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LOOMING DETECTORS IN THE HUMAN VISUAL PATHWAY[1]

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Abstract—Inspecting a target whose size oscillates about a constant mean value selectively depresses visual sensitivity to oscillating size. The effect transfers from positive to negative contrast and vice versa. This depression cannot be attributed to fatigued movement detectors. We propose that there are, in the human visual system, channels in which information as to changing size is selectively processed. This notion is consistent with the existence of two neural organizations (e.g., two classes of single neurons) selectively sensitive to increasing and to decreasing size, respectively.

Key Words—Vision; stereoscopic motion; motion perception; movement; size perception; visual adaptation.

INTRODUCTION

By successfully catching or hitting the ball thrown by his small child even the most unathletic father demonstrates a notably precise judgement of the direction along which a moving object moves in space, an ability that in gamesplayers can be quite remarkably developed. Few commuting drivers question the unfailing precision in directional judgements on which they depend during their daily passage through speeding traffic. We have previously reported experimental data that might partially account for this fine judgement. We found evidence for psychophysical information-processing channels that handle motion in depth (Beverley and Regan, 1973a,b, 1975; Regan and Beverley, 1973) forming a stereoscopic system for motion that is quite distinct from the well-established stereoscopic system for static depth in which static disparity information is processed (Wheatstone, 1838, 1852; Julesz, 1960). On this basis, we tentatively suggested that, in the human visual pathway, there are binocularly-driven neurons responsive to changing disparity and *sensitive to the direction of motion in depth*.[2] For example, one class of these neurons would respond only to motion directed between the nose and the left eye, while another class would respond only to motion directed between the nose and right eye. Subsequently, neurons sensitive to opposite-directed motion in the two eyes were found in monkey visual cortex, though these neurons seem rare (Zeki, 1974). However, since the two eyes were never stimulated simultaneously with oppositely-directed motion, the binocular interactions in point could not be observed in these physiological experiments. Simultaneous stimulation of both eyes has recently uncovered neuronal properties in area 18 of cat visual cortex that go far to explain our chief psychophysical findings in man, and these neurons seem not uncommon (Cynader and Regan, 1978). In spite of the uncertainty of neurophysiological predictions based on psychophysical data alone, it is encouraging to find this degree of correspondence at single-neuron level.

However, all these studies were of somewhat unreal situations in that the only cue to depth movement was the relative velocity of the retinal images in the

[1] This work was presented at the April 1977 ARVO Meeting, Sarasota.

[2] We should emphasize a caveat that psychophysicists assume but do not always explicitly state when they cite the result of some psychophysical experiment as evidence "consistent with" (or even "for") the existence within the human visual pathway of individual neurons that are preferentially sensitive to some stimulus feature. A psychophysical experiment can provide strong evidence that some restricted visual information is preferentially processed in a "channel", but this evidence is much weaker support for the existence of single neurons that operate as "feature filters" or "feature emphasizers" by virtue of being preferentially excited or inhibited by some particular stimulus feature. For example, a number of psychophysical adaptation experiments might be explained in terms of a population of neurons, each of which responds, perhaps rather similarly, to two or more stimulus features. We would suppose the pattern of relationships between the activities of different neurons in this population to differ in consistent ways for the different stimulus features: one particular pattern of relationships would neurally-represent (i.e., "stand for") its corresponding stimulus feature. Such hypothetical relationships might take a variety of forms, limited only by the imagination of the reader and to some extent perhaps by the known physiological facts.

Our point here (not a new one, but sometimes overlooked) is that psychophysical experiments do not, in themselves, distinguish between the presence or absence of "feature detecting" single neurons unequivocally sensitive to a single "trigger feature". Psychophysical evidence is indeed "consistent with" the existence of neurons preferentially sensitive to a single "trigger feature" whose activities underlie the specific visual sensitivity in point. But this argument gains much of its force from the assumption that one is already persuaded (e.g., by single-unit evidence) that neurons with these properties do exist and that their activities do underlie specific visual sensitivities in man. For psychophysical evidence alone is also "consistent with" a number of other neurophysiological hypotheses including in the extreme case, models that do not involve unequivocally feature-sensitive neurons (or even neural mechanisms) at all. For example, a quite acceptable psychophysical "channel" can in principle amount to no more than an interaction between two (physical) neural mechanisms rather than the activity of a single physical mechanism (a case in point may be very narrow spatial-frequency channels, see Spitzberg and Richards, 1975).

left and right eyes. In the real world there are many other visual cues to movement in depth, including changing size. The importance of cues other than changing disparity is evidenced by, for example, the continuing international career of the Nawab of Pataudi (the Indian cricket captain) following his loss of vision in one eye. In this article, we emphasize (a) the effectiveness of a cue other than binocular disparity and (b) the importance of visual sensitivity to the rate and direction of change of stimulus parameters, in achieving precise and reliable oculomotor performance in our 3-dimensional world.

We report below psychophysical evidence that, in the human visual pathway, changing image size is handled in information-processing channels separate from either motion or flicker information. On this basis, we tentatively propose the existence of neural mechanisms specifically sensitive to changing size.

METHODS

Our stimulus consisted essentially of a square whose mean side length was 0.5°. The sides oscillated to and fro at a frequency set by the experimenter with an amplitude that could be varied by the subject. When all sides of the square oscillated in phase, the square appeared to move as a whole along the lower right-upper left diagonal but remained constant in size. When opposite sides oscillated in antiphase, the square appeared to oscillate in size, but remained in the same position.

While viewing a moving stimulus, it is possible that the eyes might move in synchrony with the target. In order to avoid artifacts due to such eye movements the stimulus was arranged as in Fig. 1A. Two 0.5° squares were set on either side of a fixation spot along a diagonal with the nearest corners 2.8° apart. Squares and fixation spot were green, and of luminance 27 cd/m^2 (0.9 log ft. lamberts). The squares were superimposed on a white adapting background subtending roughly 15° × 10° and of luminance 4.3 cd/m^2 (0.1 log ft. lamberts). The viewing distance was 145 cm (57 in.). The squares were electronically generated on a Tektronix model 604 CRO (type 31 Phosphor). For oscillatory motion stimulation, the movements of the squares were equal and opposite, so that eye movements could not simultaneously track the motion of both squares. All adapting stimuli consisted of 6 min arc peak-to-peak sinewave oscillations of the square's edges (except in the ramp experiments, see below). Subjectively, this was a strong stimulus. The percentage elevation of visual threshold was calculated for each test frequency in the following way:

Percentage elevation of threshold

$$= 100\left(\frac{\text{threshold after adaptation}}{\text{threshold before adaptation}} - 1\right)$$

Thus, an elevation of 0% meant that adaptation did not affect visual sensitivity.

We used a slightly different stimulus both in the experiments dealing with positive *versus* negative contrast and in the experiments when a ramp waveform rather than a sinewave was used to modulate size and position. In these experiments subjects viewed a white adapting background (15° × 10°) of luminance 6.4 cd/m^2. Superimposed on this was a green patch of luminance 2.7 cd/m^2 in the middle of which was a single 1° × 1° square of luminance 5.4 cd/m^2 (approximately 30% positive contrast) or a 1° × 1° square of luminance 0 cd/m^2 (approximately 30% negative contrast). In ramping experiments the adapting stimulus was a rate of size change of 24 min arc sec^{-1} with a ramp time of 1.0 sec. The test ramp time was also 1.0 sec. There was a 0.25 sec blanking period between successive ramps.

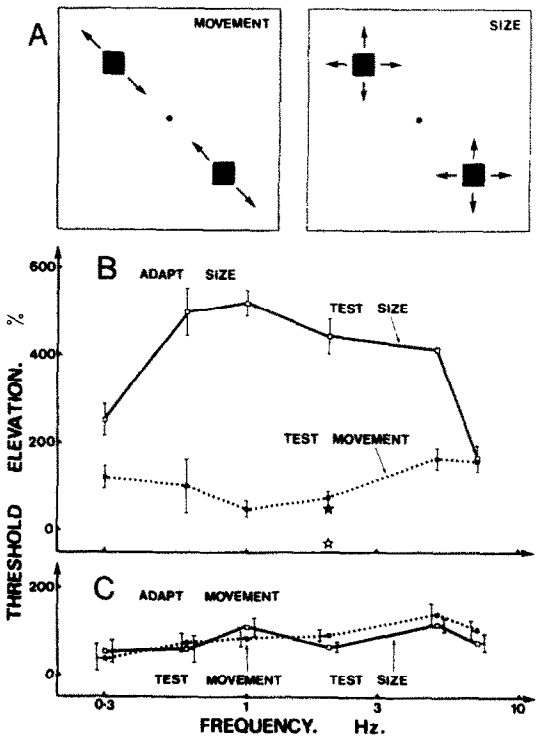

Fig. 1. Adapting to oscillating size preferentially depressed visual sensitivity to oscillating size. The stimulus was two identical squares on either side of a fixation spot (A). Ordinates plot percentage elevations of visual threshold produced by 25 min adaptation to 2 Hz oscillating size (B) and to 2 Hz oscillatory motion (C). Test frequencies are plotted as abscissae. Vertical lines show 1 SE. The large filled star and large open star show threshold elevations produced by adapting to 2 Hz flicker upon sensitivity to oscillating size and oscillatory motion, respectively. Subject D.R.

The calculations of threshold changes for ramps call for separate explanation. After adapting to a square whose size changed with a ramping waveform there was no motion-in-depth aftereffect providing that the adapting stimulus was weak. Following such adaptation to e.g. a size-increasing ramp, a size-increasing test square was more difficult to detect whereas a size-decreasing test square was easier to detect. In this case it was straightforward to calculate the respective values of threshold elevation and threshold reduction from the equation above. However, we encountered a problem in calculating threshold reductions in excess of −100%, in other words when our adapting stimuli were so strong that they produced a motion-in-depth after-effect (Regan and Beverley, 1978). In this situation the presence of a negative after-effect hindered the measurement of threshold depressions. For example, after gazing at such a size-increasing test square, a static test square appeared to be in continuous motion away from the head. As the ramping rate of size increase of the test square was gradually raised, a value was reached (d_1 deg sec^{-1}) for which the square appeared to be just detectably moving away from the head. On further raising the rate of size increase, the test square appeared to be stationary, and for some higher rate (d_2 deg sec^{-1}) it just detectably moved towards the head. [The interval ($d_2 - d_1$) was considerable for lower ramp rates, though for the highest rates it approached zero.] In the present experiments we separately used the values of d_1 and d_2

Table 1. Threshold elevations caused by adapting to a ramping increase or a ramping decrease in the size of a square. Adapting and test squares were of two types, namely dark (30% negative contrast) and bright (30% positive contrast). Positive elevations mean that adaptation made the test stimulus more difficult to detect while negative elevations mean that the test stimulus was easier to detect (see Methods). Underlined numerals indicate that adapting and test conditions were identical

Sinewave stimulation

			Test			
			L eye		R eye	
		Contrast	+	-	+	-
Adapt	L eye	+	+216	+198	+149	+128
		-	+170	+164	+114	+114

Ramp stimulation

			Test			
			Increasing		Decreasing	
		Contrast	+	-	+	-
Adapt	Increasing	+	+354	+333	-307	-211
		-	+291	+447	-189	-253
	Decreasing	+	-413	-379	+463	-369
		-	-252	-485	+340	+445

to calculate threshold elevations and depressions in the presence of a negative after-effect. This calculation was as follows. We had recorded the pre-adaptation thresholds for increasing size (I_t deg sec^{-1}) and for decreasing size (D_t deg sec^{-1}). The threshold elevations for increasing size were derived straightforwardly from the values of d_2 and I_t. A formal estimate for the threshold reduction for decreasing size was then obtained by inserting the values of d_1 and D_t in the equation above. These are the threshold reductions that appear in Table 1 as negative quantities numerically larger than -100%.

All experimental findings were confirmed several times by two experienced subjects, over a total of 70 one-hour experimental sessions.

RESULTS

Adaptation to size oscillations and to oscillatory motion

Subjects gazed steadily at the fixation mark for 25 min while the squares oscillated in size at 2 Hz, each edge moving through 6 min arc with a sinewave motion. (Prior experiment showed that 25 min was sufficient to saturate the threshold elevation: a longer adaptation period was no more effective.) Visual sensitivities to size oscillation and to oscillatory motion were measured both before and after the adaptation period. Subjects were allowed 5 sec to make a setting, and 1 min stimulation by either the adapting stimulus or (for baseline measurements) stationary squares intervened between successive settings. Visual sensitivities were measured for six test frequencies between 0.3 Hz and 7 Hz.

Fig. 1B shows the results of adapting to oscillating size and Fig. 1C the results of adapting to oscillatory motion.

The continuous line in Fig. 1B shows the percentage elevation of visual threshold to size oscillations caused by adapting to sinusoidally oscillating size. For subject D.R. the sensitivity loss was clearly very marked, reaching a threshold elevation of 520% near the adapting frequency of 2 Hz. This was significant at better than the 0.001 level. Our other subject (K.B.) gave a somewhat smaller threshold elevation, reaching 330% between 1 and 2 Hz, but with similarly high significance levels.

Of course, this finding is not sufficient to support a proposal that there is, in the human visual pathway, an information-processing channel for changing size. Three plausible alternative hypotheses spring to mind. One alternative explanation for our finding that does not invoke the notion of a changing-size channel is that the perception of threshold oscillations of size is mediated entirely by motion detectors. This explanation would have the merit of parsimony, since there is already strong psychophysical evidence for the existence of motion channels in the human visual pathway (Wohlgemuth, 1911; Pantle and Sekuler, 1968; Sekuler, Pantle and Levinson, 1976). We checked this explanation by comparing visual sensitivities to oscillatory motion and oscillating size before and after adapting to the oscillating size stimulus. (In fact, the two test stimuli were alternated one after the other during every experiment.) The dotted line in Fig. 1B clearly shows that adaptation to oscillating size depressed visual sensitivity to oscillatory motion much less than it depressed visual sensitivity to size oscillations up to 7 Hz. This experiment shows that the depression of visual sensitivity to size oscillations cannot be explained in terms of motion channels (or motion detectors).

There is a second and independent argument that adaptation of motion channels cannot explain the depression of visual sensitivity to size oscillations shown in Fig. 1B. This argument is based on the data of Fig. 1C. Here we measured visual sensitivity to size oscillations and to oscillatory motion both before and after 25 min adaptation to oscillatory motion. Fig. 1C shows that visual sensitivity was depressed for both oscillatory motion and size oscillations, and that the percentage depressions were not greatly different.

A comparison of Figs. 1B and 1C demonstrates our main finding: the effects of adaptation to oscillating size were quite different from the effects of adapting to oscillatory motion.

We should emphasize a point that is central to the interpretation of our data. This point is that the to-and-fro movements of the edges of the oscillating-size and oscillatory motion adapting squares were of identical amplitudes and frequencies in Figs. 1B and 1C. Furthermore, movements in opposite directions were exactly counter-balanced in both cases. The only difference between the size and motion adapting stimuli was that the *phase difference* between movements of opposite edges of a square was 0° in the case of oscillatory motion, and 180° in the case of size oscillations. In other words, the adapting stimuli differed only in the *relation* between the motion of opposite edges.

Control experiments

A trivial explanation for our findings would be that our adaptation and test procedure might produce an artifactual depression of sensitivity due, for example, to local retinal adaptation to light level, or to Troxler fading.[3] In order to estimate the size of this effect, i.e., to set a "procedural baseline", we repeated our adaptation experiments with the difference that the adapting squares neither moved nor changed size. In other words, we inspected static squares for 25 min. Data corresponding to the plots of Fig. 1B gave a sensitivity change at a test frequency of 2 Hz of only 6% (S.E. = 6%) which was quite negligible compared with the large depressions of sensitivity to oscillating size shown in Fig. 1B and the sensitivity depressions of Fig. 1C.

A second, again rather trivial, explanation of our finding might be couched in terms of the known effect of adaptation to flicker (Smith, 1970; Pantle, 1973). Size oscillations must necessarily be accompanied by luminance flicker (if total light flux is kept constant) or by flicker of the total light flux (if luminance is kept constant) or by some mixture of the two. In our case, the luminance of the size-oscillating adapting squares flickered with a peak-to-peak amplitude of about 55% from the mean. If a flicker channel contributed to the visual detection of size oscillations, and if the adapting stimulus depressed the sensitivity of this flicker channel, then flicker adaptation would masquerade as adaptation to size oscillations. In order to check this explanation we carried out an adaptation experiment similar to that of Fig. 1, excepting that we adapted for 25 min to stationary squares flickering at 2 Hz (peak-to-peak intensity change was 76%). We then measured visual sensitivity to size and motion stimuli and also to flicker at 2 Hz and at 7 Hz (Fig. 3, left-hand side). Visual sensitivities to size and motion stimuli were little affected. On the other hand, visual sensitivity to 2 Hz flicker was substantially depressed with a significance exceeding the 0.001 level for both subjects (210% for D.R. and 196% for K.B.) although sensitivity to flicker at 7 Hz was not significantly changed. We then adapted to flicker at 7 Hz and repeated the test measurements at 7 Hz and 2 Hz (Fig. 3, right-hand side). Again, size and movement sensitivities were not significantly changed. This time flicker threshold at 7 Hz was elevated with a significance exceeding the 0.001 level (281% for D.R., 286% for K.B.). This control experiment showed that the selective depression of visual sensitivity to oscillating size could not be explained in terms of adaptation to flicker. As a minor point it also confirmed Smith's (1970) finding that flicker adaptation is selective for temporal frequency.

Interocular transfer

Some estimate of the neuroanatomical site of a visual mechanism can be reached by measuring interocular transfer. Accordingly, we measured visual sensitivities in both adapted and non-adapted eyes before and after 25 min adaptation to oscillating size. Our chief finding was that adaptation to oscillating size showed substantial interocular transfer. Detailed results, all significant at the 0.01 level, were as follows. For subject D.R. transfer was 14% from left to right and 58% from right to left. For subject K.B. transfer was 33% from left to right, and 26% from right to left. The pointing test (Mitchell *et al.*, 1975) showed subject D.R. to be strongly dominant and subject K.B. to be weakly dominant in the right eye.

Positive and negative contrasts: sinewave and ramping size changes

In separate experiments we asked whether the threshold elevation for changing size (Fig. 1B) was specific to the sign of spatial contrast. In these experiments the stimulus was a single square (see Methods).

Table 1 summarizes the results. In brief, monocular adaptation to a bright square whose size oscillated sinusoidally produced approximately the same threshold elevation in an oscillating-size test square, independently of whether the square was bright or dark (and similarly for a dark adapting square).

Secondly, adapting to a bright square whose size increased with a ramp waveform elevated threshold for both bright and dark test squares whose sizes *increased* with a ramp waveform: thresholds were not elevated for *decreasing* size. Similarly, adapting to a dark square whose size increased with a ramping waveform elevated thresholds for both dark and bright test squares whose size increased with a ramping waveform whereas thresholds were not elevated for decreasing size. Again, threshold elevations caused by adapting to decreasing size were qualitatively independent of the sign of test or adapting contrast.

Retinal localization

Although we made no quantitative measurements of the lateral spread of adaptation to oscillating size, the effect seemed to be restricted to an area of the visual field little larger than the stimulus square. This held both for the adapted eye and for the interocularly-transferred effect. The localization was made evident by moving the point of gaze from the fixation spot in a perpendicular direction to the line joining the two squares. This movement produced an immediate and marked increase in the subjective magnitude of size oscillations, an effect that was not noticeable before adaptation.

Temporal tuning

Figure 2 plots visual sensitivity to oscillatory motion and to size oscillations in the absence of adaptation. Visual sensitivities for both measures rose to a broad peak between about 0.6–4 Hz. These data for oscillatory movement agreed with previous reports (Tyler and Torres, 1972; Regan and Beverley, 1973a,b). Figure 2 shows that sensitivity to size oscillations differed appreciably from movement sensitivity only between about 1 Hz and 5 Hz.

The temporal selectivity of the adaptation to a 2 Hz oscillating-size stimulus can be estimated from the data of Fig. 1B[4]. Temporal tuning was broad, with upper and lower half-sensitivity points at about 0.3 Hz and 6 Hz. Figure 4 shows corresponding data for

[3] A few seconds very steady fixation causes a target to disappear. This effect (Troxler fading) is easier to observe when the target is small and located peripherally rather than foveally.

[4] We thank the referees for suggesting a fuller discussion of this point.

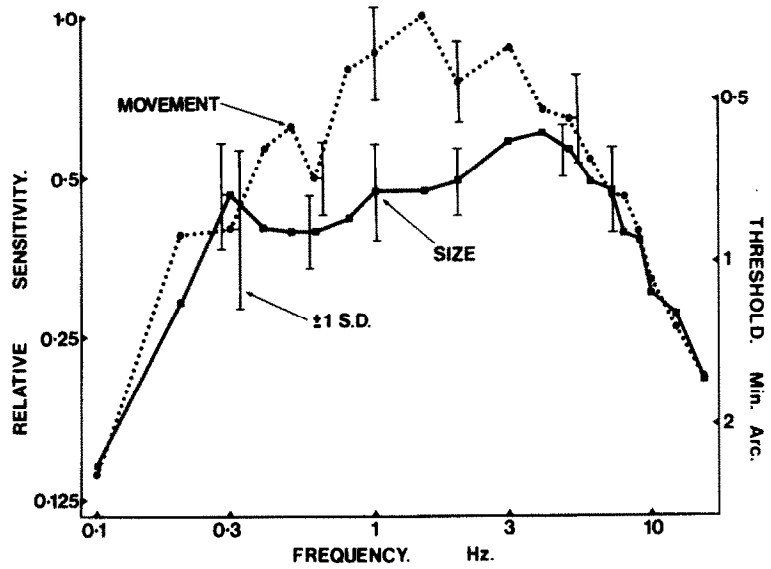

Fig. 2. Motion detection thresholds (in min arc) versus stimulus oscillation frequencies for size oscillations (continuous line) and for oscillatory motion (dotted line). The stimulus was as in Fig. 1. Vertical lines show 1 SD. Subject D.R.

subject K.B. (half-sensitivity points at 0.5 Hz and 4 Hz). Figures 1B and 4 also show that any elevation of *motion* threshold following size adaptation had comparatively little temporal selectivity compared with the elevation of threshold to oscillating size, suggesting that the continuous-line plots of Figs. 1B and 4 closely approximate the temporal selectivity of the stage specifically sensitive to oscillating size, relatively unconfounded with the temporal selectivity of any peripheral motion-sensitive stage that might be common to the motion and size channels.

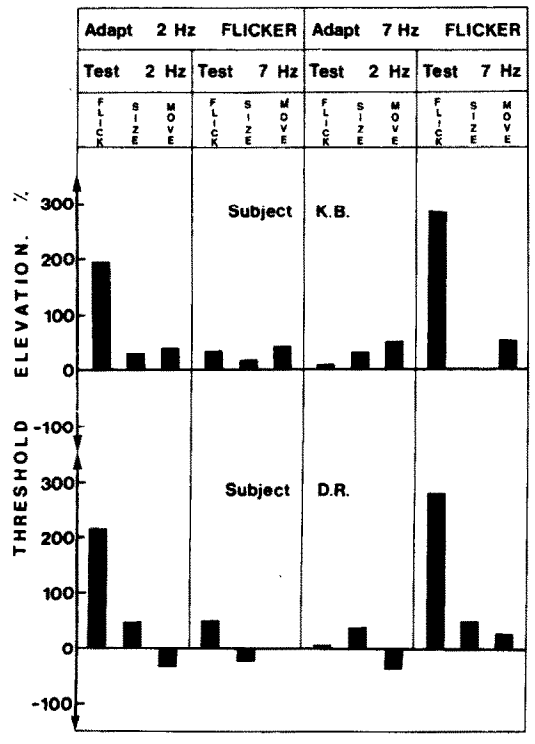

Fig. 3. Adapting to flicker had no effect on the visual sensitivities to oscillating size or oscillatory motion. Although threshold for flicker detection was elevated, this effect was specific for temporal frequency.

DISCUSSION

Historically, at least four types of psychophysical evidence have been cited for the existence of information-processing channels, as succinctly summarized by Blakemore and Sutton (1969). In this article we report two types of evidence, namely (a) *selective* threshold elevation following adaptation to changing size, and (b) progressive attenuation of the magnitude of sensation of oscillating size during adaptation. On this basis we propose that there are channels within which psychophysical information as to dynamically changing size is preferentially processed, and that these channels are distinct from the known movement channels. This is our chief conclusion. Our ramp data support the notion that increasing and decreasing size are processed in different channels: threshold depressions are consistent with inhibition between these channels. Elsewhere we report two further types of supporting evidence, namely (c) distortion of perception after adaptation, and (d) a negative after-effect (Regan and Beverley, 1978; Beverley and Regan, 1979).

More tentatively, our evidence is consistent with the existence, within the human visual pathway, of neural mechanisms (for example, classes of single neurons) preferentially sensitive to increasing or to decreasing object size, respectively. That a substantial proportion of these neurons would be binocularly-driven is indicated by our finding that adaptation to changing size shows interocular transfer. This would locate the neurons either in colliculus or at, or more central to, primary visual cortex. On this point, it is interesting to note that Zeki (1974) has reported single neurons sensitive to changing size in monkey visual cortex, although it is not clear how unequivocally his neurons would signal size change.

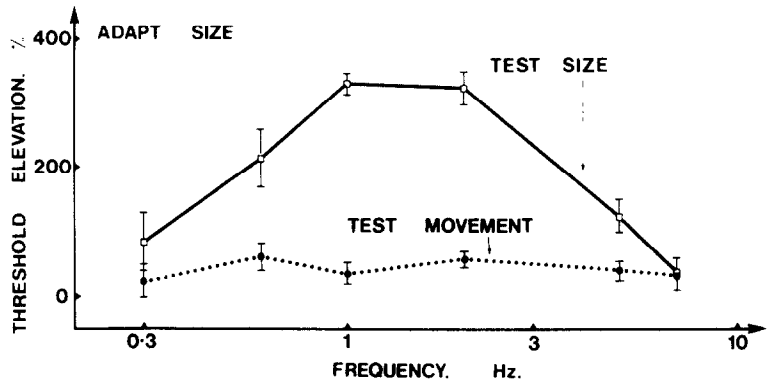

Fig. 4. Temporal tuning of adaptation to size oscillations. Subject K.I.B. Otherwise as for Fig. 1B.

Several explanations at the single-neuron level are ruled out by taking together our findings that (a) *independently* of whether contrast is positive or negative, thresholds for ramping size changes are elevated when adapting and test ramps have the same direction but not when adapting and test ramps have opposite directions, and (b) adaptation to changing size is quite distinct from adaptation to flicker.

The first class of explanation that can be discounted is cast at the level of the lateral geniculate body in terms of concentrically-organized receptive fields. For example, a centre-on neuron would indeed be excited by increasing the size of a bright square falling within its field centre. On the other hand, increasing the size of a dark square would have the opposite effect. But we find that the threshold elevation effect transfers from a ramping increase in the size of a bright square to a ramping *increase* in the size of a dark square rather than to a ramping decrease in the size of a dark square. Similarly, for a ramping decrease in size, the threshold elevation transfers independently of the sign of contrast. A second argument against this geniculate-level explanation is that adaptation to flicker does *not* transfer to an oscillating-size test square, and vice versa.

Turning to cortical level, many cells (simple cells) respond better to movement than to flicker (Hubel and Wiesel, 1962). Explanations in terms of their centre-surround organization are again ruled out by our findings for positive and negative contrasts.

One mechanism that might correspond to our changing-size filters would be a type of neuron or neural organization that received inputs from two different regions of the visual field. When these two regions were simultaneously stimulated by contrast borders (either light-dark or dark-light) that moved in *opposite* directions the neuron would respond, either by excitation or inhibition. [According to Bishop, Coombs and Henry (1971) some 50% of simple cells in cat respond to one direction of motion independently of contrast, and complex cells with this property are also well known. Perhaps such cells might converge onto the changing-size cell]. Stimulation of either region alone or simultaneous stimulation by similarly-directed movements would have comparatively little effect. These two regions that together constitute a "receptive field for changing size" might be separated by a distance of up to several degrees, and the neuron's special sensitivity to changing size would be revealed only by simultaneously stimulating the two regions with oppositely-directed motion.

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