INTRODUCTION

Relative motion requires differential movements of observed elements of the visual field. Such motion has a vital role in visual processing. It has been implicated as a monocular depth cue (Eibl-Eibesfeldt, 1956, 1957, Yakayama and Loomis, 1964; Koenderink and van Doors, 1976; Longuet-Higgins and Prazdny, 1980; Rogers and Graham, 1979, 1982). In figure-ground separation (von Holst-Holste, 1925; Reichardt and Poggis, 1977; Reichardt et al., 1963), and discrimination of self-motion from object motion, allowing perceptual disability during eye, head, and body movements (Bridgeman, 1972; Miezent et al., 1982; Frost and Nakayama, 1983).

Neurons sensitive to relative motion have been isolated electrophysiologically in various visually responsive areas of the brain. Frost and Nakayama (1983) examined pigeon optic tectum and observed single visual neurones which code opposing motion independent of direction. Hammond and MacKay (1977) found in cat striate cortex that 70% of simple cells showed a change in responsiveness to conventional bar stimuli when these were presented in moving rather than stationary static noise backgr-

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grounds, and that complex cells had their direction bias modified according to the direction and velocity of background motion. Hammond and Smith (1982) further examined these relative motion effects in monkey striate cortex (Bridgeman, 1972); cat striate cortex (Burns et al., 1972), and cat superior colliculus (Mandl, 1974) neurones have been examined whose responsiveness is greater when the stimulus moves with respect to a structured background.

Matter and Mountcastle (1961) noted a possible mechanism for relative motion sensing in the posterior parietal (area of macaques where "opponent vector organization" was common among light sensitive neurones with bilateral response areas, that is, direction sensitivity vectors point in opposite directions in the two half-fields of these cells. Such cells would probably be most active during translations of the head forward or backward in a complex visual environment. Miezent et al. (1982) examined area MT (the middle temporal area) in owl monkeys, where most cells responded best to the preferred direction of motion in the receptive field against a stationary background or a background moving in the opposite direction. These cells did not respond to the preferred direction of motion if the background also moved in that direction. This centre-surround organization for motion could play a role in the processing of motion parallax.

Electrophysiological evidence such as that cited above provides a basis from which to examine human psychophysical motion perception data; conversely, electrophysiological and anatomical data from ani-
mals are evaluated in the wake of psychophysical reports from humans. Attempts are thereby launched at integrating behavior and substrate into a consistent and meaningful framework.

As a step in determining the extent to which electrophysiological findings in monkeys can realistically be extrapolated to humans, we undertook a psychophysical comparison of the motion detection abilities of rhesus monkeys and man.

We selected a form of relative motion, "shearing motion," with potentially broad relevance. Shearing motion is a form of relative motion in which the velocity of the moving elements varies, or changes sign, as a function of position along the axis perpendicular to the axis of motion. Shearing motion is implicated in foreground-background separation and the extraction of depth from motion parallax (Graham and Roberts, 1979), and thus is an important relative motion cue for spatial perception available to a moving organism.

**Methods**

Shearing motion stimulus

The stimulus consisted of a random dot display on the face of a cathode ray tube (H.P. 1311B) with a visible screen measuring 15 cm horizontally by 19 cm vertically. Random dots were used to minimize familiar positions cues and to isolate detection of motion from the contrast-modulating effects of position sensitivity (Lippin and Bell, 1974; Nakayama and Tylke, 1981). Pixel size was 2 microns horizontally by 2.4 microns vertically. At the most common viewing distance used (53 cm), the pixels were 12 microns horizontally by 14 microns vertically and the entire screen subtended an angle of 15 arc sec horizontally by 19 deg vertically. Mean luminance of the display was approximately 24 cd/m^2 with contrast approximately 50%.

The method of motion generation was essentially the same as the one used by Nakayama and Tyler (1981). The refresh rate was 400/sec. Only horizontal
shearing motion was used. Shearing motion was mediated by two function generators. One was syn-
chronized to the vertical sweep of the random dot generator and was connected to the horizontal oscillo-
scope axis, creating a displacement of dots with a spatial frequency corresponding to the carrier fre-
quency of the function generator. This function gen-
erator was then amplitude modulated by another function generator, whose frequency thus represented the temporal frequency of shearing motion. Gener-
ally a single sinuoidal cycle triggered as the first zero crossing was used for temporal modulation. The spatial waveform was also sinusoidally varying with the top of the screen synchronized to the first zero crossing. For the spatial frequencies used in these experiments from just below 1 to just over 33 cycles were visible on the screen. In essence, the motion of the dots was that of a transverse standing wave with amplitude, temporal frequency and spatial frequency under experimental control. Figure 1 illustrates the parameters of the motion involved.

Subjects

Our subjects included two male rhesus monkeys (Macaca mulatta) represented as M83-1 and M83-2 in the figures, and the five human subjects R.A., B.G., D.M., B.K., and A.W. The monkeys were refracted under cycloplegia, and found to be esmometropic, with no astigmatism. All human subjects had normal or corrected vision.

Motion detection task

The monkeys and humans performed a reaction-
time task for motion detection which was adminis-
tered under computer control. Subjects sat in a chair (a primate chair for macaques) at either 57 or 200 cm from the screen. All experiments were performed with binocular viewing conditions. When the stationary random dot display flashed on, the subject fixated the display and pulled back a lever. A variable foreperiod ensued, randomly distributed among seven foreperiod classes ranging from 500 to 3500 msec. At the end of the variable foreperiod the display sheared whereupon the subject released the lever. The re-
sponse was monitored by computer. A Hit was scored if the lever was released within the allotted reaction-
time window after motion onset (150-800 msec was used). Following each Hit the screen blanked, a computer controlled noise was sounded, and, for the animal subjects, a drop of apple juice was delivered through a feeding tube. A False Alarm was registered when the lever release preceded the response window or was made within the first 150 msec of the reaction-
time window. A Miss was registered if the response succeeded the response window. A No Response signified that no lever pull had occurred within 1200 msec after display onset (the screen was then blanked). A No response was not counted as a Trial; the Trial category embraced False Alarms, Misses and Hits. Randomized intertrial intervals of 500, 1000, or 1500 msec were used. These randomized trials ensured that the animal was looking at the display when it appeared rather than pulling back the key using a timing behavior. There were no differential time outs for False Alarm and Hit trials. 30 Trials were performed for each amplitude tested at a specified spatial and temporal frequency of shearing motion. Amplitudes were measured as the peak-to-
peak distances of the shearing modulations (Fig. 1(b)). The results from several amplitudes permitted the plotting of hit percentages as a function of amplitude of motion (Fig. 2(a)). All data were col-
clected and displayed on line by a DEC PDP 11/34 computer.

Threshold determination

The "Hit %" (percent hits out of 50 trials) was scored for several amplitudes for a given spatial and temporal frequency, leading to a psychometric func-
tion plot; a semilog rendition of the data revealed a linear region flanked by transitions to minimum and maximum response zones (Fig. 2).

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Fig. 2. (a) Individual curve shows data from one set of conditions for a monkey subject. Hit % is the percent of correct detections the animal made within the reaction-time window plotted as a function of log amplitudes-of-motion. (b) Cumulative curve demonstrates consistency of data across testing days. The same curve was superimposed on the collared data of subject M83-1 as an amplitude of 0.4 mm (c). Threshold determination was done by finding the amplitude of motion corresponding to 20% Hit response. 50% Hit values were also used.
We ascended both the 50° and 20° Hit amplitudes (those amplitudes of motion for which, respectively, the subject responded correctly with a Hit in 50°, and 20° of the Trials, Fig. 2(c)) based on a linear regression of the linear portion of the curve, that is, those data points representing between about 20 and 85% Hits.

The probability of getting a randomly correct response for the 650 msec response window over the range of trial durations was calculated by \[1 - \frac{1}{2}(FP + D)] \times (D - RT)/(FP + D - A)\] where RT is the first 150 msec of the response window that is always a False Alarm, A is the first foreperiod of 500 msec plus the RT and represents the initial 650 msec after the key is pulled back (and it always a False Alarm), D is the response delay that includes the 650 msec reaction time hit window plus RT, and FP is the foreperiod range of 3500 msec. The 15% probability of a hit made by this calculation was compared to the real situation by running the animal on several sets of trials in which there was no shearing motion at all. These tests were interleaved with trials with motion so the animal did not change his strategy or become frustrated. We found the Hit rate to be 14-18% under these stimulus conditions and thus in good agreement with the calculated values.

The method of adjustment for threshold determination was also used, for comparison to the reaction-time method just outlined. This involved figuring the display with continuous shearing motion while manually adjusting the motion amplitude via a logarithmic potentiometer until a subjective determination of threshold had been reached.

RESULTS

Spatial frequency curve

In the first experiment we determined the motion sensitivity of both monkeys and humans as a function of spatial frequency of the shearing motion. A single temporal sinusoidal cycle of shearing motion was used, at 2 Hz, for the several spatial frequencies. We hoped to compare the spatial motion abilities of rhesus monkeys to those of man, and to previous results for man. A temporal frequency of 2 Hz was selected for this comparison because it yielded the lowest threshold values in previous experiments with humans (Tyler and Torres, 1972; Nakayama and Tyler, 1981).

Results were similar for man and monkey and are portrayed in Fig. 3. Both demonstrated a smallest threshold somewhere in the range of 0.1-0.4 cycles of visual angle, at 57° of viewing distance. The threshold amplitudes increased on either side of this optimum. The actual threshold value varied among individuals by up to a factor of four. Those with lower values consistently showed lower values throughout the testing, and those with higher thresholds were similarly constant. Consistency of data across testing days can be seen in the psychometric curve of Fig. 2(b). Additionally, those whose best spatial frequency was at the low or high end of the optimum frequency range maintained this characteristic for all temporal frequencies in all shearing motion paradigms used. Although there is some individual variation in the optimum spatial frequency and considerable individual variation for absolute threshold amplitudes, in general the "U"-shape of the spatial frequency sensitivity curve was apparent for all individuals tested. The monkey thresholds and optimum spatial frequencies fell within the range of the human data.

Temporal frequency

In agreement with Nakayama and Tyler's (1981) experiments with humans we found the lowest thresholds for the optimum spatial frequencies to be at temporal frequencies of approximately 2 Hz, with thresholds increasing for higher and lower temporal frequencies. The macaques resembled the human sub-
jects in this regard (Fig. 4). The shape of the spatial frequency sensitivity curve was independent of the temporal modulation in the range of 0.5-10 Hz; the only systematic changes recorded among these curves were in the absolute levels of the thresholds (Fig. 5).

Multiple temporal cycles and method of adjustment.

Nakayama and Tyler (1981) did not report an upturn in the spatial frequency threshold curve for low spatial frequency values for human subjects. They used a method of adjustment procedure in which thresholds were determined by viewing multiple temporal cycles in the stimuli. To determine whether their lack of a low frequency rise might be due to such multiple cycles of motion, we allowed the sinusoidal motion to continue for more than one cycle during the detection period of the trials. The number of temporal cycles possible is limited by the time allotted for the monkey to release the lever during the detection time window. This put different number-of-cycle constraints on different temporal frequencies of motion, while allowing the same time-of-viewing-motion for each, thus inverting the considerations of the single-cycle situation.

We compared single- and multiple-cycle motion thresholds. There is obvious parallelism in the spatial frequency profiles for single- and multiple-cycle motion (Fig. 6), thus multiple-cycle viewing does not remove the low frequency elevation in threshold. A superiority was seen in multiple-cycle performance above single-cycle performance at the lower temporal frequencies tested (5-5 Hz) which reversed between 5 and 10 Hz whereupon single cycles elicited better motion detection performance. This single-cycle superiority faded by 20 Hz by which point single- and multiple-cycle motion were equally effective stimuli. This performance pattern was present for both the monkey (M3-1) and human (B.G.) subjects tested. Despite the persistence of the low frequency upturn in the face of multiple cycles, there could conceivably remain factors in the method-of-adjustment which might eradicate the upturn found with our reaction-time paradigm. To examine this possibility our human subjects tried the method of adjustment (Fig. 7). The low frequency upturn persisted.

The screen size and pixel limitations were such that 57 cm was inadequate for obtaining high spatial frequency thresholds, and 2 m was too distant for low ones. Subjects were tested at both positions and the

![Graph](image)

Fig. 4. Temporal frequency profiles for monkey (M3-1) and human (B.G.) at a spatial frequency of 0.14 c/deg. All subjects exhibited best performance at around 2 Hz (1-5 Hz range).

![Graph](image)

Fig. 6. Comparison of single cycle (SC) with multiple-cycle (MC) motion at 3 Hz (subject M3-1) revealed parallelism of the respective spatial frequency sensitivity profiles. The threshold advantage seen for multiple-cycle motion was maximum at this 3 Hz value, decreasing with lower or higher temporal frequencies, nearly reversing at a value between 5 and 10 Hz, and finally equalizing by 20 Hz, for both the human and monkey subjects tested. At all temporal frequencies tested, regardless of whether single or multiple cycles were used, there was an elevation in threshold at the low spatial frequencies.

![Graph](image)

Fig. 5. Spatial frequency plots for M3-2 showed the characteristic U-shaped curve for all temporal frequencies in the range of 0.5-10 Hz.
thresholds were found to be comparable for com-
parable spatial frequencies, suggesting that the data
from each distance could be used to extend the results
from the other distance (Fig. 8). Together the data
describe a U-shaped relationship of threshold ampli-
tude as a function of spatial frequency over the range
0.04-6.5 c/deg.

DISCUSSION

The rhesus monkey (Macaca mulatta) showed psy-
chophysical threshold properties similar to those of
man for shear-motion detection. Both monkeys
tested were similar to human subjects in spatial and
temporal frequency preferences and in actualthresh-
old values. This observation extends previous reports
claiming similarity of rhesus monkeys to man for
such visual functions as acuity (Weinstein and
Grether, 1940; Cowey and Ellis, 1967), stereoview
(Santiago, 1975), binocularity and color vision (De
Valois et al., 1974a), and visual spatial abilities
(Smith et al., 1982; De Valois et al., 1974b).

Both monkey and man deviated from the pre-
viously reported view of Nakayama and Tyler (1981)
that, for man, there is no low frequency upturn in
thresholds for shear-motion but instead a flatten-
ing. We attribute this discrepancy largely to the
range of spatial frequencies that they used.

Nakayama and Tyler took their lowest spatial fre-
quency reading at about 0.15 c/deg, whereas we ex-
plored the region nearly four times lower than this
value. For some individuals the threshold elevation,
though present, was not great at this spatial fre-
quency. It should be noted that 0.04 c/deg, the lowest
spatial frequency we tested, the areas of
maximum differential motion are 13.5 deg apart and
the pickup of motion must require the peripheral
visual system which has higher motion amplitude thresholds
(De Valois and Nakayama, 1983). Indeed, Rogers and
Graham (1982) found identically shaped tuning
curves to those reported here for an identical stimulus
in a somewhat different experiment; they required
human subjects to determine thresholds at which
depth sensations were first detected in random dot
patterns that shifted in phase with the swaying
motion of the head. The Rogers and Graham thresh-
olds were high compared to ours, possibly due to
components of common motion generated by the
retinal slip that resulted from the head motion; small
amplitude of common motion added to shear-
motion have been shown to increase thresholds sub-
stantially for shear motion detection (Nakayama,

We can also compare our results to an analogu-
ese set of experiments on the spatial frequency tuning
of binocular disparity sensitivity. Tyler (1976) found
much lower bandwidths than the profile for
contrast sensitivity. The similarity in the shape of the
curves for stereopsis and motion parallax is another
instance of the similarity of the depth sensations produced by shear-
and disparity in random dot have led Rogers and
Graham (1979) to propose that the two pathways
are convergent or derivative at some point in the
nervous system. Our absolute thresholds for shear
motion are thus similar to theirs for stereocuity across all spatial frequencies tested, ad-
ing support to this hypothesis.

The earliest stages in the nervous system which
may be involved in motion detection are at the very
front end of the system. The retinal ganglion cells
respond to small movements within their receptive
fields (Scobee and Henlow, 1972). Cells in striate
cortex add the feature of directional selectivity, par-
cicularly for cells in layers 4b and 6 (Oots, 1974;
Livingstone and Hubel, 1984). These neurons project
to the middle temporal area (MT), an extrastriate
visual field that appears to be specialized for motion
analysis (Zeki, 1974; Van Essen et al., 1981; Maunsell
and Van Essen, 1983a; Albright et al., 1984). The
response of some MT cells indicate that the spatiot-

problem may be solved at this level in the visual pathway since cells in this area have been found which respond to the overall direction of motion of an object irrespective of the component motions of its local contours (Movshon et al., 1985).

One would predict that lesions to the striate cortex would greatly increase the thresholds reported here by delaying the remainder of the nervous system access to the results of the early stages of motion processing. Moreover, by comparing spatial frequency sensitivity profiles for shearing and compression motion, Nakayama et al. (1984) propose that the basic motion detectors have receptive fields similar in shape to those of striate cortical neurons. No loss in sensitivity after such a lesion would suggest that the collicular-pretectal pathways can provide a parallel path for fine motion sensitivity.

On the other hand, lesions to area MT may also severely affect the thresholds measured in this experiment by interfering with the perception of motion. A current hypothesis holds that motion information is funneled into this area from striate cortex and that MT is one of the major access routes for motion information available to the perceptual and motor systems. Lesions to humans, in an area that may be homologous to area MT in monkeys, can produce a motion blindness in the absence of overt defects in pattern vision (Zeki et al., 1983). Chemical lesions of MT in monkeys disrupt their ability to estimate velocity or direction of movement in visual pursuit tasks (Newcombe et al., 1983). Area MT projects to premotor areas including the frontal eye fields and prefrontal cortex and thus has access to some motor systems that V1 does not. However, there are alternative pathways from V1 to the frontal lobe through other extrastriate visual areas including V2 (Mausmiller and Van Essen, 1983).

MT may be in part responsible for the extremely low thresholds seen for relative motion. Thresholds for absolute motion are much higher than for relative motion, at least in the foveal region (Nakayama, unpublished). Miezen et al. (1982) have found that the cells of MT have opponent surrounds for the motion of texture fields. Thus MT neurons are maximally activated when the direction of the surround is opposite to that of the center of the receptive field and likewise these neurons are often completely inhibited with motion in the same direction for center and surround. This center-surround organization for motion has also been observed in V2 and V1 but to a lesser degree in terms of sensitivity and size of the receptive fields. Thus, the added sensitivity to relative motion may be a result of such a receptive field structure in MT. The reduced sensitivity to shearing motion at very low spatial frequencies may be another consequence of this center-surround antagonism.

Finally, we do not know the role spatial summation plays in the extremely low thresholds reported in these experiments. If spatial summation is a factor, and since the maximum sensitivity for motion is at very low spatial frequencies, it would be expected that large receptive field sizes would be required. Large receptive fields exist in MT and may boost perceptual sensitivity by correlating the activity in groups of convergent V1 neurons. We have calculated the expected size of an opponent center-surround motion receptive field from our threshold-spatial frequency data. The center diameter was estimated to be 0.66 deg and the surround diameter 6.6 deg.

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