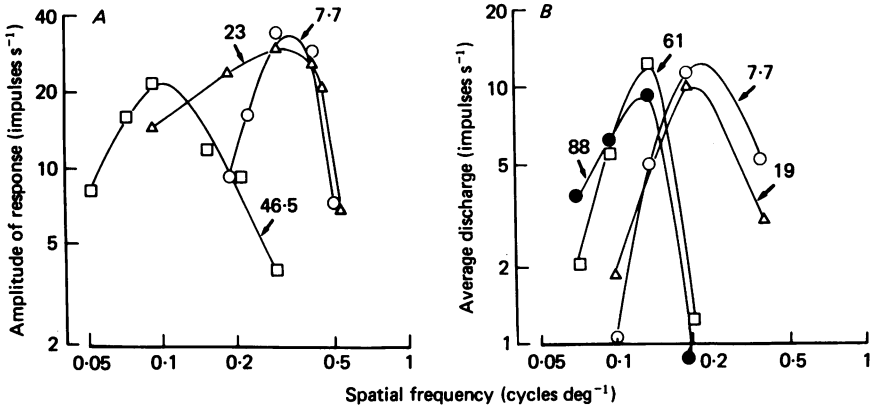

Fig. 2. Spatial-frequency tuning curves of a simple-like cell (*A*) and a complex cell (*B*) of area 18. Each curve is obtained with drifting gratings of constant velocity. Numbers in the Figure indicate the velocities in deg s^{-1}. *A*, velocity: ○, 7·7 deg s^{-1}; △, 23 deg s^{-1}; □, 46·5 deg s^{-1}. Contrast 0·17. *B*, velocity: ○, 7·7 deg s^{-1}; △, 19 deg s^{-1}; □, 61 deg s^{-1}; ●, 88 deg s^{-1}. Spontaneous firing rate 0·2 impulses s^{-1}. Contrast 0·4. Mean luminance 7 cd m^{-2}.

Neurones of area 18 do not exhibit a clear distinction into simple and complex cells as neurones of area 17 do. They have been subdivided into two classes, simple-like and complex cells (Tretter, Cynader & Singer, 1975). Our classification is based on the response to drifting gratings (see Methods). With respect to neurones of area 17, neurones of area 18 generally prefer higher stimulus velocities and are tuned to lower spatial frequencies (Movshon *et al.* 1978; Orban, Kennedy & Maes, 1981; Berardi *et al.* 1982).

Fig. 2*A* and *B* shows the spatial tuning curves of a simple-like and a complex cell respectively for various velocities of the drifting grating. It can be easily noted that both types of cell become responsive to lower spatial frequencies when the velocity of the grating increases. The cell loses responsiveness on the side of high spatial frequencies but decisively gains on the side of the lower ones.

Fig. 3*A* and *B* shows for a simple-like and a complex cell the spatial-frequency tuning curves obtained when instead of the velocity (Fig. 2) the temporal frequency of the drifting grating is kept constant. It is clear that when the temporal frequency is increased, the spatial-frequency tuning curves, similarly to the results reported in Fig. 2, shift towards the lower spatial frequencies.

The shift of the spatial-frequency tuning curve of neurones of area 18 along the spatial-frequency axis, however, is conditional on the temporal variations induced by the drifting motion of the grating, since when the equivalent temporal variations

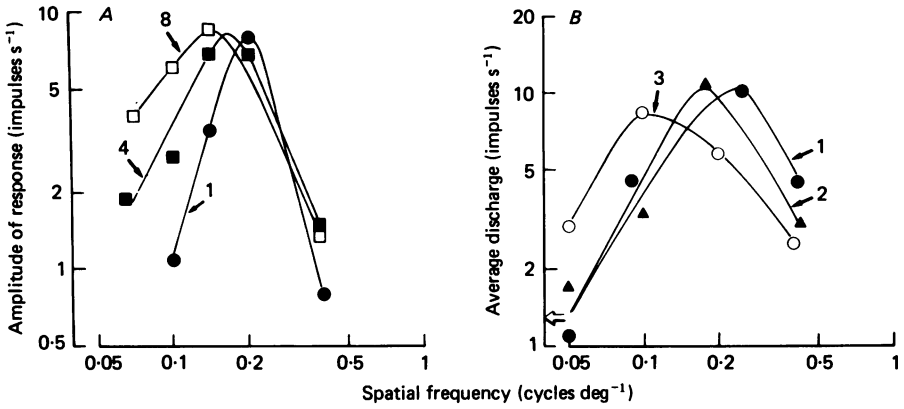

Fig. 3. Spatial-frequency tuning curves of a simple-like cell (*A*) and a complex cell (*B*) of area 18. Each curve is obtained with gratings drifting at a constant temporal frequency. Numbers in the Figure indicate the temporal frequencies in Hz. *A*, temporal frequency: ●, 1 Hz; ■, 4 Hz; □, 8 Hz. Contrast 0·4. *B*, temporal frequency: ●, 1 Hz; ▲, 2 Hz; ○, 3 Hz. Contrast 0·17. Mean luminance 7 cd m^{-2}. In *B* the spontaneous firing rate of the cell is indicated by an arrow on the ordinate axis.

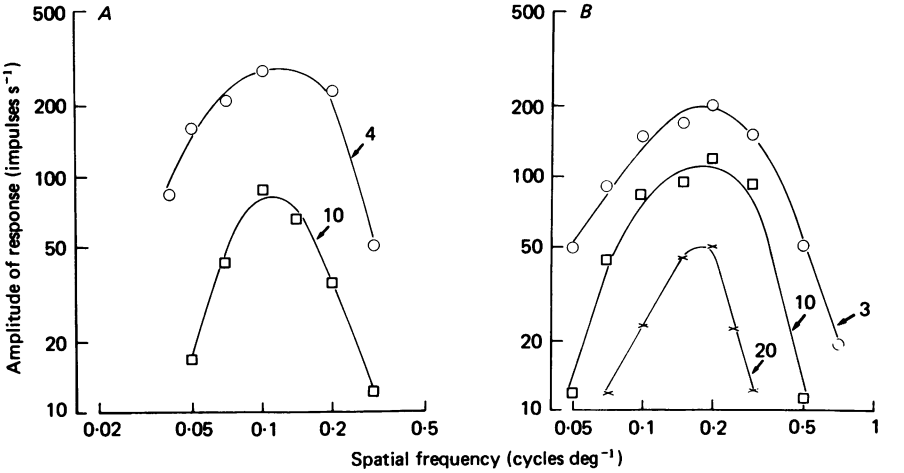

Fig. 4. Spatial-frequency tuning curves of a simple-like cell (*A*) and a complex cell (*B*) of area 18. Each curve is obtained with square-wave alternating gratings of constant temporal frequency. Most of the simple-like cells respond to each reversal (second harmonic) of the alternating grating as complex cells do. The second harmonic amplitude of the cell discharge is reported as a function of the spatial frequency. Numbers in the Figure indicate the temporal frequencies in Hz. *A*, temporal frequency: ○, 4 Hz; □, 10 Hz. Contrast 0·07. *B*, temporal frequency: ○, 3 Hz; □, 10 Hz; ×, 20 Hz. Contrast 0·17. Mean luminance 7 cd m^{-2}.

are obtained by alternating in phase a stationary grating, there is no evident shift along the spatial-frequency axis of the spatial-frequency tuning curve. In this case the behaviour of neurones of area 18 is similar to that of neurones of area 17. An example for a simple-like and a complex cell is reported in Fig. 4*A* and *B*.

The results reported in Fig. 2 and 3 indicate that for a single cell the response to

a given spatial frequency is present only in a limited range of velocities. In order to illustrate better this point we have plotted the response of a complex cell at a fixed spatial frequency as a function of the velocity of the stimulus (Fig. 5*A*). The various curves in Fig. 5*A* and *B* refer to different spatial frequencies of the stimulus.

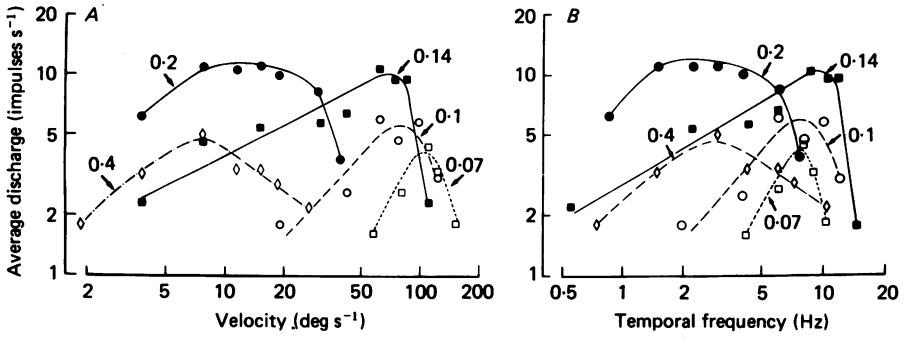

Fig. 5. *A*, velocity tuning curves for a complex cell of area 18 at five different spatial frequencies. Numbers in the Figure indicate the spatial frequencies in cycles deg^{-1}. Spatial frequency: □, 0·07 cycles deg^{-1}; ○, 0·1 cycles deg^{-1}; ■, 0·14 cycles deg^{-1}; ●, 0·2 cycles deg^{-1}; ◇, 0·4 cycles deg^{-1}. Spontaneous firing rate 0·2 impulses s^{-1}. Contrast 0·4. Mean luminance 7 cd m^{-2}. *B*, the same data as in *A* reported on a temporal-frequency scale. Numbers in the Figure indicate the spatial frequencies in cycles deg^{-1}.

It can be seen that for very low spatial frequencies of the grating the cell responds only to very high velocities. When the spatial frequency is increased the cell becomes responsive to a lower range of velocities.

In Fig. 5*B* the same results have been reported as a function of the temporal frequency of the drifting stimulus. For low spatial frequencies (from 0·07 to 0·14 cycles deg^{-1}) the cell maintains approximately the same peak at a high temporal frequency. Then it shows a shift towards lower temporal frequencies. The data in Fig. 5*B* refer to a cell for which the shift of the temporal-frequency tuning curves along the temporal-frequency axis was particularly evident. For other cells this shift along the temporal-frequency axis was less marked, but we never found that the peak temporal frequencies of the tuning curves remained invariant by changing the spatial frequency of the stimulus. The temporal characteristics of area 17 neurones are largely independent of the spatial frequency of the stimulus (Tolhurst & Movshon, 1975).

Temporal-frequency responses of cortical neurones of area 17 and 18 for drifting and alternating gratings

The most common modality to excite cortical neurones with gratings is either to drift or to alternate them in phase. The temporal properties of most neurones of area 17 are very similar when obtained either with drifting or alternating gratings. An example is reported for a simple cell in Fig. 6*A*. Conversely, the temporal properties of neurones of area 18 are usually different for the two modalities of stimulation (Fig. 6*B*).

The temporal characteristics of neurones of area 18 can also vary with the direction

of motion of the drifting grating. We have found several examples of simple-like and complex cells in which by changing the direction of motion, both the optimum temporal frequency and in particular the response at low temporal frequencies, can substantially change. Even the direction selectivity of the cell can invert by changing the range of temporal frequency.

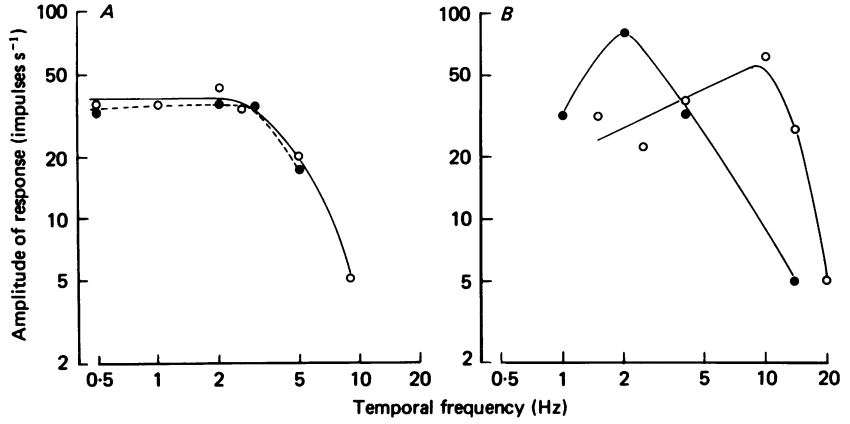

Fig. 6. Temporal-frequency tuning curves for a simple cell of area 17 (*A*) and for a simple-like cell of area 18 (*B*). Stimulus: ○, drifting grating; ●, alternating grating. *A*, spatial frequency 0·53 cycles deg^{-1}. Contrast 0·1. *B*, spatial frequency 0·33 cycles deg^{-1}. Contrast 0·14.

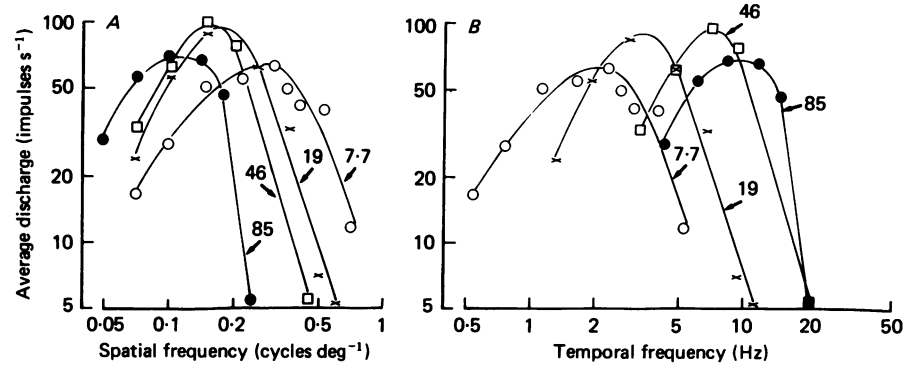

Fig. 7. *A*, spatial-frequency tuning curves of a complex cell of area 18. Each curve is obtained at a constant velocity. Numbers in the Figure indicate the velocities in deg s^{-1}. Velocity: ○, 7·7 deg s^{-1}; ×, 19 deg s^{-1}; □, 46 deg s^{-1}, ●, 85 deg s^{-1}. Contrast 0·17. *B*, the same data as in *A* reported on a temporal-frequency scale (temporal frequency = velocity × spatial frequency).

DISCUSSION

The most important result reported in this paper is that neurones of area 18 shift their spatial-frequency response characteristics to lower spatial frequencies when the velocity or the temporal frequency of the stimulus is increased. The effect of an increase either of velocity or temporal frequency is to slide the cell spatial-frequency tuning curve down the spatial-frequency scale, keeping relatively constant the

strength and band width of the response. This effect is not observed in neurones of area 17. The position of their spatial-frequency tuning curves does not change along the frequency axis as a function of the temporal variables of the drifting grating.

This difference between area 17 and 18 is likely to derive from their different inputs (for a reference see Stone, Dreher & Leventhal, 1979; Raczkowski & Rosenquist, 1983). Area 17 receives retinal information from all the three classes of retinal ganglion cells, X, Y and W, but only through the lateral geniculate body. Area 18 receives only Y and W inputs and these arise from the geniculate, the medial interlaminar nucleus and the pulvinar. One of the reasons for the difference between area 17 and 18 responses could be that area 18 lacks the X-cell projection that is thought to underlie the analysis of fine patterns. The extrageniculate input and the more robust W-cell projection to area 18 should, however, also be taken into consideration.

Several authors have advanced the hypothesis of a dichotomy of function between areas 17 and 18. Area 17 would be involved in pattern detection and area 18 in movement detection. Our results suggest that the role of area 18 may be somewhat complementary to that of 17. The neural mechanisms of area 18 could be responsible for the perception of patterns during movement (or despite movement).

When we see an object in movement, the details of the object, i.e. its high spatial frequencies, are not perceived. Vision becomes confined to the general 'Gestalt' of the object as described by its low spatial frequencies. The faster the velocity of the object, the more dramatic the attenuation of high spatial frequencies. At very high velocities only a very rough silhouette of the moving object can be perceived.

Recently, Burr & Ross (1982), in a series of experiments partly carried out in this laboratory, have described the dependence of human contrast sensitivity upon the grating velocity. They have found that by increasing the velocity of the stimulus neither the bandpass nor the maximum of the human contrast-sensitivity curve decreased. The effect of motion is simply that of sliding down the spatial-frequency window toward lower spatial frequencies. By increasing the velocity of the stimulus there is a loss in sensitivity at high spatial frequencies *and* an *increase* in sensitivity at lower ones. Thus the effects of varying the velocity of the stimulus are similar for human and single neurones of area 18. The relevant parameter in the perception of a moving grating seems to be the temporal frequency of the stimulus, since when the contrast-sensitivity curves for different velocities are plotted on a temporal-frequency scale they largely superimpose (Burr & Ross, 1982). The responses of neurones of area 18 at different velocities do not behave in this way, indicating that the velocity of the stimulus is a parameter relevant to the processing of a moving object. Unlike the psychophysical result, the spatial-frequency tuning curves of neurones of area 18 do not superimpose when reported on a temporal-frequency scale (Fig. 7). The conclusion that the velocity is a relevant parameter for area 18 cells is also supported by the fact that the spatial-frequency tuning curves of cells in area 17 and 18 are very similar, if constructed from the response to contrast modulation of a stationary grating (they do not shift along the spatial-frequency axis).

Our results permit us to propose a new hypothesis on the neurophysiological basis of pattern analysis. Neurones of area 17 would be responsible for pattern analysis in the range of low velocities. In these conditions the object is perceived in all its

details. At high velocities of the moving object, neurones of area 17 do not respond any longer and the task of pattern analysis is carried out by neurones in area 18. The task of the latter is not a detailed analysis of the object, but the recognition of it. To accomplish this task neurones of area 18 possess a special plasticity. At increasing velocity they tune their spatial-frequency response to the spatial frequencies relevant for perception in that particular situation. Obviously the same task could be performed by progressively shifting the analysis of the pattern to neurones tuned to lower spatial frequencies as the velocity of the stimulus increases. The two mechanisms could coexist even if the first seems to be more parsimonious.

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