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SPATIAL AND TEMPORAL SELECTIVITY OF THE HUMAN MOTION DETECTION SYSTEM

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Abstract—Measurements were made of spatial frequency, orientation and temporal frequency selectivity of the visual motion system. The results suggest: (1) There exists in the motion system mechanisms selective for spatial frequency. The preferred spatial frequency varies considerably and extends down to at least 0.06 c/deg. (2) At all spatial frequencies (from 0.1 to 10 c/deg) there exist detectors selective for orientation which vary in (directed) orientation tuning to encompass 360°. (3) The bandwidth of both spatial frequency and orientation selectivity vary inversely with spatial frequency: the lower the spatial frequency, the broader the bandwidth. (4) There exist two classes of temporally tuned detectors, one lowpass (sustained) and one bandpass (transient), of preferred temporal frequency of 7–13 Hz (depending on spatial frequency).

Motion Spatial selectivty Temporal selectivity Bandwidth Orientation

INTRODUCTION

There is now adequate evidence for the existence in the visual system of independent mechanisms tuned to different spatial frequencies and orientations, at least in the medium to high spatial frequency range. The evidence derives primarily from adaptation, masking and summation studies (e.g. Blakemore and Campbell, 1969; Stromeyer and Julesz, 1972; Shapley and Tolhurst, 1973; King-Smith and Kulikowski, 1975; Legge, 1978, 1979).

However at low spatial frequencies, below 1.0 c/deg, the picture is less clear. Blakemore and Campbell (1969) found that adaptation to frequencies below 3 c/deg produced threshold elevation peaking at 3 c/deg suggesting that this value was the lowest adaptable frequency at which a tuned detector could be found. Tolhurst (1973), however, showed that the exact value of the "lowest adaptable channel" is dependent on the spatial extent of the grating, and on motion. Using a larger screen he demonstrated a lowest adaptable channel for stationary gratings at 1.5 c/deg. For moving gratings (both adaptation and test), threshold elevation peaking at the adapting spatial frequency could be demonstrated at 0.66 c/deg, suggesting that there exist channels for low spatial frequencies which are movement dependent. Tolhurst (1973) interpreted these results as evidence for two distinct populations of detectors, one restricted to relatively high spatial frequencies, responsible for the analysis of spatial pattern, and the other of lower spatial frequency preference, responsible for motion detection.

Recent evidence suggests that the degree of spatial selectivity is less at lower than at higher spatial frequencies: both orientation and spatial frequency bandwidths increase with decreasing spatial frequency (Furchner *et al.*, 1977; Stromeyer *et al.*, 1982; Wilson *et al.*, 1983; Sharpe *et al.*, 1973). However, Legge and Foley (1980) point out that as sensitivity to gratings varies with the number of visible cycles (e.g. McCann *et al.*, 1973, 1978; Savoy and McCann, 1974; Hoekstra *et al.*, 1974), the larger bandwidth estimates at low spatial frequencies may be an artefact of the limited number of cycles, which often occurs with low spatial frequency measurements.

Most psychophysical studies have been confined to the higher spatial frequency range of the visible spectrum (above 1.0 c/deg), the range in which vision is most sensitive to stationary images. However, when motion is introduced, the most sensitive frequency range may be much lower. For example, a grating drifting at 800 deg/sec is best seen when its spatial frequency is 0.01 c/deg (Burr and Ross, 1982), and sensitivity at this frequency is as high as sensitivity to a 3.0 c/deg stationary grating. The degree of spatial selectivity for mechanisms sensitive to movement, particularly those which respond to very low spatial frequencies, remains unclear.

A grating drifting at a constant velocity (v) has a single spatial frequency (SF) and temporal frequency (TF): $TF/SF = v$. To understand motion fully, it is important to investigate both spatial and temporal selectivity. Using a discrimination task, Watson and Robson (1981) observed that only two temporal frequencies, one high and the other low, can be perfectly discriminated. From this they concluded that the temporal frequency dimension is served by only two discrete sets of mechanisms, one selective for high temporal frequencies, the other for low. This interpretation is consistent with earlier proposals (e.g. Tolhurst, 1973; Kulikowski and Tolhurst, 1973; Breitmeyer and Ganz, 1976; Green, 1981). Other studies have suggested that multiple temporal channels (possibly more than two) may exist (e.g. Smith, 1970, 1971; Tolhurst *et al.*, 1973; Nilson *et al.*, 1975). Temporal tuning at different spatial frequencies has not been systematically investigated.

In this study we examine the spatial frequency, temporal frequency and orientation selectivity of the motion system. Our measurements extend to the low frequency range, where previous studies (e.g. Burr and Ross, 1982) have shown the human motion system to be particularly sensitive. We use the now common technique of masking, in which sensitivity to a sinewave grating is measured with and without a superimposed high contrast mask grating of variable orientation, spatial frequency or temporal frequency. Selective masking (for example to a specific spatial frequency range) is taken as evidence for spatial frequency selective mechanisms. The theoretical justifications for using this technique have been argued elsewhere (e.g. Legge and Foley, 1980; Graham, 1981). For thorough reviews of the concepts of channels in vision, masking and effects of temporal modulation, the reader is referred to Graham (1980, 1981).

METHODS

Stimuli

All waveforms were generated by computer (Cromemco Z-2D) and displayed on the face of one or two oscilloscopes (Joyce Electronics), using a raster technqiue (100 frames/sec, 1000 lines/frame). The oscilloscope faces were of mean luminance 490 cd/m^2, masked to a 30 cm diameter circle by a 1.5 m square screen, floodlit to the same mean luminance (490 cd/m^2).

The test stimulus for all measurements was a drifting vertical sinusoidal grating. For the measurements of spatial frequency and orientation selectivity, it drifted at 5 Hz. For the temporal frequency measurements, temporal frequency was varied. For spatial and temporal frequency measurements, direction of drift was randomised between trials. For orientation measurements, the test stimulus was made to drift from left to right. Spatial frequency was varied in all experiments.

A different mask was used for each experiment. For measurements of spatial frequency selectivity, the mask was a vertical sinusoidal grating of 0.25 contrast* positioned randomly from frame to frame, so that it appeared to jitter. This gave it a flat temporal frequency spectrum (up to 50 Hz), ensuring strong representation of all visible temporal frequencies, and also randomized its phase with respect to the test. The spatial frequency of the sinewave varied from trial to trial (to measure masking with spatial frequency). The mask waveform was produced with one computer D/A and added electronically with the test, which was produced with another.

To measure orientation selectivity, the mask was low pass filtered (cut off 1.5 c/cm) one dimensional noise, of 0.16 contrast caused to drift at 0.8 times the velocity of the test. Its random profile ensured that all spatial frequencies (up to 1.5 c/cm, which was always 6 times higher than the test) and all temporal frequencies up to 50 Hz were represented. Causing the mask to drift at a different speed from the test aided in the detection of the test when the orientations and directions of drift coincided. The orientation of the mask varied from trial to trial, through 360°: vertical, and drifting from left to right like the test was defined as 0°, and vertical drifting from right to left was defined as 180°C. The waveform was displayed on a second oscilloscope, equipped with a rotatable yoke to vary orientation. The two oscilloscopes were superimposed optically with a half silvered mirror.

For temporal frequency measurements, the mask was unfiltered one-dimensional vertical noise of contrast 0.21, caused to reverse in contrast sinusoidally (i.e. white bars become black and vice-versa). The temporal frequency of contrast reversal varied from trial to trial. The waveform was added electronically to that of the test.

Procedure

In all conditions, the display accommodated five cycles of test grating. Spatial frequency at the eye was varied by varying viewing distance, from 9 cm to 35 m, using a front silvered mirror for the longer viewing distances. As a control, additional measurements were made with 10 and with 20 cycles of grating on the screen, but these gave substantially the same results. At very close viewing distances, geometric distortions arising from the flat screen caused the spatial frequency to vary from centre to periphery. In this study, spatial frequency was calculated from the most peripheral 6 cm of the screen (the region occupied by one cycle of grating), as the frequency of the test grating is artificially highest in this region.

Measurements were made in a semidarkened room. Observers fixated monocularly a large fixation spot with their dominant (right) eye, the other eye being occluded. Natural pupils were used, and no correction was made for accommodation at close viewing distances, as the optical blur would have little effect on the low spatial frequencies measured at those distances (e.g. Campbell and Green, 1965).

Threshold settings were made by the method of adjustment. Observers turned a hand held attenuator, until the direction of drift of the test grating was just

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*Sinusoidal contrast is defined as Michaelson contrast, $(L_{max} - L_{min})/(L_{max} + L_{min})$, and noise as r.m.s./L. Luminance distributions of the noise waveforms were measured with a Spectra Pritchard (model 1980A-PL) photometer. The noise patterns were caused to dirft slowly past the slit aperture of the photometer while the computer read the photometer output, from which it calculated the mean and standard deviation of the luminance distribution, and hence the contrast of the noise. Throughout this series of experiments, the mask was held at constant contrast, rather than being related to contrast threshold (as some previous studies have done). However, this should not influence the results, as Legge and Foley (1980) show that the mask contrast does not affect the form of the masking function. In any event, under the conditions of this experiment, sensitivity does not vary with spatial frequency except at the very highest spatial frequencies.

discernible. The criterion for threshold was always the detection of the direction of drift.

The procedure for all experiments was to choose at random a spatial and temporal frequency for the test, attenuate the mask contrast to zero, and measure the contrast detection threshold for the test alone. The contrast of the mask was then restored, and threshold measurements of the test were made for all relevant spatial frequencies, orientations or temporal frequencies of the mask. Thresholds for the test alone were again measured at periodic intervals. The strength of masking was taken as the ratio of the average threshold of the test grating in the presence of the mask to that of the test grating alone. The test was then varied in spatial and/or temporal frequency, and the process repeated. The whole procedure was repeated five times for each observer.

Two observers were used, one unaware of the aims of the experiment. A.R. is emmetropic with 6/5 vision. S.A. is slightly astigmatic (0.75 D), but was corrected to 6/5 vision with a negative cylindrical lens. To avoid a restricted field of view, no correction was worn at the closest viewing distance (9 cm), but this should not affect sensitivity of the low frequency patterns observed at those distances (e.g. Campbell and Green, 1965). Both observers were known to have normal (scotoma free) visual fields.

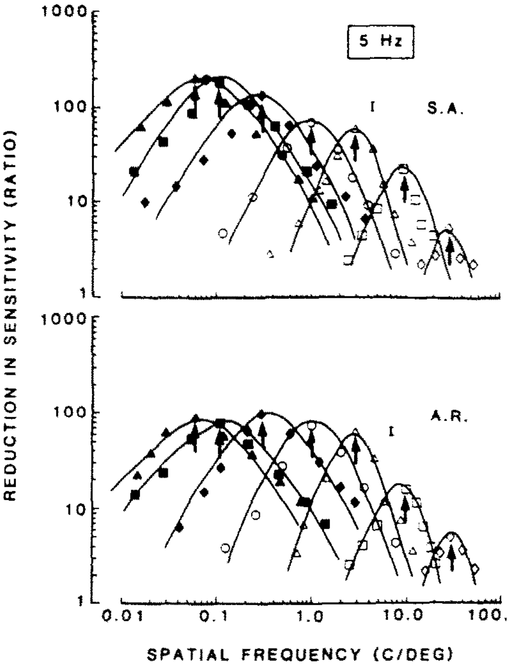

Fig. 1. Masking as a function of spatial frequency of the mask. The test was a vertical sinusoidal grating drifting at 5 Hz, and having the spatial frequency indicated by the arrows. The mask was a vertical "jittering" sinusoidal grating, whose spatial frequency is indicated on the abscissa. The error bar represents 2 standard errors of the mean, averaged over all conditions. Masking is defined as the ratio of the threshold for just discerning the direction of motion of the test in the presence of the mask to its threshold when viewed alone.

RESULTS

Spatial frequency selectivity

Figure 1 summarises the results of measurements of sensitivity to gratings in the presence of masks of varying spatial frequency. The arrows indicate the spatial frequency of the test grating. The various symbols show for tests of different spatial frequency the relative reduction in sensitivity (by masks of various frequencies). Smooth curves were drawn through the symbols by eye.

For tests of medium and low frequencies (below 3 c/deg), masks of the same spatial frequency as the test reduced sensitivity by about a factor of 100 (2 log units). For A.R. maximum masking was constant for all test frequencies below 3 c/deg, while for S.A. masking increased slightly at low spatial frequencies. For the higher frequencies, 10 and 30 c/deg, masking decreased for both observers, reflecting reduced sensitivity at those frequencies.

For every spatial frequency of the test, masking is maximal when the test and mask frequencies coincide, and steadily decreases as the spatial frequency of the masks differs from that of the test. These results are taken to imply the existence of detectors of selective spatial frequency tuning, whose sensitivity is reduced by the presence of a mask of similar spatial frequency.

The results of Fig. 1 suggest that there is spatial frequency selectivity even at very low spatial frequencies, as low as 0.06 c/deg. However, selectively is less at low than at high spatial frequencies. This is depicted more clearly in Fig. 2, which shows interalia how bandwidth (defined as the full width of the masking functions at half height) varies with spatial frequency. Spatial frequency bandwidth decreases monotonically with spatial frequencies from about 3 octaves at 0.06 c/deg to about 1 octave at 30.0 c/deg. Orientation and temporal frequency bandwidth will be discussed later.

In this experiment, the number of cycles of grating did not vary with spatial frequency. Test spatial frequency was varied by decreasing viewing distance, not decreasing screen frequency. It therefore seems likely that the reported bandwidths reflect real variations in the visual system, rather than artifacts resulting from a restricted sample of grating, as suggested by Legge and Foley (1980).

An unavoidable consequence of maintaining at least five grating cycles at all frequencies was that the field of view increased at low frequencies, to 118 deg at 0.06 c/deg. A stimulus of this extent clearly involves both central and peripheral vision. However, preliminary measurements (which will be reported in detail in a forthcoming report) indicate that there are no great differences between central and peripheral retina with low spatial frequencies. Sensitivity drops slightly with eccentricity, but the shape (and hence

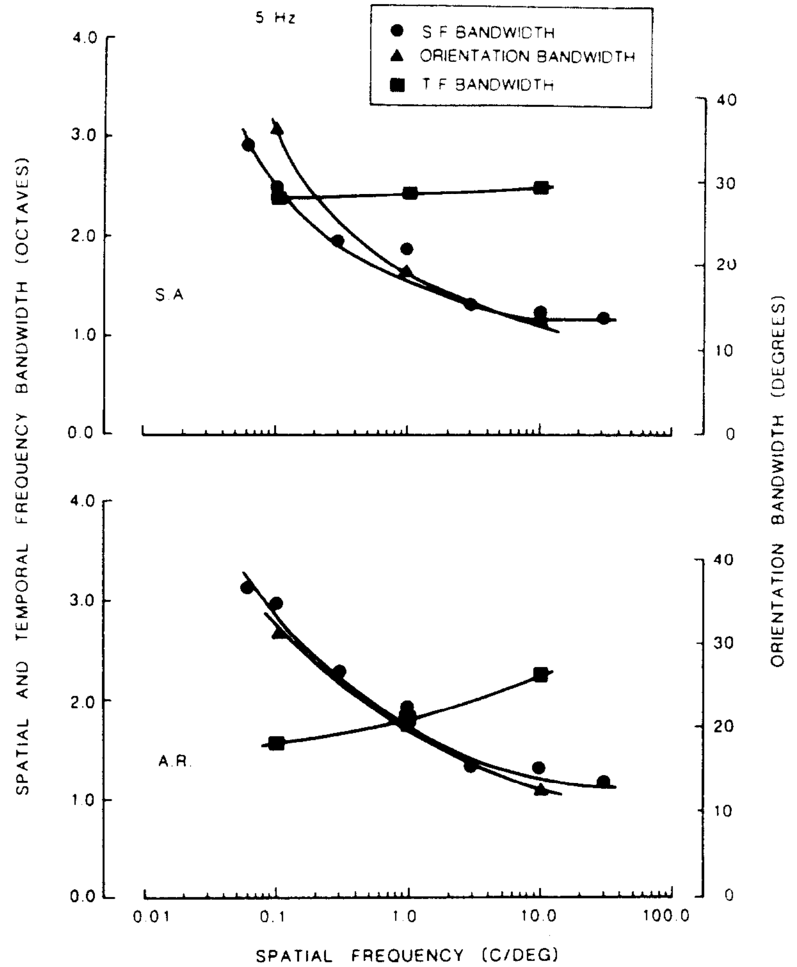

Fig. 2. Bandwidths of spatial frequency selectivity (from Fig. 1), orientation selectivity (from Fig. 3) and temporal frequency selectivity (from Fig. 5). Bandwidth is defined as the full width of the masking funciton at half hight. For temporal frequency, the bandwidth was measured from the curves for a 5 Hz test grating.

bandwidth) of the masking functions remains virtually unchanged.

Orientational selectivity

The results of masking a vertical sinusoidal test grating by a noise grating of variable orientation are shown in Fig. 3. At all spatial frequencies of the test, masking was greatest when test and mask coincided in orientation. This implies the existence of orientation selective detectors at all the spatial frequencies measured.

In addition to the major peak in the masking function at 0° (where test and mask were vertical and drifting in the same direction), at all spatial frequencies there is a smaller secondary peak at 180° (where drift direction is opposed).

As with spatial frequency selectivity, orientation selectivity increased with spatial frequency. Both the primary and secondary peaks of Fig. 3 become more narrow as spatial frequency increases from 0.1 to 10 c/deg. Figure 2 shows the change in orientation bandwidth (of the primary peaks) as a function of spatial frequency. Bandwidths vary from about 36° to 12° as spatial frequency varies from 0.1 to 10 c/deg. Again, this effect is not considered to be an artifact of the number of cycles of sinusoid in the stimulus display, as there were always 5 cycles on the screen.

Temporal frequency selectivity

For temporal frequency measurements, the test was a vertical grating of 0.1, 1 or 10 c/deg, caused to drift at a constant temporal frequency (indicated by the arrows of Fig. 4). The mask was one dimensional vertical noise caused to reverse in contrast at a variable temporal frequency. This mask was chosen to parallel that used for the spatial frequency selectivity studies to allow for later comparison of the data.

Temporal frequency masking (Fig. 4) follows a quite different pattern from spatial frequency or orientation masking. Whereas for the previous two experiments masking was always maximal when the test and mask coincided in spatial frequency or orientation with the test, here the masking functions for all temporal frequencies tend to have a common

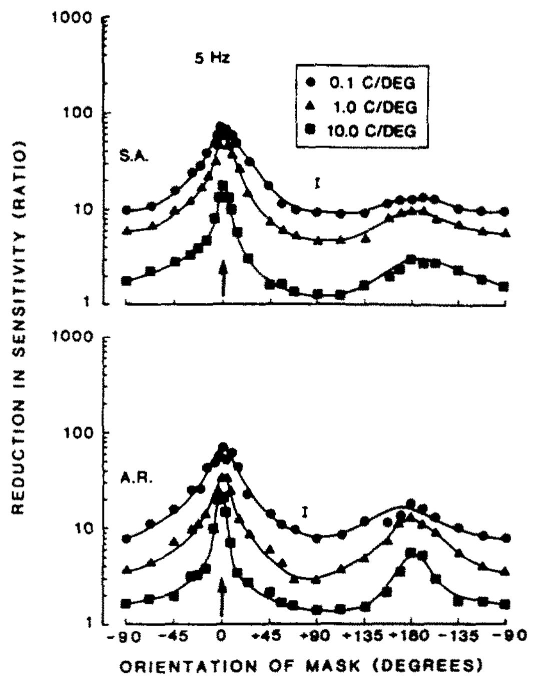

Fig. 3. Masking as a function of orientation. The test was a vertical sinusoidal grating caused to drift (from left to right) at 5 Hz. The mask was lowpass filtered one-dimensional noise caused to drift at 0.8 times the speed of the test, and varied in orientation. Three spatial frequencies of the test were measured. The error bar represents 2 SEM.

peak. The peak is relatively indifferent to the temporal frequency of the test for frequencies above 1 Hz. It does, however, change slightly with the spatial frequency of the test, decreasing with increased spatial frequency: about 7 Hz at 10 c/deg, 10 Hz at 1 c/deg and 13 Hz at 0.1 c/deg.

The change of temporal frequency bandwidth (measured from the functions at 5 Hz) with spatial frequency is shown in Fig. 2. Temporal frequency bandwidths do not follow the tendency of spatial frequency and orientation bandwidths to increase with decreasing spatial frequency. Rather, temporal frequency bandwidths decrease slightly with decreasing spatial frequency.

For very low temporal frequencies (below 1 Hz), masking does not have a specific peak. This is seen more clearly in Fig. 5, which shows masking functions for a representative low temporal frequency (0.7 Hz) and high temporal frequency (10 Hz), for the three spatial frequencies. While the high temporal frequency function is bandpass (high and low frequency attenuation), the low temporal frequency function is lowpass (only high frequency attenuation). Interestingly, however, the high frequency cutoff is about the same for the bandpass and lowpass functions. Another point of interest is that whereas at high spatial frequencies (10 c/deg), the lowpass function is higher than the bandpass function, at low spatial frequencies (0.1 c/deg), the reverse holds.

Interrelationship between spatial frequency and orientation tuning

As Fig. 2 shows, both spatial frequency and orientation bandwidths vary inversely with spatial frequency. The similarities between the two are brought out more clearly in Fig. 6, which plots spatial frequency bandwidth (in octaves) against orientation bandwidth (in degrees). The six data points are taken from the two observers for the three spatial frequencies at which complete measurements were made (0.1, 1 and 10 c/deg). There is a strong positive correlation between orientation and spatial frequency bandwidths ($r = 0.93$).

DISCUSSION

The results of this paper provide evidence for the existence of motion sensitive units selectively tuned for spatial frequency, orientation and temporal frequency. The units vary in spatial frequency selectivity from 0.06 c/deg (or lower) to at least 30 c/deg, and cover 360° of orientation. Tuning bandwidths vary with spatial frequency preference: orientation and spatial frequency bandwidths decrease with increasing spatial frequency, while temporal bandwidths increase slightly.

Spatial selectivity

The results showing broader orientation and spatial frequency tuning at low spatial frequencies agree with and extend those of previous psychophysical studies (e.g. Phillips and Wilson, 1982; Wilson *et al.*, 1983). They are also in general agreement with single unit electrophysiological studies. Tuning bandwidths for simple cells in the cat (Kulikowski and Bishop, 1981) and in the monkey (De Valois *et al.*, 1982a) primary visual cortex are smaller at higher spatial frequencies. Spatial frequency bandwidths in man as revealed by evoked potential recordings (Fiorentini *et al.*, 1983) also decrease with increasing spatial frequency.

Orientation and spatial frequency bandwidths are well correlated. This agrees with De Valois *et al.* (1982b), who reported correlations for orientation and spatial frequency bandwidths in single cells of macaque visual cortex.

The orientation masking functions of Fig. 3 are bimodal: they peak when test and mask orientation and direction of motion coincide, and again when direction of motion is opposed. The secondary peak could be explained by the action of detectors tuned for orientation, but not direction of motion. Detectors of this sort are regularly found in cat and monkey visual cortex (e.g. Hubel and Wiesel, 1962; De Valois *et al.*, 1982a). It is also possible, however, that the results could be explained by inhibitory interactions between detectors of opposing directional selectivity, which has also been observed in cat cortex (Dean *et al.*, 1980). It is not easy to compare

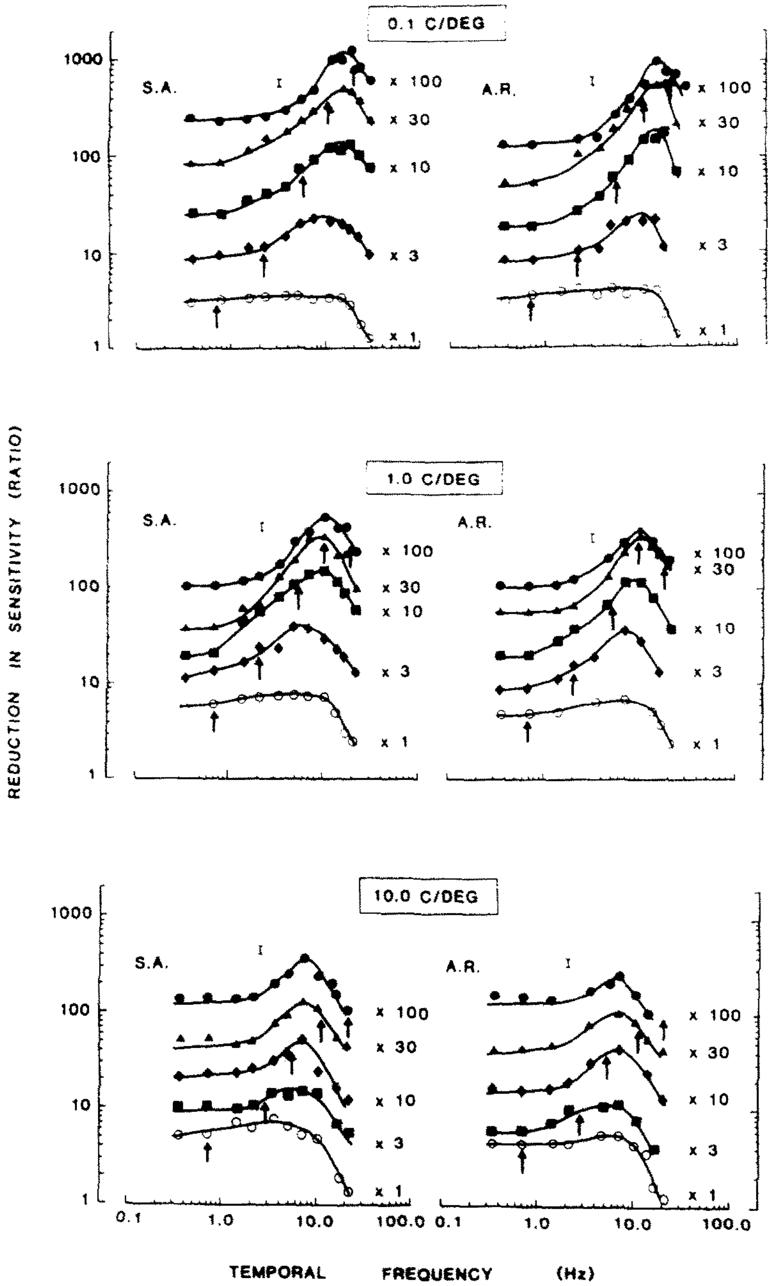

Fig. 4. Masking as a function of temporal frequency. The test was a vertical sinusoidal grating of 0.1 (upper), 1.0 (middle) or 10.0 (lower) c/deg, caused to drift at variable temporal frequencies (indicated by the arrows). Direction of drift was randomised. The mask was one-dimensional random noise caused to reverse in contrast at variable temporal frequency (abscissa). The curves are successively displaced by half a log unit for clarity. The error bar represents 2 SEM, averaged over all conditions.

the size of the secondary peak for the three spatial frequencies, as the functions differ in overall height and shape. However, the ratio of height of the secondary to the primary peak is slightly higher at low than at high spatial frequencies, suggesting that detectors are slightly less directionally selective at low spatial frequencies. This result agrees with physiological findings (De Valois *et al.*, 1982a,b), but not with previous psychophysical research (Watson *et al.*, 1980; Thompson, 1984).

Temporal selectivity

The results of temporal frequency masking differ markedly from those for spatial frequency and orientation. Instead of masking being maximal at the test frequency, a wide range of test frequencies yielded a single peak of 7–13 Hz (depending on spatial frequency). For very low temporal frequencies (less than 1 Hz), there was no peak to the masking function. Instead masks of all temporal frequencies up to a maximum of about 13 Hz were equally effective.

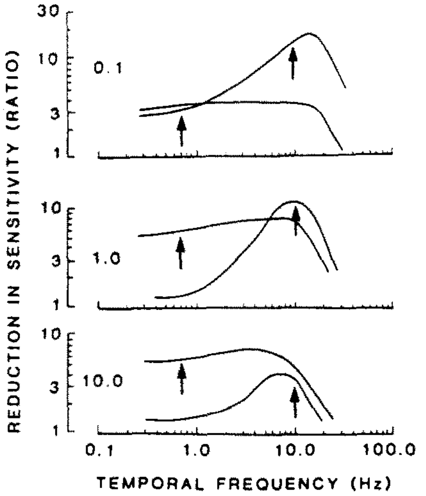

Fig. 5. Selected curves from Fig. 4. For each spatial frequency, the masking functions at 0.7 and 10 Hz are plotted with no vertical displacement. This reveals two basic types of functions, lowpass and bandpass.

These results suggest the existence of two groups of temporally tuned visual detectors: one bandpass, with a peak around 10 Hz, and the other lowpass. The results are consistent with previous ideas of two groups of detectors, "transient" and "sustained" (e.g. Keesey, 1972; Tolhurst, 1973; Kulikowski and Tolhurst, 1973; Levinson and Sekuler, 1975; Watson and Robson, 1981; Thompson, 1983). A recent evoked potential study (Regan, 1983) further complements our results. Figure 5 also shows that the lowpass masking functions are higher than the bandpass functions at high spatial frequencies, and lower at low spatial frequencies. This result is also consistent with Tolhurst's (1973) notion that transient detectors predominate at low spatial frequencies.

It is interesting that the lowpass masking functions extend to temporal frequencies as high as the bandpass functions. This results shows that masks of high temporal frequency mask low temporal frequency tests, but not vice-versa (at least at 1 c/deg and above). This could imply that "sustained", lowpass detectors respond to frequencies as high as the bandpass detectors. However, it could also imply the existence of inhibitory interactions between the two classes of units, in which the bandpass units inhibit the lowpass units, allowing for masking of low by high temporal frequencies, but not vice-versa (as suggested by Breitmeyer and Ganz, 1976, in another context).

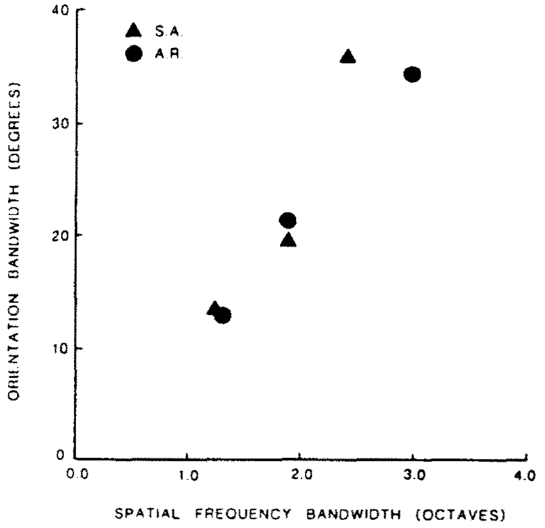

Fig. 6. Orientation bandwidth for the two observers at the three spatial frequencies as a function of spatial frequency bandwidth. The correlation for the six data points is 0.93.

At very low spatial frequencies (0.1 c/deg), the evidence for two classes of detectors is not clear. The masking function for a 0.7 Hz test is at no point higher than the tail of the masking functions for higher frequency masks. These results could be accounted for by a single temporal channel peaked at about 13 Hz, which attenuates very gradually at very low temporal frequencies.

Our results provide evidence to support broadly the popular notation of distinct sustained and transient channels, the transient channels predominating at lower spatial frequencies. However, our results also show that the so called "transient channels", or movement dependent channels are equipped by virtue of their tuning not only to provide information about motion, but also about spatial structure. Detectors tuned for motion, like those which prefer stationary patterns, are tuned for both orientation and spatial frequency. Even at low spatial frequencies, detectors are selective for orientation and spatial frequency, although the selectivity is less than that at high spatial frequencies. Thus, in theory at least, motion detectors are capable of analysis of form.

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