DIFFERENCES IN THE PROCESSING OF SHORT-RANGE APPARENT MOTION AT SMALL AND LARGE DISPLACEMENTS

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Abstract—Using random dot patterns we have compared performance on direction discrimination tasks for single and multi-step sequences of apparent motion at a range of displacement sizes. Performance was measured by varying the correlation between the frames. For “small” displacements we found that no improvement in performance occurs with stimulus duration (number of frames) if the movement of individual elements within the pattern was restricted to one step, whereas if elements undergo multiple steps, performance improves with duration. For “large” displacements, on the contrary, performance improves with increasing stimulus duration irrespective of whether individual elements are restricted to single steps. These results suggest that small and large displacements are processed in different ways. We review possible psychophysical and physiological correlates of this suggestion.

INTRODUCTION

The perception of motion depends on the integration of visual information over space and time. The spatial and temporal properties of this integration can provide important clues as to how the visual system is organized. Previous studies of spatial integration raise the possibility of distinct processes within the motion system. In the present study we provide evidence from temporal integration properties that support such a distinction.

A number of studies suggest that the spatial integration of motion information is anisotropic. Chang and Julesz (1983), testing the maximum displacement threshold \( d_{\text{max}} \) in a random dot kinematogram, found that performance was better for rectangular strips elongated parallel to the direction of motion rather than perpendicular to it. Van Doorn and Koenderink (1983) reported a similar finding, using a signal/noise threshold for motion detection as a measure. These results suggest that spatial integration occurs over a greater range parallel to the motion axis than perpendicular to it.

However, the results of Nakayama, Silverman, MacLeod and Mulligan (1985) seem exactly opposite. They measured thresholds for detecting the spatial modulation of motion in patterns where velocity varied sinusoidally in space and time. This threshold rose with the spatial frequency of the modulation, but did so much more steeply when the motion was shearing (i.e. at right angles to the direction of modulation) than rarefaction/compression (motion parallel to the direction of modulation). Nakayama et al. interpret this result as indicating “receptive fields” for motion which are elongated perpendicular to the motion axis.

The apparent discrepancy between these two sets of results might be due to the difference in the velocities or displacements involved. Nakayama et al., since they measured minimum thresholds necessarily worked with low velocities and displacements; Chang and Julesz were measuring \( d_{\text{max}} \) and therefore much larger displacements. Van Doorn and Koenderink used displacements between these limits (1.25 min per 10 msec).

There are a number of lines of evidence that low and high velocities are detected by distinct sub-processes (see Bonnet, 1982). These studies both show that thresholds for motion perception may be governed by either a minimum amplitude of motion, or by a minimum velocity of motion. It is therefore possible that the differences between the experiments discussed...
above may reflect different spatial integration properties of these two mechanisms.

We have previously reported on the integration of motion information by examining performance in multi-frame sequences of random dot kinematograms (Snowden & Braddick, 1989a, b). Here we examine such integration as a function of displacement size, to see if there is any evidence for different temporal integration properties over different ranges of displacement. The use of random patterns avoids the problems of possible positional cues (Nakayama & Tyler, 1981).

Two modes of integration

Snowden and Braddick (1989b) have produced results which indicate that the temporal integration of motion signals may proceed by two modes of integration. The first is believed to occur because any one velocity is detected by units which, though tuned to the same velocity, have different temporal and spatial properties. Consider what will happen for short duration motion sequences. Units with fast temporal properties will be activated whilst those with slow temporal properties will not. As the motion sequence is extended in time, units with slower temporal properties will be activated. (In our previous paper this was termed hetero recruitment as it involves detectors of varying spans and delays.)

It is possible to eliminate such a process by allowing the individual elements of the dot pattern to be coherently displaced only once. This can be achieved by coherently displacing 50% of the dots from one pattern to the next, the other 50% being randomly repositioned on the screen. By alternating the 50% of elements which are displaced from step to step no single dot survives from pattern 1 to pattern 3 (or from pattern 2 to pattern 4 etc.). However, Snowden and Braddick (1989a, b) have demonstrated that a form of temporal recruitment still occurs in such sequences for large (near the maximum displacement limit) or more moderate (7 min) displacements. We therefore decided to see whether the minimum displacement limit could be lowered as the number of displacements in the sequence is increased.

METHODS

Stimuli

On each trial a sequence of patterns was presented. For the first pattern, 1000 (or 400) dots were assigned random $X$ and $Y$ co-ordinates. For the second pattern, a fixed percentage of the dots were selected randomly and the $X$ co-ordinate was incremented (or decremented) by a set amount (the displacement level). Any element that now fell outside the original area was wrapped around to the opposite side of the display. The remaining dots were given fresh random $X$ and $Y$ co-ordinates. For sequences larger than two patterns each pattern was derived from the preceding pattern by a similar operation. However, the dots to be displaced after the second pattern could be chosen according to three alternative rules: (1) select the dots to be displaced randomly, independent of their history ("random" condition); (2) select the dots to be displaced to be the same as those displaced on the previous displacement ("same" condition); (3) select the dots to be displaced only from those that were not displaced on the previous displacement ("different" condition). Unless otherwise stated the "random" condition was used. Results are reported in terms of the percentage of elements which were coherently shifted (we ignore any of these elements which were wrapped around, hence there is a small but systematic bias for reported thresholds to be higher than if we compensated for this effect).

The dots, of diameter 0.5 mm, were all of a high luminance value and were displayed on a HP 1319 c.r.t. (P31 phosphor) controlled by a Sigma QVEC display processor attached to a PDP 11/10 host computer. In Experiments 1-3, the square display area was 0.95 deg (from 3 m viewing distance) and 400 points were plotted in each pattern (dot density 440 dots/deg$^2$). In Experiments 4 and 5 the square display area subtended 3.7 deg and 1000 points were plotted in each pattern (dot density 73 dots/deg$^2$). The screen was refreshed at 100 Hz, hence pattern durations are multiples of 10 msec. Except where stated otherwise, each pattern was presented for 10 frames (100 msec).

The screen was viewed under conditions of dim illumination such that the edge of the screen and laboratory equipment was still visible. Subjects sat under these conditions for approximately 2 min prior to formal testing.

Procedure

Each trial commenced with a 0.5 sec fixation dot. The stimulus appeared at the offset of this point. Subjects gave a binary choice as to the direction of the displacement (left or right) by
depressing one of two buttons. No feedback was provided. In Experiments 1-3 the Method of Constant Stimuli was used. A number of displacement values chosen to span the required threshold (roughly determined in pilot experiments) were presented 50 times each, with all conditions (the number of displacements) and displacement levels randomly interleaved. These results are presented simply as the percentage of errors as a function of displacement size for each of the conditions. In Experiments 4 and 5 the displacement size was held constant and the percentage of dots undergoing this displacement was varied according to a Staircase procedure. Each staircase began with 50% correlation. If an incorrect response occurred this was incremented, whereas if two consecutive correct responses occurred it was decremented. Two or more correct followed by one incorrect response was termed a reversal. The increment/decrement level was based upon the logarithm of a "signal to noise ratio" scale (signal to noise ratio = % correlation/1 - % correlation). Before the first reversal it was 0.2 log units, this fell to 0.1 log units between reversals 1 and 2, and to 0.05 log units for all further trials. Each staircase was terminated after 11 reversals. All stimulus levels after the 3rd reversal were recorded and the mean and standard deviation calculated. Several staircases were presented randomly interleaved in one block. Standard deviations for data points of an individual subject were always less than 0.1 log unit.

Subjects
All subjects were experienced psychophysical observers, but were naive to the precise aims of the experiments (except the author R.S.). All had normal, or corrected to normal, vision except J.B. who has a history of optic neuritis in her right eye. All viewed the display binocularly without any restraints.

EXPERIMENTS 1 AND 2: EFFECTS OF INCREASING NUMBER OF FRAMES ON THE LOWER THRESHOLD MOTION

Experiment 1
Sequences containing 1, 2 or 3 displacements (2, 3 or 4 patterns) were presented to subjects. Six displacement levels were selected (from pilot studies), chosen to span threshold, and were presented 50 times each, hence 900 trials were presented to each subject (3 x 6 x 50). The dots to be displaced were chosen according to the "different" rule, so that no individual dot underwent more than one displacement before being destroyed.

The results for three subjects are plotted in Fig. 1 (three other subjects showed essentially similar results). The graphs plot the percentage of errors as a function of the size of each displacement. As the size of the displacement increased the number of errors decreases. The functions for sequences containing 1, 2 and 3 displacements show no systematic variation in the minimum displacement limit per step.

This result suggests that the processes that serve to increase the maximum displacement limit in a sequence of more than two frames do not improve performance when assessed by the minimum displacement limit. This can be contrasted to the improvement in performance found when the upper displacement limit is used as a threshold (Nakayama & Silverman, 1984; Snowden & Braddick, 1989a).

Experiment 2
The result of Experiment 1 suggests that $d_{min}$ might be governed by the excursion taken by the individual elements rather than the pattern movement (i.e. the displacement per step of the coherently moved elements multiplied by the number of steps).

In order to assess such a possibility we repeated Experiment 1 under conditions in which the number of displacements (and therefore excursion) of an individual element was varied. Again sequences of random dot kinematograms were presented with only 50% of the dots undergoing coherent displacements. However, the dots to be displaced were selected by the "same" rule. To further encourage the integration of movement over successive steps the duration of each pattern was reduced to 20 msec.

The results of this experiment are plotted in Fig. 2. The upper section of this figure (A) plots the data in the same way as Fig. 1, that is the displacement size per displacement is plotted against the number of errors. As should be expected, the results for a single displacement are very similar to the single displacement condition in the previous experiment. However, we now see that increasing the number of displacements in the sequence has a marked effect on the errors versus displacement function, such that increasing the number of displacements produces lower thresholds. In the lower half of Fig. 2 (B) the data have been replotted in terms of the total excursion of individual dots.
Fig. 1. Percentage errors are plotted against the size of the displacement (per displacement) for sequences containing 1, 2 or 3 displacements in a sequence. The stimuli were squares of side 0.95 deg and contained 400 dots. The duration of each frame was 100 msec, therefore stimuli were of 200, 300 or 400 msec duration for sequences containing 1, 2, and 3 steps respectively. Only 50% of the dots were coherently shifted from frame to frame, the others were randomly repositioned. The dots to be shifted were always different from frame to frame.

This manipulation brings the functions into close proximity (although there appears to be a tendency for the fewer number of displacements to have smaller thresholds for subject A.W.). Thus it appears that subjects can integrate the movement over a number of displacements for individual pattern elements. Further, this finding confirms that $d_{\text{max}}$ is an amplitude based threshold rather than a velocity based threshold (Boulton, 1987).

These results suggest that the temporal integration of motion information proceeds differently at the extreme ends of the displacement range for short-range apparent motion. We suggest that for small displacements, as a motion sequence is extended in time, motion detectors with longer temporal properties can be stimulated. If such a process is eliminated, as in experiment 1, no improvement in performance occurs as the number of displacements in the motion sequence is increased. Near the upper limit of displacement ($d_{\text{max}}$) it seems unlikely that increasing the number of displacements of individual elements would improve performance as the displacement between elements $t$ frames apart is on the order of $2 \cdot d_{\text{max}}$. In agreement with this suggestion Snowden and Braddick (1989a) show that the increase in $d_{\text{max}}$ with increasing number of frames does not depend upon whether individual elements undergo more than one displacement. To explain the increase in performance in this case Snowden and Braddick (1989a) suggest a process of cooperative interactions between motion detectors (termed homo recruitment). These results therefore suggest that there is a difference in the temporal integration of motion information between the upper and lower...
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Displacement limits of apparent motion in random dot patterns.

**EXPERIMENT 3:**
RECRUITMENT AND THE MAXIMUM DISPLACEMENT FOR A SMALL FIELD SIZE

One possible explanation of the lack of improvement in motion sensitivity when individual element motion is restricted is that the field size of the pattern might affect recruitment. Nakayama and Silverman (1984) show a greater recruitment effect with greater field sizes, therefore it is possible that the small field size used in the present experiments gave too small an effect to be detected, compared to the 3.6 deg field used by Snowden and Braddick (1989a).

Experiment 3 therefore measured the temporal recruitment effect at "large" displacements under precisely the same conditions as in Experiment 1.

Plotted in Fig. 3 are the errors versus displacement functions for stimuli containing one or two displacements. The two-displacement function is shifted along the abscissa (note the change of scale from Figs 1 and 2) to higher displacements than the one displacement function. $d_{max}$ (taken as 25% errors) is approximately 25% greater for the two displacement condition, a figure similar to our previous study. Thus the lack of improvement in performance found in Experiment 1 does not appear to be due to the small field size.

**Discussion**

From the present data and previous research (Chang & Julesz, 1983; Van Doorn & Koen-derink, 1983; Nakayama et al., 1985) it appears that the integration of motion signal differs in both its temporal and spatial properties at the extreme ends of the displacement range. It is...
therefore tempting to postulate that different mechanisms might operate in processing small and large displacements.

EXPERIMENT 4:
TEMPORAL INTEGRATION AS A FUNCTION OF DISPLACEMENT SIZE

Having demonstrated that extended motion sequences are treated somewhat differently at the upper and lower limits of displacement detection we were interested to find out how more intermediate displacements are processed.

In measuring recruitment effects as a function of displacement size it is clear that displacement must be the independent variable. We have followed Van Doorn and co-workers (Van Doorn & Koenderink, 1983; Van de Grind, Van Doorn & Koenderink, 1983) in using a correlation or “signal to noise ratio” measure as the dependent variable, as outlined in the Methods section. We presented subjects with such sequences containing either 1 or 2 displacements. If subjects have lower thresholds for the two displacement stimulus over for the one displacement this suggests motion information has been integrated across displacements.

Field size was now set to 3.6 deg and each pattern was of 100 msec duration. Dots to be displaced were chosen according to the “random” rule.

Figure 4 portrays the results of this experiment. The results, averaged over three subjects, are displayed in (B) whilst the functions for the individual subjects are plotted in (A) so as to show the inter-subject variability. Curves for both the single and double displacement stimuli show a U-shaped function, with the minima occurring for displacements of 8 min. The function rises sharply towards 100% threshold correlation when the displacement is around 30 min for a single displacement, which agrees well with our earlier $d_{max}$ estimates at this field size (Snowden & Braddick, 1989a). The function for a double displacement appears to head to 100% threshold correlation at a slightly larger displacement, again our earlier findings of a larger $d_{max}$ for a double displacement stimuli agrees with such a finding. Over the majority of the displacement range lower thresholds are found when the stimuli has two displacements rather than one. However, for small displacements this is not the case. At displacements of less than 2 min the curves come together.

To summarize this change we have plotted the ratio of the single and double displacement thresholds in Fig. 4(C). The open circles represent the averaged data, whilst the solid circles are data from the individual subjects. For small displacements the ratio is near 1, indicating thresholds were highly similar. At larger displacements the ratio is near 2, indicating better performance (lower thresholds) for the double displacement stimuli.

Discussion

The U-shaped curves obtained in this discrete displacement paradigm qualitatively resemble those obtained by Van de Grind et al. (1983) using random dot stimuli which were displaced every 10 msec for an unlimited period of time. They report optimal velocities ($v_{opt}$; the velocity at which thresholds were lowest) for foveal
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viewing of around 1 deg/sec. This figure was relatively unchanged for field sizes between 0.5 and 2 deg despite large changes in the maximum velocity ($v_{\text{max}}$). As the stimulus was displaced every 10 msec this $v_{\text{opt}}$ corresponds to a $d_{\text{opt}}$ (optimal displacement) of 0.6 min; over a factor of 10 different from the present estimate! The discrepancy might be explained by the "non-independence" of displacements in their paradigm. It seems possible that the most sensitive detectors might be stimulated, not by correlations between successive patterns, but by correlations between patterns several frames removed from each other. What then would be the spatial properties of the units most likely to govern threshold performance of a pattern moving at 1 deg/sec? Earlier work by the same group give an insight into a possible answer (Van Doorn & Koenderink, 1982a, b). These papers attempted to estimate the span and delay of bi-local motion units underlying the detection of a given velocity. They suggest that although a particular velocity is subserved by a range of spans, and therefore delays, the mean of these can be calculated by the formulas

$$S = 4 \cdot V^{0.61}$$
$$D = 48 \cdot V^{-0.2}$$

**Fig. 4.** Threshold percentage correlation is plotted against the size of the displacement (both scales are logarithmic) for (A) three individual subjects and (B) averaged over subjects. The stimuli were squares of side 3.6 deg and contained 1000 dots. The dots were chosen to be coherently shifted independently of their history (random condition). Frames were of 100 msec duration. Data for single steps are shown in solid lines and solid symbols, and those for a double step in broken lines and open symbols. Note that all functions are U-shaped with a minima around 0.1–0.2 deg (6–12 min). The functions are similar at small displacements but diverge for larger displacements so that thresholds are lower for the double step stimuli. The ratio of the single to double step thresholds (C) show this divergence. Open symbols are the averaged group data, whilst solid symbols represent individual datum points.
where $V$ (velocity) is in deg/sec, $S$ (detector span) in mins and $D$ (time delay of detector) in msec. Hence a pattern moving at 1 deg/sec optimally stimulates units with a span of 4 min and a delay of 50 msec. Though this result is still not the same as the 8 min of the present experiment it is at least probably reconcilable given stimulus differences and the uncertainty in locating the minima of the curves.

A recent paper (Newsome & Paré, 1988) reports threshold correlation for direction discrimination against displacement size for monkeys. The results are almost identical to those described here, adding to the increasing evidence that performance of humans and macaques is very similar for visual motion tasks (Golomb, Andersen, Nakayama, MacLeod & Wong, 1985; Siegel & Andersen, 1988).

Using a quite different stimulus and criterion, that of threshold contrast of a single edge or line, King-Smith and Riggs (1978) measured contrast thresholds as a function of amplitude for discrete and continuous motion. Despite the differences in stimuli and criteria the results are concordant with the above data. For discrete displacement threshold contrast was lowest for 8 min displacement, whereas it was lowest at 1 deg/sec for continuous motion.

The finding of lower threshold correlations for medium and large displacements when a two displacement stimulus is used is consistent with earlier findings (Nakayama & Silverman, 1984; Snowden & Braddick, 1989a, b). Similarly the absence of a difference at small displacements is in line with the data of Experiment 1 and suggests that different processes might be responsible for threshold performance. The question of whether the change is gradual or abrupt is a little less clear cut. The data from two subjects seem to show a fairly sharp transition, whereas the third shows a more gradual change between the displacements at which performance is superior for the two displacement stimuli. However, it is clear that qualitative change in performance does occur, and the change occurs at around displacements of 2-4 min.

**EXPERIMENT 5: THE TIME COURSE OF INTEGRATION**

If a dichotomy exists between the processing of small and large displacements, we should expect to find comparable results over a range of displacements in which we believe threshold is mediated by one particular process. For example if one process involves recruitment over particular duration, then all displacements that show this recruitment effect should also be bound by the same temporal constraints. Hence the next experiment measures the duration over which two displacements may integrate information. This experiment also serves to check whether the absence of improvement found in earlier experiments was due to some temporal constraint, i.e. that the effects for small displacements are short-lived and therefore missed with the temporal parameters so far employed.

The procedure was copied from the experiments of Nakayama and Silverman (1984). Three patterns were presented to the subject. The first and last patterns of the stimulus were each displayed for 100 msec, and the duration of the middle pattern was the independent variable [see Fig. 6(A)]. In the present experiment, however, the dependent variable was the percentage correlation, so that thresholds could be measured away from the displacement limits. Each subject was tested on a small selection of displacements varying from 1.3 min up to 27.8 min (each displacement size was presented in separate blocks). On each experimental run a staircase method was employed. Several durations of the middle pattern durations were selected, intended to sample the curve for the interesting region (following pilot experiment on R.S.). Trials were randomized within a block as was the order of the blocks.

The results of this experiment can be found in Fig. 5. For displacements of 6.9 min and above, thresholds fall with increasing middle pattern duration, remaining depressed for some period of time and then rise once again to a steady level. The rise in the curve occurs at around 200–300 msec. Nakayama and Silverman (1984) find a similar figure for the duration of their temporal recruitment effect when measuring $d_{\max}$. The data for displacements of 2.2 min and less do not show this trough at intermediate middle pattern durations.

**Discussion**

The overall form of the curves for large displacements in Fig. 5 resemble those produced by Nakayama and Silverman (1984). The initial improvement in performance was interpreted as a velocity limit by Nakayama and Silverman (1984). In the present experiment poor performance at short middle pattern durations can be
explained in terms of the temporal conditions of each individual displacement. The stimulus can be considered as two separate displacements, as in Fig. 6(B) and (C), each containing a 100 msec pattern and a pattern of variable duration. Baker and Braddick (1985b) found that $d_{\text{min}}$ fell if the variable pattern duration was below 30 msec in sequences like (B), and below 10 msec in sequences like (C). Thus the drop in thresholds with increasing middle pattern duration might be accounted for by the enhanced ability to process each displacement independently, and there are not necessarily any implications about the onset of temporal recruitment. Given this expectation that very brief patterns might lead to poorer motion processing it is somewhat surprising that the data for the small displacements (> 3 min) does not show some deterioration for short middle pattern durations. We suggest two possible explanations. (1) As the dots to be "signal" are chosen randomly, a small proportion undergo both displacements. These would fall into a range of displacements to which we are more sensitive (see Fig. 4) and so lower the threshold. Alternatively (2) the short pattern durations might not change $d_{\text{min}}$ in a parallel manner to their change upon $d_{\text{max}}$. Experiments on $d_{\text{min}}$, similar to those of Baker and Braddick (1985b) on $d_{\text{max}}$, would be needed to answer this question.

The finding that the duration of motion integration remains constant over a four fold change in displacement (from 6.9 to 27.8 min) is consistent with the notion that these displacements are being detected at threshold by qualitatively similar mechanisms. The findings of elevated $d_{\text{min}}$ over a similar time-course (Nakayama & Silverman, 1984) further suggests that $d_{\text{max}}$ is being determined by the same type of process.

The results then conform to the predictions on the assumption of two processes. Within each process the nature of the recruitment is invariant, whereas between the two processes there are large differences. The experiment further suggests that the crossing point in terms of displacement between these processes found in Experiment 4 was not dependent upon the temporal parameters employed.

**GENERAL DISCUSSION**

The above results suggest that small and large displacements are encoded at threshold by processes with different properties.
The postulation of two processes within the motion system is not a new idea, though the current experiments are a novel route to such an idea. Both Exner (1875) and Brown (1931) suggest that motion might be sensed on the basis of the changing position or upon the velocity per se. Similar ideas have been put forward in a succession of papers by Bonnet (1975, 1977, 1982). Bonnet describes a two mechanism theory, his two mechanisms being that of a movingness analysing system (M.A.S.) and the displacement analysing system (D.A.S.). The D.A.S. is said to process the spatial components of any motion or the amplitude of translation. The information concerning the amplitude is obtained by comparing the actual position of the target with its sensory trace of a previous position. The M.A.S. processes the motion information as such. One reason for such a distinction is Bonnet's observation that displacement threshold is dependent upon exposure time of the stimulus only above a critical time $T_c$, an observation echoed by other workers (Johnson & Leibowitz, 1976). Below $T_c$, displacement threshold is constant, whereas above $T_c$ it varies so as to be a constant velocity. Using a measure of contrast threshold to a oscillating single edge or line, King-Smith and Riggs (1978) show an amplitude/temporal frequency trade-off for moderate velocities (2.13 deg/sec), but for low velocities (0.26 deg/sec) sensitivity declines as temporal frequency increases. In conclusion King-Smith (1978) proposes that slow motion, or low amplitude displacement, is detected on the basis of amplitude, whilst larger velocities and displacements are detected on the basis of velocity. Our current finding confirms that displacement is detected upon the basis of amplitude (see Experiment 2).

Boulton (1987) also suggests two mechanisms can govern the detection of slow motion depending on visual field location. For foveal viewing displacement thresholds are a constant amplitude as stimulus duration is varied, whereas at peripheral locations (32 deg) displacement thresholds vary with stimulus duration so as to be a constant velocity. This occurs for both gratings and random-dot patterns.

Can the notion of thresholds being based either upon the amplitude of motion or upon the velocity of motion be related to the dichotomy we proposed on the basis of different recruitment effects? Clearly this is a possibility. The work of King-Smith and Riggs (1978) is described above. It is notable that the displacement at which the threshold for the two temporal frequencies of motion break apart (and by inference the change from amplitude to velocity based thresholds) is 2 min. Nakayama (1981) measured differential motion thresholds for shearing motion as a function of the common image motion. At large common image motions differential motion thresholds obeyed Weber's law with respect to velocity, but at low values of common image motion thresholds were governed by a minimum amplitude difference between sections of the pattern. The change from amplitude dominated behaviour to velocity dominated behaviour always occurred for total image displacements of 2 min even when variations in pixel size and motion duration (12–200 msec), and hence velocity, were introduced. These previous studies, using very different stimuli and thresholds, suggest a change in processes governing threshold when a displacement are around 2 min. Our finding of a change in recruitment behaviour at displacements of 2–4 min is suggestive that these hypotheses might be related.

It is also of interest to consider the postulated differences in processing to the better known distinction of short- and long-range processes (Braddick, 1980). It is clear that both our processes fall within the upper spatial limit of the short-range process (as $d_{max}$ is the definition of the upper limit), so there is no one to one correspondence. It appears that both processes are within the short-range process, and we tentatively suggest that they may simply be manifestations of the systems ability to code movement by amplitude or velocity.

**Physiological considerations**

Recent attention has focussed on the primary visual cortex (V1) and the middle temporal area (MT or V5) as regions containing motion sensitive neurons, with MT receiving information both directly and indirectly from V1, and itself projecting to another motion sensitive area MST. We shall examine the possibility that V1 and MT might be the physiological substrates of the different processes suggested by psychophysical evidence.

Receptive field sizes increase as one moves up the hierarchical structure from V1 to MT to MST. Receptive field sizes are, perhaps, up to 10 times larger in area in MT than V1 (Gattas & Gross, 1981). This trend continues into MST.
to show similar phenomena to \( d_{\text{max}} \), and cells of displacements then we might expect cells of VI MT to show similar phenomena to \( d_{\text{max}} \). Two elements. Analysed in terms of the individual patterns global processing of the pattern rather than the elements are displaced only once, suggests a global interaction may take place, as these cells look at a larger section of the visual world.

The first of these possibilities has been examined. Mikami, Newsome and Wurtz (1986b) measured \( \delta x \), the maximum displacement of a stimulus that will retain the property of directional selectivity for a given cell and found that MT cells tolerate far larger displacements than V1 cells at corresponding eccentricities. If temporal parameters are similar in V1 and MT, this would mean differences in the maximum speed to which the two areas give directional responses. Mikami, Newsome and Wurtz (1986a) show the maximum temporal delays to be similar between the areas. In addition, van Essen (1985) has observed that the optimal speeds for stimuli moving in preferred direction are greater in MT than in V1. Thus the suggestion that MT processes faster speeds and larger displacements than V1 is borne out. As such the two areas seem possible candidates for the two processes.

Newsome, Mikami and Wurtz (1986) provide some interesting comparisons between psychophysical displacement thresholds and physiologically measured displacement thresholds of individual cells. They measured the maximum spatial displacement for the sensation of motion (\( d_{\text{max}} \); human psychophysics) or directional selectivity in single cells (\( \delta x \); macaque neurophysiology) at different rates of movement of discontinuous stimuli. The psychophysical threshold appeared to be governed by the response of V1 cells at slow rates of movement, but governed by the response of MT cells at fast rates of movement.

The second possibility of larger receptive fields outlines above, that of more global processing, is also in accord with the current data. Improvement in performance with increasing number of displacements, even when individual elements are displaced only once, suggests a global processing of the pattern rather than the individual elements. Whereas the data for the small displacements suggest that the patterns is analysed in terms of the individual patterns elements.

If V1 and MT are indeed the physiological substrates of thresholds for small and large displacements then we might expect cells of V1 to show similar phenomena to \( d_{\min} \), and cells of MT to show similar phenomena to \( d_{\text{max}} \). Two observations appear relevant. Firstly, both \( d_{\text{max}} \) for humans and \( \delta x \) for macaque MT cells increase with respect to eccentricity with similar scaling factors (Baker & Braddick, 1985a; Mikami et al., 1986b). This is steeper than the cortical magnification factor for V1 (Rovamo & Virsu, 1979) which has proved useful in modelling changes with eccentricity of many other visual dimensions. The change in \( \delta x \) with eccentricity for V1 cells is not as rapid as the change in \( d_{\text{max}} \) with eccentricity. Baker and Braddick (1985a) further show that \( d_{\min} \) increases rather slowly with eccentricity, more in line with the V1 magnification factor. However, at present we know of no studies which compare changes in the minimum stimulus displacement to elicit directional selectivity in single cells with eccentricity. Hence, the two thresholds \( d_{\text{max}} \) and \( d_{\min} \) appear to scale with eccentricity in a similar fashion to MT and V1 respectively. Secondly, the strength of the directionality of response of MT cells has been noted to increase with number of displacements, to the extent that some cells that are strongly direction to multi-displacement or continuous movement are non-directional to single displacements (Mikami et al., 1986b). However, the contribution of the two forms of recruitment suggested psychophysically in this study and previous work (Snowden & Braddick, 1989b) to this effect is as yet unclear. Further, similar experimentation on V1 cells in lacking.

In conclusion the hypothesized link between the detection of small displacements and V1, and between the detection of large displacements and MT has some support. However, the parcellation of functions into discrete areas may well prove to be rather naive and awaits further evidence. The roles of other areas with a substantial percentage of cells affected by stimulus motion (e.g. V2 and V3; see Maunsell & Van Essen, 1983) must also be considered before a coherent picture of primate motion information processing may be drawn.

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