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Perceptual Signs of Parallel Pathways [and Discussion]

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Perceptual signs of parallel pathways

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Previous physiological work has shown that the X and Y cells found in the visual pathways of cats and monkeys have properties that might explain the perceptual distinction between 'sustained' and 'transient' mechanisms. However, when the sensitivities of X and Y cells are measured under conditions comparable with those used in psychophysical experiments, one finds that the properties thought to be relevant to the perceptual dichotomy do not in fact distinguish the two types of cell.

One of the most important psychophysical grounds for distinguishing 'sustained' from 'transient' mechanisms is that there appear to be two distinct thresholds for detecting grating patterns, depending upon whether the observer is asked to detect the spatial or the temporal properties of the stimulus. However, if thresholds are measured under conditions where the observer's criterion is tightly controlled, the two thresholds converge.

These experiments question the existence of qualitatively distinct 'sustained' and 'transient' mechanisms.

Introduction

One of the most influential recent ideas in visual psychophysics is that qualitatively different mechanisms underlie the detection of grating patterns of low and high spatial frequency, and that these mechanisms have different temporal properties: the mechanisms sensitive to low spatial frequencies have a fast and 'transient' response, while those sensitive to higher spatial frequencies have a slower, more 'sustained' response (Tolhurst 1973; Kulikowski & Tolhurst 1973). It has also been suggested that the 'transient' pathway might be specialized to convey information about movement, while the 'sustained' pathway conveys information about form (Tolhurst 1973, 1975).

The distinction between two classes of mechanism has drawn considerable support from recent phsyiological work, which shows that in the principal pathway from the retina to the cortex there exist populations of neurons that are physiologically quite distinct. Two of the cell types discerned in the cat, the X and the Y cells (Enroth-Cugell & Robson 1966; Cleland *et al.* 1971), which probably have counterparts in the macaque monkey (De Monasterio 1978), possess properties that have made them popular substrates of the 'sustained' and 'transient' mechanisms distinguished psychophysically. However, few of the physiological results are of a type that permit comparison with psychophysics.

In the first part of this paper I take for granted the psychophysical distinction, and examine the differences between X and Y cells that are thought to be relevant to it; I shall show that, when stimulated under conditions comparable with those used in psychophysical experiments, several properties thought to underlie their distinctive perceptual roles do not reliably distinguish the two types of cell. In the second part of the paper I examine some of the psychophysical evidence for distinct 'sustained' and 'transient' mechanisms. I shall describe the results of two experiments that I think weaken the psychophysical basis of the distinction.

Physiological substrates of 'sustained' and 'transient' mechanisms

Psychophysical experiments that bear upon the distinction between 'sustained' and 'transient' mechanisms have been reviewed by Breitmeyer & Ganz (1976), MacLeod (1978), Legge (1978) and Graham (1979). Here I shall deal only with those findings that have been thought to reflect a physiological distinction between X and Y cells. The relevant psychophysical observations fall broadly into two groups: (1) those that show a pronounced loss of sensitivity to gratings of low spatial frequency when their temporal frequency is low, and (2) those that suggest faster transmission of information by mechanisms sensitive to gratings of low spatial frequency.

These observations are consistent with the idea that the perception of high spatial frequencies depends upon X cells, which are thought to have slow responses and good sensitivity to low temporal frequencies, while the perception of low spatial frequencies, especially at higher temporal frequencies, depends upon Y cells, which are thought to have fast responses and poor sensitivity to low temporal frequencies. The following experiments examine these suggestions.

Methods

The general techniques were conventional. Adult cats were anaesthetized initially with an injection of Vetalar (ketamine hydrochloride, 20–25 mg kg^{-1}, intramuscular) and preparatory surgery was carried out under Saffan anaesthesia (alphaxalone and alphadolone acetate, intravenous). A loading dose of urethane (300 mg kg^{-1}) was given, and during the experiment further urethane (20 mg kg^{-1} h^{-1}) was given in a saline mixture containing dextrose and Flaxedil (gallamine triethiodide, 10 mg kg^{-1} h^{-1}) to immobilize the eyes. The cervical sympathetic trunks were cut and a small hole was made in the skull above the optic tract.

The pupils were dilated with atropine sulphate and the corneae were protected with transparent contact lenses. An artificial pupil (diameter 2 mm) was placed immediately in front of each eye, behind such supplementary lenses as were necessary to bring stimuli into focus on the retina. Action potentials, recorded by glass-coated tungsten microelectrodes placed stereotaxically in the optic tract, were counted by a computer.

Visual stimuli

Sinusoidal gratings patterns were generated by standard techniques (Campbell & Green 1965) on the screen of an oscilloscope that had a P31 phosphor. The computer generated a waveform to modulate the luminance of the screen, and also triggered each frame of the display. The phase of the modulating waveform, relative to the trigger pulse, could be varied as required, thus allowing the production of stationary grating patterns in any spatial phase, or of patterns that moved steadily across the screen. The contrast of the grating was controlled by multiplying the modulating voltage by a second signal from the computer, the product being fed to the *Z*-axis of the oscilloscope. In most experiments the screen subtended 16 × 19° and, when no modulating signal was applied, was uniformly illuminated at 225 cd m^{-2}; in some early experiments the illumination was 45 cd m^{-2}

Identification of X and Y cells

Two tests were used to establish the cell type unequivocally. In the first, grating patterns moved steadily across the receptive field. If the spatial frequency of the patterns was less than about

0.7 cycles/deg all cells gave modulated responses to the passage of bars across the receptive field, but if the spatial frequency was higher, the modulated responses of Y cells gave way to a steady discharge more rapid than that occurring in the presence of the uniformly illuminated screen (Enroth-Cugell & Robson 1966; Hochstein & Shapley 1976*a*). In the second test, stationary sinusoidal gratings of spatial frequency higher than that to which the cell was most sensitive were modulated by a temporal sinusoid to produce a standing wave. These stimuli were presented at different positions on the receptive field, and responses averaged for each position. One can find for X-cells a position of the pattern where temporal modulation elicits no response from the cell, but such a 'null' position cannot be found for Y cells (Hochstein & Shapley 1976*a*; Enroth-Cugell & Robson 1966). By the application of these tests all fibres studied in the optic tract were readily classified as X or Y type.

Sensitivity to temporal frequency

It is well established that the shape of the curve relating human contrast sensitivity to spatial frequency depends upon the temporal frequency; when patterns are moved or flickered rapidly, sensitivity to gratings of low spatial frequency improves. Sensitivity to gratings of intermediate and higher spatial frequencies is rarely improved by increasing temporal frequency (Robson 1966; Kelly 1977). This is consistent with the notion (Tolhurst 1973) that the mechanisms subserving the detection of low spatial frequencies are less sensitive to low temporal frequencies (i.e. they give more transient responses) than those sensitive to higher spatial frequencies. The 'transient' properties of such mechanisms relate only to their insensitivity to low temporal frequencies. A transient mechanism need not (although it has often been supposed to) have high sensitivity to high temporal frequencies.

X cells have smaller receptive fields than do Y cells and in general are more sensitive to high spatial frequencies (Enroth-Cugell & Robson 1966; Cleland *et al.* 1971). These properties suggest a possible connection between X cells and the 'sustained' mechanism and Y cells and the 'transient' one. However, to establish this link satisfactorily, we have to show that X cells are less sensitive than Y cells to low spatial frequencies (especially at higher temporal frequencies).

Figure 1 shows measurements of contrast sensitivity to moving gratings, made individually on nine X cells and eleven Y cells. Each curve shows the reciprocal of the contrast required for a discernible modulation of response plotted against the spatial frequency of the grating. Since within each of the two classes of cell there is no great scatter of curves on the abscissa (all receptive fields lay between 5° and 15° from the area centralis), it is convenient for our present purposes to consider the summary graph, which shows the sensitivities of X and Y cells averaged separately. It is clear that, for gratings moving at 2.6 Hz (close to the optimum rate for all units studied) the X cells are most sensitive to spatial frequencies of near 0.4 cycle/deg, while for Y cells the best spatial frequency is below 0.2 cycle/deg. Sensitivities of X and Y cells are strikingly different for spatial frequencies near 1 cycle/deg: the distributions do not overlap. At low spatial frequencies, however, Y cells are not significantly more sensitive than X cells, which causes one to ask whether the shapes of the curves depend upon temporal frequency, and whether Y cells were penalized by low temporal frequencies of stimulation.

I have made some measurements of spatial contrast sensitivity at different temporal frequencies, from which it appears that, except at the very highest temporal frequencies, the principal effect in both X and Y cells is to scale the contrast sensitivity equally for all spatial frequencies.

The question of whether Y cells are relatively less sensitive than X cells to stimulation at low temporal frequencies can therefore be answered by measuring contrast sensitivity for gratings of optimal spatial frequency at different temporal frequencies, and thus producing a graph relating contrast sensitivity to temporal frequency. Measurements of this kind made on seven X cells and eight Y cells are shown in figure 2. As in figure 1, the ordinate is the reciprocal of the contrast required for a threshold modulation of response. However, in this case the thresholds were calculated by computer because the experimenter could not guarantee a stable criterion for threshold at different temporal frequencies. The computer first analysed samples of the spontaneous discharge in the presence of the uniformly illuminated screen, to find the distribution of amplitudes of the Fourier components at the temporal frequencies used in the experiment. Then it set, for each frequency of interest, a criterion amplitude that had to be reached for a response to be detected reliably. Where this method of estimating threshold has been compared with the subjective method, it has given similar results.

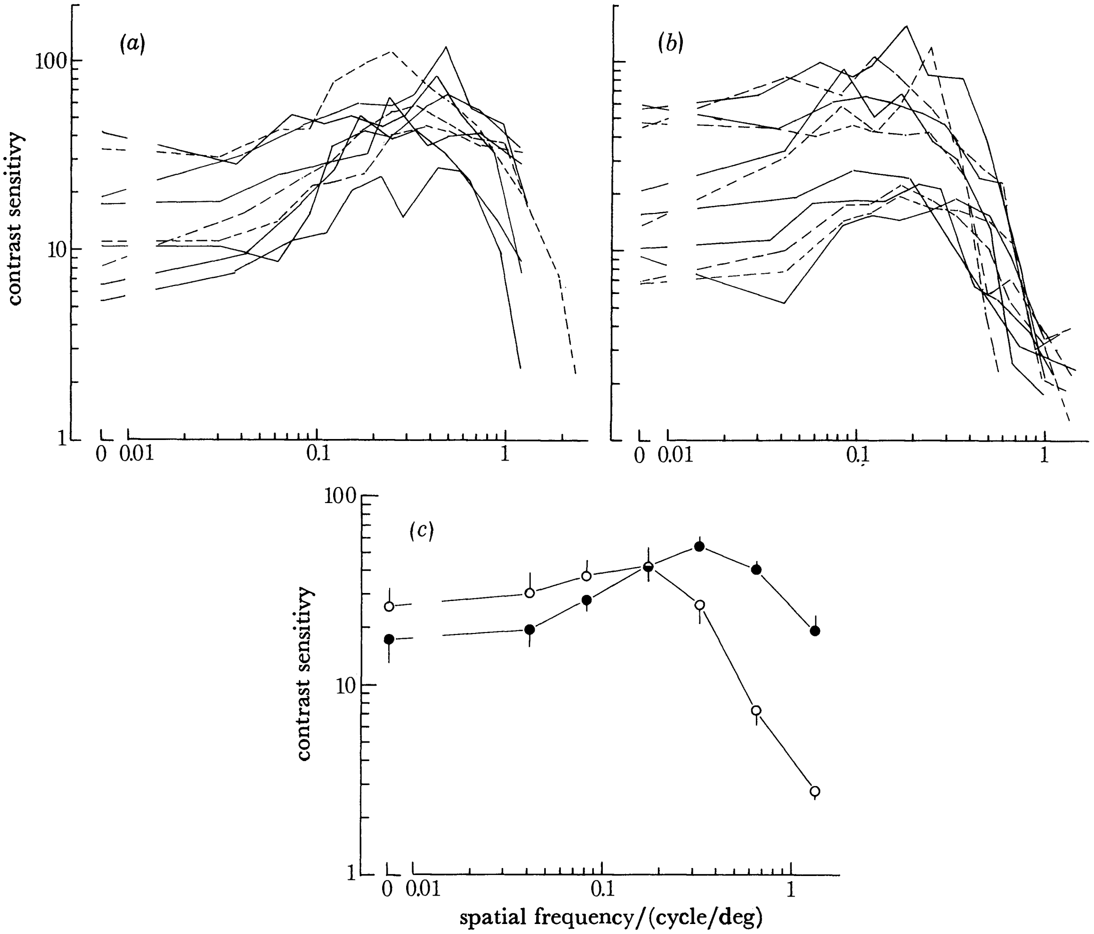

Figure 1. Spatial contrast sensitivities of X and Y cells, for gratings moving at 2.6 Hz. In all cases sensitivity was the reciprocal of the contrast required for the experimenter to hear a modulation of response. (*a*) Individual curves for X cells. (*b*) Curves for Y cells. (*c*) Curves averaged separately for X cells (●) and Y cells (○). Vertical bars mark 1 s.e. of the mean.

The individual curves for X and Y cells (figure 2*a*, *b*), which are quite similar, are averaged separately in figure 2*c*. Plainly, the temporal contrast sensitivities of X and Y cells are indistinguishable at all but the highest temporal frequencies, where Y cells have a slight advantage.

The observations in figure 2 might be thought odd in view of the evidence (Cleland *et al.* 1971, 1973) that Y cells can be distinguished from X cells by their more transient responses, which suggest poorer sensitivity to low temporal frequencies. Two factors probably account for the discrepancies. The observations that most clearly show Y cells to give more transient responses have generally used strong incremental (or decremental) spots of optimal size, and the time-scale of response has been of seconds. If one is interested in responses likely to be relevant to psychophysical thresholds, one should probably consider responses that are just strong enough to cause a reliable perturbation of the maintained discharge measured over a period of 1 s or less. Some such responses obtained from five X cells and five Y cells are shown in figure 3.

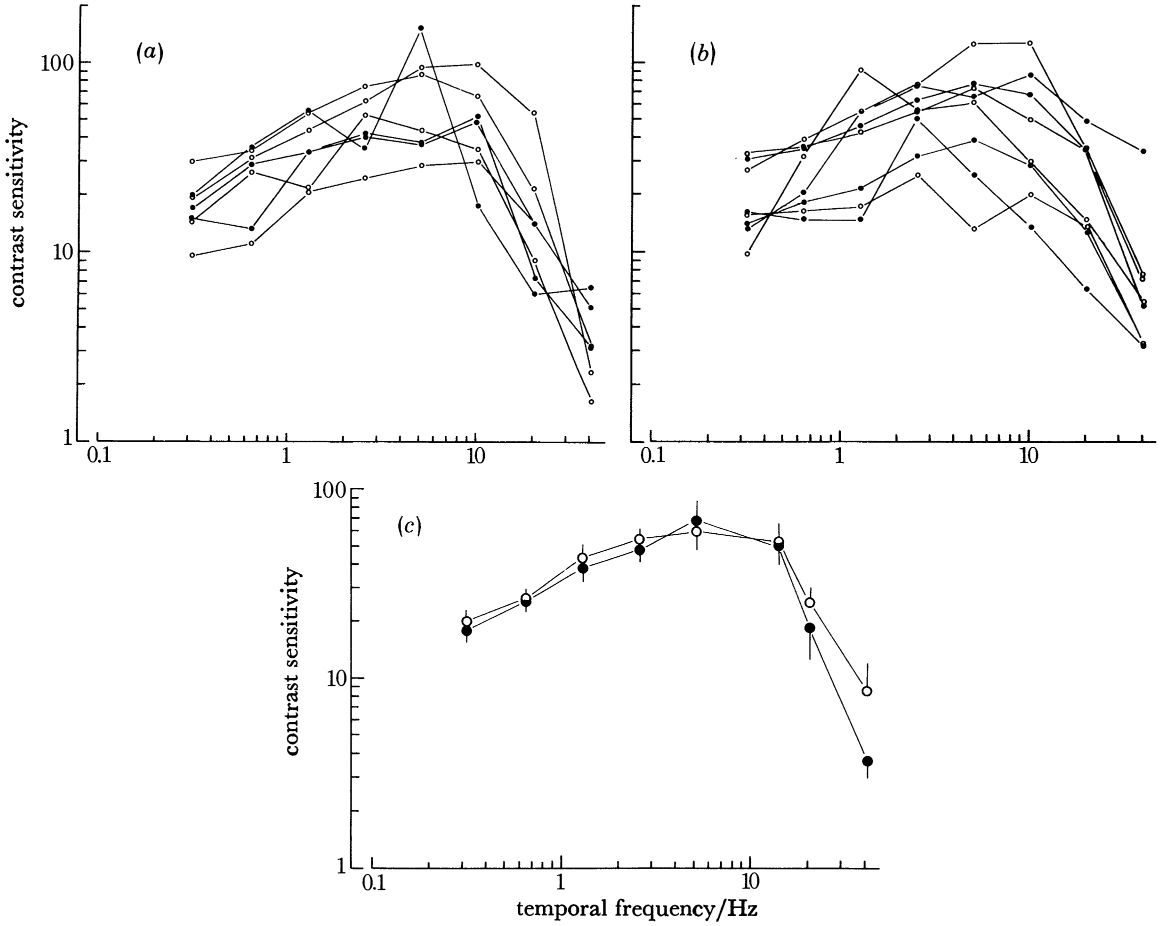

FIGURE 2. Temporal contrast sensitivities of X cells (*a*) and Y cells (*b*) for moving gratings of optimal spatial frequency. Open and closed symbols are used only for clarity. (*c*) Curves averaged separately for X cells (●) and Y cells (○).

In each case the stimulus was an optimally positioned grating of optimal spatial frequency, which was switched on for one second then off again; its contrast just exceeded that required to elicit a threshold response on 50 % of stimulus presentations. The post-stimulus time histograms obtained from X cells (left) and Y cells (right) are quite different, but the difference lies principally in the rate of the underlying spontaneous discharge (very much higher in X cells) and not in the form of the response to the stimulus (the extra impulses above the spontaneous rate). The cell giving the most transient response is a Y cell and that giving the most sustained response is an X cell, but it would be hard to classify cells reliably by the 'transientness' of their responses to the threshold stimuli used here. Hochstein & Shapley (1976*a*) have also drawn attention to some difficulties associated with this index.

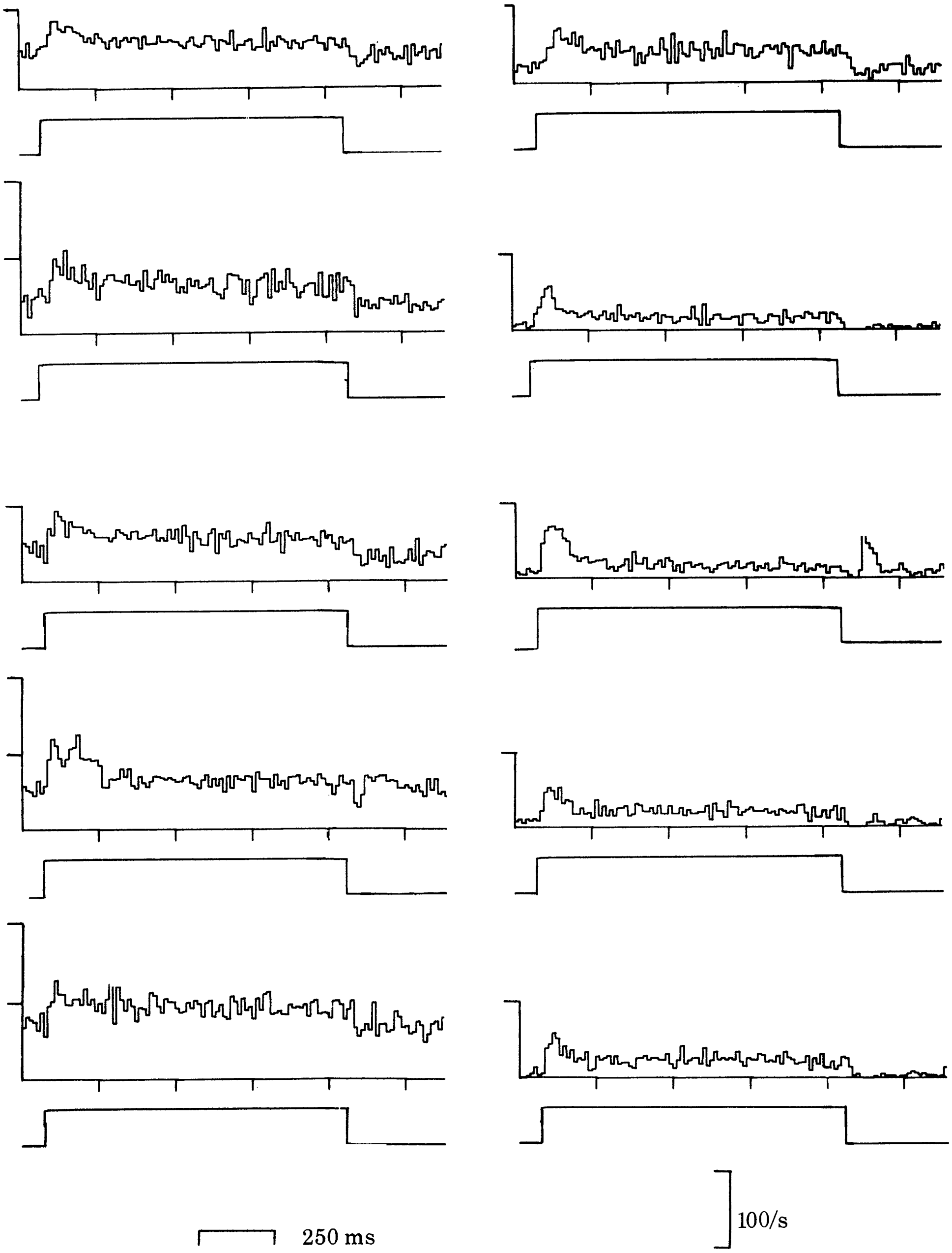

FIGURE 3. Averaged responses to 30 presentations for 1 s of gratings of optimal spatial frequency placed in even symmetry about the centre of the receptive field. Contrast was set to give a just suprathreshold response. Left, X cells, right, Y cells. Bin width, 10 ms.

The more transient responses of Y cells to strong stimuli are probably due to the action of the 'subunits' that exist within and beyond the classical receptive field (Hochstein & Shapley 1976*b*). These mechanisms generate rectified responses (i.e. they increase the discharge of a cell at both onset and offset of a stimulus), are relatively insensitive to low temporal frequencies and are probably densely distributed throughout the receptive field and beyond it. Although the manner in which subunits bring about more transient responses in Y cells is complex (Shapley & Victor 1978), they seem to be relatively much more effective when stimulated by gratings of high contrast.

Other factors explain why, despite the insensitivity of subunits to low temporal frequencies, the temporal contrast sensitivity curves of X and Y cells are so similar when measured by using continuously moving gratings (figure 2): a moving grating of spatial frequency optimal for the classical receptive field is not a particularly effective stimulus for subunits (its spatial frequency is too low). Moreover, it excites different subunits at different times, so the population of them contributes an unmodulated component to the discharges of Y cells.

It might be argued that, since subunits endow Y cells with the temporal properties that can distinguish them from X cells, the temporal properties of subunits are of greatest interest in drawing parallels with psychophysics. I think that this is wrong, because the spatial frequency for which a Y cell has the highest contrast sensitivity (and presumably therefore the greatest chance of contributing to vision) reflects the properties of the classical receptive field and is generally too low to be an effective stimulus for subunits.

These results suggest that unless signals from X and Y cells in the retina are subjected to different temporal filtering at higher stages in the visual pathway, they cannot provide the properties required of the presumed 'sustained' and 'transient' mechanisms, respectively.

Latency of response

The simple reaction time to the onset of a grating pattern is appreciably shorter when the gratings are of low spatial frequency than when the frequency is high, implying that mechanisms sensitive to low spatial frequencies transmit information faster (Breitmeyer 1975; Vassilev & Mitov 1976; Lupp *et al.* 1976). Other psychophysical results concerning backward masking (Breitmeyer & Ganz 1976; Rogowitz 1978) and saccadic suppression (Matin 1974) have also been interpreted in terms of the activity of a fast-responding mechanism sensitive to low spatial frequencies and a slower-responding mechanism sensitive to higher spatial frequencies. These ideas are consistent with the notion that X and Y cells respectively are the mechanisms sensitive to high and low spatial frequencies, for it is well established (Cleland *et al.* 1971) that the axons of Y cells conduct impulses faster than do those of X cells. Thus, other things being equal, one would expect impulses originating in Y ganglion cells to reach the lateral geniculate nucleus (l.g.n.) and cortex sooner.

However, the important functional latency is not conduction time, but the latency of a response to light. Since the bulk of the visual latency arises in the retina distal to the ganglion cells, differences between the conduction speeds of X and Y cells could be trivial. Ikeda & Wright (1972) found X cells to have the shorter visual latencies when stimulated by spots, but in their experiments X cells were probably more strongly stimulated.

J. B. Troy and I have made some measurements of the latencies of responses of X and Y cells to the abrupt onset of a grating pattern of optimal spatial frequency and spatial phase, and of contrast that produced small responses of peak amplitude about 50 impulses/s above the spontaneous discharge: a little stronger than would be required for threshold.

Latency was measured by the method shown in the inset to figure 4. One starts by counting, from some arbitrary time, the number of impulses discharged spontaneously in the presence of the uniformly illuminated screen; a cumulative count of impulses discharged is then plotted against time from the start of the counting period. The averaged counts are shown by filled circles and the slope of the straight line drawn through them gives the rate of the maintained discharge. If a stimulus is now presented and impulses are counted from the moment of its delivery, we find, as we should expect, that initially the stimulus has no effect upon the discharge and the cumulative counts follow the line for the spontaneous discharge. However, at some point there is an abrupt change of slope, indicating a change in discharge rate. The point of divergence of the two lines, usually sharply defined, marks the onset of response, and this we take as the latency. This measurement was made on eight X cells and eleven Y cells, with the result shown in figure 4. X cells have shorter latencies on average. Bearing in mind that these latencies were measured at a point in the optic tract just anterior to the l.g.n., by which time Y cells have a conduction advantage of perhaps 3 ms, it is unlikely that between the l.g.n. and cortex the faster conduction of impulses by Y cells could reverse the difference; neither are Y cells in the l.g.n. likely to be capable of exerting a prior inhibitory influence on X cells when weak visual stimuli are used (cf. Singer & Bedworth 1973).

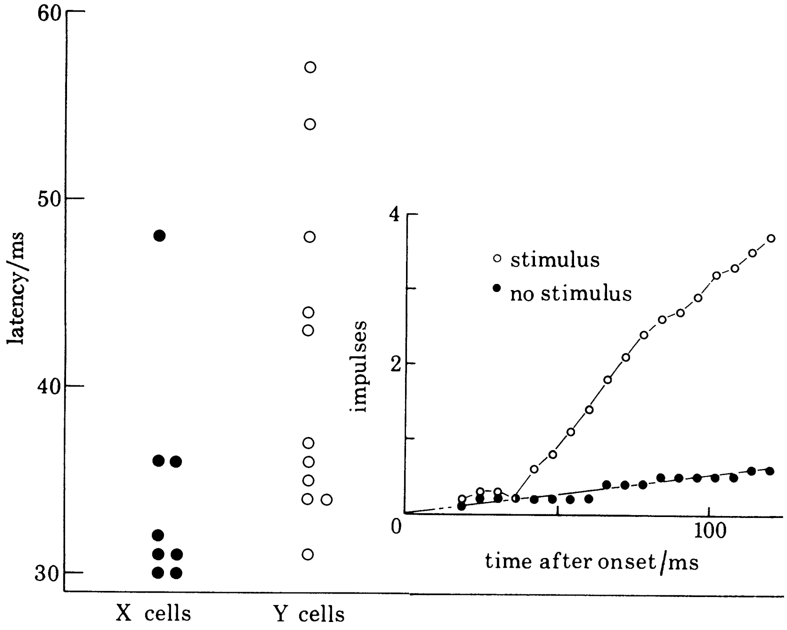

FIGURE 4. Latencies of just suprathreshold responses to the onset of gratings, measured by the method illustrated in the inset and described in the text. Counts were accumulated in 5 ms intervals. The latencies of X cells (average 34.2 ms) were significantly shorter than those of Y cells (average 41.2 ms).

It would be unwise to conclude from these results that the X system is functionally faster than the Y system, because the measurements take no account of the variability of response, which has a substantial effect on the latency for a reliable change in discharge. Moreover, the work of

Shapley & Victor (1978) suggests that, as stimulus contrast is raised, the latencies of responses of Y cells decrease faster than those of X cells. It seems most likely that the difference between the conduction velocities of X and Y cells has little significance for the speed of visual responses.

These observations suggest that, unless their responses become relatively very much faster with increasing contrast, Y cells cannot be the embodiment of the 'fast' mechanism hypothesized by Breitmeyer & Ganz (1976) to produce masking, and by Matin (1974) to produce saccadic suppression.

Psychophysical evidence for 'sustained' and 'transient' mechanisms

The weakening of the apparently close relationship between physiological and psychophysical results prompts one to review the psychophysical evidence for the distinction between 'sustained' and 'transient' mechanisms. A good deal of it is based on observations that show a graded change in temporal properties with increasing spatial frequency. It is therefore worth asking if any of the psychophysical results could reflect the operation of a single class of mechanisms all having the same temporal properties.

One notion consistent with many of the observations is that mechanisms sensitive to high spatial frequencies have the same temporal properties as those that detect low spatial frequencies, but that small eye-movements, even those occurring during attempted steady fixation, introduce a temporal modulation of the retinal image sufficient to render quite visible the image of a grating that is stationary on the oscilloscope. Thus the apparently 'sustained' response arises from these fortuitous movements of the image (Arend 1976). This idea accounts qualitatively for the changes in shape of the spatial contrast sensitivity curve that accompany changes in temporal frequency (Robson 1966), for the effect of exposure duration on the shape of the spatial contrast sensitivity curve (Legge 1978) and for some effects of subthreshold summation (Tolhurst 1975). It is also rendered attractive by the physiological observation (see above) that changes in temporal frequency seem to affect contrast sensitivity of ganglion cells uniformly at all spatial frequencies. However, quantitative considerations are less encouraging: 'sustained' properties have been inferred for mechanisms subserving the detection of spatial frequencies as low as 1.5 cycles/deg (Legge 1978), where eye movements during fixation would be expected to have little effect upon sensitivity. The explanation in terms of eye movements is also weakened by the finding that, when the retinal image is stabilized (Kelly 1977; Tulunay-Keesey & Bennis 1979) sensitivity for intermediate and high spatial frequencies is only slightly reduced at low temporal frequencies.

A second possibility, which has not been explored experimentally, is that the progression to more transient properties with decreasing spatial frequency reflects a change in the retinal distribution of mechanisms that detect the gratings. Suppose that peripheral mechanisms are less sensitive to low temporal frequencies. In a typical experiment where grating displays are, say, 10° in diameter, regions more than a small distance from the fovea will contribute little to the detection of patterns of high spatial frequency, at any temporal frequency, but may contribute much more to the detection of low spatial frequencies when the temporal frequency is higher, i.e. there is greater probability summation across space when the temporal frequency is high.

A number of observations showing low temporal sensitivity in mechanisms sensitive to low spatial frequencies might be explained by one or other of the above ideas, but some others are more difficult. The most compelling argument for there being *qualitatively* different mechanisms that have different visual functions is based on the observation that there appear to be two distinct thresholds for perceiving grating patterns: when low spatial frequencies are presented, the temporal properties of the stimulus are easily seen at the threshold for detection, but one requires supra-threshold contrast to discern the spatial structure (van Nes *et al.* 1967; Keesey 1972; Tolhurst 1973; King-Smith & Kulikowski 1975). For higher spatial frequencies, on the other hand, the spatial structure of the stimulus seems to be readily discerned at the threshold for detection but supra-threshold contrast is required for perception of the temporal properties.

Perceptually distinct thresholds might arise because observers find it hard to maintain a stable criterion as spatial and temporal properties are varied. If an observer is forced to maintain a stable criterion (as in Nachmias's (1967) experiment where spatial contrast sensitivity was measured by a forced-choice technique that required the observer to identify the orientation of a grating), there is little fall in sensitivity for spatial frequencies below the optimum. It therefore seemed worthwhile to establish whether distinct thresholds are revealed in experiments where the observer's criterion is constrained.

Qualitatively distinct threshold percepts

Detection of the movement of threshold stimuli

This experiment was undertaken to establish the conditions under which the direction of movement of a grating could be discerned at the threshold for detection. I was particularly interested to know how the spatial frequency of the gratings affected performance.

The observer sat with his head held steady by a chin rest and temple support, and viewed binocularly an oscilloscope screen (mean luminance 27 cd m^{-2}) on which could appear side by side two gratings (each 4° wide by 4° high, viewed from 57 cm). These were separated by a narrow region of uniform illumination with a fixation spot in the middle. The threshold for detection of gratings was established in the first part of the experiment: on each trial a moving grating was presented in one or both halves of the screen, and the observer had to indicate, by pressing a key switch, whether one grating or two had appeared. A trial lasted 5 s, during which time gratings appeared at full contrast for 1.5 s with slow onset and offset (figure 5, inset). A single experimental session consisted of 560 trials, in which one or two gratings were presented equally frequently in random order (if a single grating was presented it appeared randomly on the left or right while the other side of the screen remained uniformly illuminated) at seven different levels of contrast. The results were plotted as a graph of the frequency with which one or two gratings were correctly detected, against the contrast of the stimulus. A probit regression line was fitted to these points, and threshold was taken as the contrast giving 80% correct detection.

In the second part of the experiment exactly the same procedure was followed, but this time two gratings were always presented. On a single trial they moved either in the same direction (both leftwards or both rightwards) or in opposite directions (one leftwards, one rightwards) and the observer had to decide whether they moved in the same or opposite directions.

The experiment therefore provides estimates of two thresholds, one for the detection of a grating and one for identifying its direction of movement. Figure 5 shows for one observer (the author) the ratio of threshold for identification to that for detection plotted against the rate of movement of the grating, for gratings of spatial frequency 0.5, 2.0 and 8.0 cycles/deg. A ratio greater than 1 means that discrimination requires more contrast than detection. Consider first the results for the highest spatial frequency (8.0 cycles/deg). When the grating was moved at 1 cycle/s the threshold for identifying its direction is nearly 1.4 times that for detection, which is in line with the previously reported observation. But notice that as gratings moved faster the difference disappeared (the horizontal bars on the graph mark limits beyond which the threshold ratio is significantly different from unity). Watson *et al.* (1980) have observed the same effects in similar experiments.

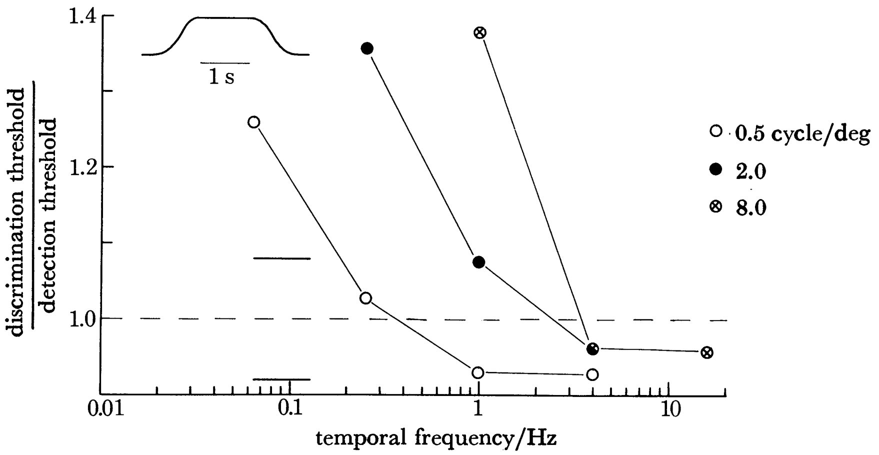

FIGURE 5. Relative thresholds for detecting a grating and discriminating its direction of motion, as a function of the rate of movement. Ratios greater than unity mean that direction of movement cannot be discerned at threshold for detection. Short horizontal lines bracket ratios not significantly different from unity. Inset shows the time course of a trial. Observer, P.L.

When gratings of 0.5 and 2.0 cycle/deg moved at 1 cycle/s, their direction of motion was identified correctly at the threshold for detection, but when these gratings moved more slowly the threshold for identifying direction of movement exceeded the threshold for detection, just as it did for the gratings of higher spatial frequency. Perhaps the simplest way to interpret these results is to suppose that the *velocity* of a grating determines whether or not its motion will be identified at the threshold for detection. Under the conditions of this experiment, motion was discriminated when the velocity was about 0.4° s^{-1}. It seems unnecessary to postulate qualitatively different mechanisms to account for the fact that gratings of high spatial frequency are not seen to move at the threshold for detection; this happens simply because their velocities are generally too low.

Detection of the form of threshold stimuli

The next experiment was designed to examine the observation that, at the threshold for detection, one apparently cannot with precision identify the spatial frequency of a low-frequency grating.

For this experiment the observer viewed an oscilloscope screen that subtended 10° × 8° and had a space average luminance of 150 cd m^{-2}. In the first part of the experiment the threshold for detecting a grating was measured by a forced-choice procedure: on each trial (marked by a tone) either a grating was presented for 250 ms or the screen remained uniformly illuminated, and the observer had to decide which of these events had happened. In a session of 400 trials, gratings and blanks were presented equally often but in random order. When gratings were presented they appeared with abrupt onset and offset. In any one experimental session gratings were all of one contrast; different contrasts were used in different sessions, and a frequency-of-seeing curve was constructed from the results of several sessions.

In the second part of the experiment the procedure was similar, but a grating appeared on the screen on every trial. The observer's task now was to indicate whether the grating was of 'standard' spatial frequency of 'higher' spatial frequency, when all gratings were equally detectable. In any one experiment the 'standard' frequency was 0.5 or 6.0 cycles/deg and the 'higher' frequency differed from the 'standard' by some specified amount. The 'standard' and 'higher' frequency gratings appeared equally often, but in random order. This procedure was repeated for a range of 'higher' frequency gratings. In figure 6 the results are plotted as graphs showing the percentage of trials on which the different 'higher' frequency gratings could be identified correctly, as a function of the degree to which their spatial frequencies differed from that of the standard grating. The question of interest is whether the graphs made with a standard frequency of 0.5 cycle/deg differ from those made with a standard frequency of 6.0 cycles/deg when all gratings are at the threshold for detection (in this case defined as the contrast that gave 80% correct detection in the first part of the experiment). The pair of graphs on the right-hand side of figure 6 show the percentage of trials on which gratings were correctly identified, against the percentage difference between the 'standard' and the 'higher' frequencies. Open circles show results for a 'standard' frequency of 0.5 cycle/deg, filled circles for a 'standard' frequency of 6 cycles/deg. It is clear that, for gratings that are equally detectable, the capacity to identify spatial frequency is no better when the 'standard' frequency is 6.0 cycles/deg than when it is 0.5 cycles/deg.

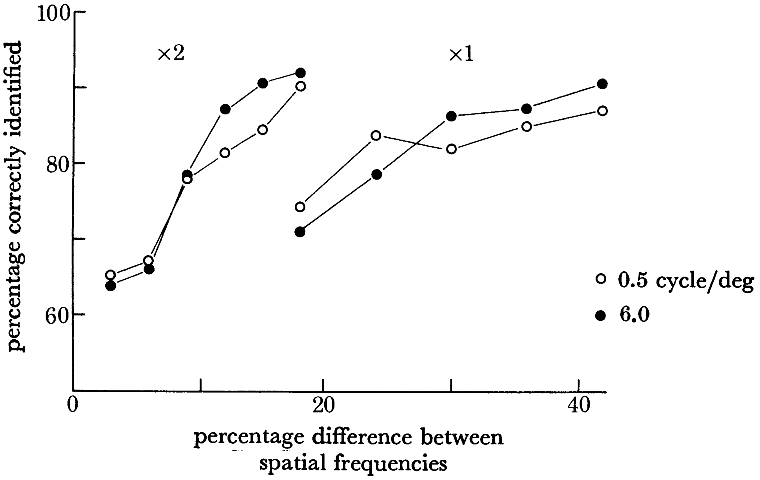

FIGURE 6. Identification of the spatial frequency of a grating at the threshold for detection (right-hand graphs) and at twice the contrast required for detection (left-hand graphs), as a function of the percentage difference between the two frequencies to be identified. ○, 'standard' frequency of 0.5 cycle/deg; ●, 'standard' frequency of 6.0 cycles/deg. Observer, P.L.

The capacity to identify spatial frequency improves as contrast is increased, but in step for the gratings of 0.5 and 6.0 cycles/deg: the graphs on the left show the percentage of trials on which gratings were correctly identified, as a function of the difference between spatial frequencies, when the contrast of all gratings was set to be twice that required for detection.

This experiment suggests that the mechanisms involved in detection of patterns of low and high spatial frequency are equally good at discriminating form. It therefore weakens the notion that the mechanisms are qualitatively different.

Conclusion

The physiological experiments described here all used stimuli that were just detected reliably. X and Y cells in the retina send more or less the same information about the temporal properties of threshold stimuli, and seem to transmit it effectively with the same speed, so unless the signals from X and Y cells are filtered differently at higher stages (for which Movshon *et al.* (1978) have provided some evidence) they seem weak candidates for the 'sustained' and 'transient' psychophysical mechanisms.

The results of the psychophysical experiments reported here suggest that the mechanisms subserving detection of spatial frequencies in the range 0.5–8 cycles/deg differ neither in their capacity to transmit information about movement, nor in their capacity to transmit information about form. Although these experiments do not impinge directly on the large body of evidence pointing to quantitative differences between the temporal properties of mechanisms subserving the detection of high and low spatial frequencies, they do weaken the evidence for the existence of *qualitatively* different mechanisms. But if one no longer requires that the underlying physiological mechanisms provide qualitatively different 'sustained' and 'transient' properties, the question remains open whether X and Y cells could subserve the detection of stimuli of low and high spatial frequency, respectively. It seems improbable that this could be the only visually significant function of a very clear-cut anatomical and physiological division of cell types. Perhaps one should look to other features that distinguish Y cells from X cells, such as their sensitivity to stimuli falling far from the classical receptive field (Fischer *et al.* 1975; Barlow *et al.* 1977; Derrington *et al.* 1979), or their different pattern of decussation (Levick 1977), for the key to their visual significance.

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Discussion

K. H. Ruddock (*Biophysics Section, Physics Department, Imperial College, London SW7 2BZ, U.K.*) In Dr Lennie's studies on the spatial properties of neural pathways selectively responsive to movement or to spatial patterns he used spatially periodic stimuli presented to a restricted retinal area. If moving, spatially non-periodic targets are employed, however, it is relatively easy to establish the activity of movement sensitive mechanisms with maximum response for spatial frequencies of around 5 cycles/deg (Barbur & Ruddock 1978). This supports Dr Lennie's thesis that movement sensitive (Y type) visual mechanisms are not characterized by low spatial frequency response. Has Dr Lennie considered employing spatially non-periodic stimuli in his own investigations?

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P. Lennie. Dr Ruddock imputes to me the suggestion that the Y system subserves the analysis of movement. I make no such claim; indeed my physiological results suggest that the Y system may be no better equipped to do this than the X system. My psychophysical results suggest that when a moving pattern is just detectable its movement can be discerned when a critical velocity is reached. I have no evidence to suggest that this critical velocity depends much upon the spatial frequency of the patterns.