EXTENSION OF DISPLACEMENT LIMITS IN MULTIPLE-EXPOSURE SEQUENCES OF APPARENT MOTION

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Abstract—In order to examine the processes by which motion signals are combined over time, we presented subjects with random dot kinematograms which could vary in terms of the number of frames in the sequence and the duration between the onset of each stationary frame. Performance (as measured by the greatest displacement at which subjects could discriminate opposite directions of movement) improved with increasing number of displacements up to around 5 displacements, whilst manipulations of the frame duration had no affect upon this figure. Thus the results cannot be described in terms of a limited integration time. By creating sequences in which no dots underwent more than a single displacement we show that the improvement is not specific to individual dot paths. We suggest that these results could be accounted for in terms of a co-operative network in which mutual facilitation can propagate between detectors tuned to a common direction of motion.

INTRODUCTION

The perception of motion, and directionally selective responses of neurons in the visual system, can be effectively stimulated by a "two-flash" sequence producing a discrete displacement, and such displays have been valuable in analysing the properties of motion-sensitive mechanisms. In particular, the maximum displacement ($d_{\text{max}}$) which leads to a directional response is a measure of the spatial range over which these mechanisms operate (Braddick, 1974; Baker & Cynader, 1986). However, most dynamic stimuli, whether discretely sampled or in continuous motion, will potentially activate a wide range of mechanisms tuned to different directions and speeds of motion. In the case of two-flash presentations of a random-dot kinematogram, this is apparent as the "correspondence problem" (Marr, 1983)—many possible pairings exist between elements in the first and second frames, corresponding to displacements of different extents and directions. The severity of this problem increases with increasing size of displacement, since more false pairings will become comparable in size to the true displacement. $d_{\text{max}}$ can thus be taken as an indicator of how successful the system is at solving this correspondence problem. It is worth emphasizing that the correspondence problem as such is a problem for sampled motion displays, but that continuous motion of any complex pattern raises a similar problem in that it contains energy corresponding to a wide range of velocities in the spatio-temporal frequency domain (Adelson & Bergen, 1985).

The problem of unambiguously determining motion in a visual sequence can be greatly eased by combining information over space and/or time. Provided that there is some coherence between the motion of nearby points, and over a certain time interval, such combination will enhance the "signal" corresponding to this coherent motion relative to the incoherent "noise" arising from chance spatio-temporal relationships in the pattern. Many motion detecting algorithms (for a review see Nakayama, 1985) include a stage of spatial and/or temporal integration. One possible form of integration is summation within a "spatio-temporal receptive field" (Burr, 1981; Adelson & Bergen, 1985; Burr, Ross & Morrone, 1986b; Harris, 1986). Another possibility is co-operative interaction...
among a population of local detectors so that the response of each detector is facilitated by others in different locations tuned to the same direction of motion, with such facilitation persisting for a finite period of time (Chang & Julesz, 1984; Williams, Phillips & Sekuler, 1986).

The purpose of the present study was to investigate the combination of motion information over time. In particular we wished to study the effects of this combination on $d_{\text{max}}$, which we have argued above to be a measure of how effectively the visual system resolves the ambiguity of dynamic stimuli. Nakayama and Silverman (1984) have provided some recent evidence that $d_{\text{max}}$ can be increased by combining information over time. They used a random-dot stimulus in which two displacements occurred, separated by a short time interval, and reported that direction of motion could be detected with a total displacement greater than twice the value of $d_{\text{max}}$ for a single displacement. This phenomenon occurred for displacements that were separated by 30–300 msec. For greater intervals the total displacement limit was simply twice that for a single displacement, ruling out simple probability summation as a possible explanation. Nakayama and Silverman use the phrase "temporal recruitment" to describe this improved performance. McKee and Welch (1985) have also proposed temporal recruitment to account for improvements in velocity discrimination with increasing stimulus duration. The present study explores this temporal recruitment governing the maximum displacement limit for multi-displacement stimuli. The possibility of a limited integration time, or a limited maximum velocity is examined. A final experiment seeks to explore the possibility that the enhancement in performance seen for multi-displacement stimuli is specific to individual dot paths, rather than a general enhancement of other elements undergoing similar displacements.

*The elements wrapped around constitute a form of noise (as they are not moving like the rest of the elements). Their number increases with increasing displacement and serves to limit the useful area for detecting the motion. As stimulus area does effect the value $d_{\text{max}}$ (Baker & Braddick, 1982) this effect will reduce $d_{\text{max}}$ by a small amount. Increasing displacement size increased the area of elements lost by wrapping, therefore the effects described in this paper (increasing $d_{\text{max}}$ with number of displacements) are somewhat smaller than would be case without this extra loss of area.

**METHODS**

**Stimuli**

Random-dot patterns were produced by software run on a PDP 11/10 minicomputer. The dots were plotted on a HP 1319 c.r.t. display (P31 phosphor) controlled by a Sigma QVEC display processor. All element positions on the x-axis were plotted relative to the same starting point using an increment procedure, the increment value being chosen randomly from one side of the display to the other,* hence all x-coordinates were constrained to fall within the display window. The y-coordinate for each element was chosen randomly. 1000 dots (dia. 0.5 mm) were displayed in an area 19.5 cm, all were of high contrast. When viewed from 3 m this subtended a 3.7 deg arc square. The processor allowed any dot to be positioned in a 1024 by 1024 matrix, thus displacements were limited to a grain of 0.22 min arc. To produce kinematograms the x-coordinate of all dots was increased by simply repositioning the starting point. Thus all displacements were horizontal. The shifted pattern was then displayed. This process could be repeated for as many exposures as were required. The effect was of uniform displacement within a window. In expt 3 random-dot kinematograms were used in which only 50% of the elements were coherently shifted. These were produced by simply reassigning new random x- and y-coordinates to half the elements. This could be done according to two rules: either the "same" dots could be coherently displaced from frame to frame, or "different" dots could be displaced from frame to frame. A further explanation of this technique is provided in the description of the experiment.

The screen was refreshed at a rate of 100 Hz, hence frame duration (the duration of the exposure of a particular pattern) and inter-frame interval (the blank interval between exposures) were multiples of 10 msec. The term stimulus onset asynchrony will be used to refer to the duration of the frames plus the inter-frame interval.

**Procedure**

In each trial a fixation point was displayed for 0.5 sec, followed by the kinematogram whose direction of displacement (left or right) was random from trial to trial. The subject reported the perceived direction by pressing one of two buttons. No feedback was provided. Subjects
viewed the display binocularly in a dimly lit room.

In expts 1 and 2 a staircase procedure was employed. Two successive correct responses for a particular staircase caused the value of the next displacement of that staircase to be incremented. A single incorrect response produced the corresponding decrement, this procedure tracks the 71% correct level. Each staircase consisted of a series of reversals (here defined as two successive correct responses followed by an incorrect response). Up to 6 staircases were run in one experimental block, with the selection of the staircase to be presented randomly chosen from trial to trial. All staircases began with a displacement value of 21.7 min arc. In order to reach the region of threshold performance quickly the increment/decrement value was 20% of the current displacement value before any reversal occurred. This dropped to 10% between reversal 1 and reversal 2, and dropped to 5% for all subsequent trials. Each staircase terminated after 11 reversals. The threshold ($d_{max}$) was taken as the mean of all displacements after the third reversal. The average standard deviation on each threshold was around 1.5 min arc. In expt 3 the Method of Constant Stimuli was used. The procedure is described before that experiment.

**Subjects**

All subjects had normal or corrected to normal vision. They were experienced observers but were not informed of the exact purpose of the experiments, except for the author (R.S.).

**EXPERIMENT 1—THE EFFECT OF MULTIPLE-DISPLACEMENTS ON $d_{max}$**

The purpose of the first experiment was to see if $d_{max}$ for individual steps would continue increasing as the number of frames within the sequence was increased. Thus the experiment measured $d_{max}$ for kinematograms containing a variable number of frames in the sequence. Frame duration was set to 10 msec with an inter-frame interval of 30 msec.

**Results**

Figure 1 shows $d_{max}$ (expressed as the maximum value of an individual displacement) plotted against the number of displacements in the sequence, for four subjects. For a single displacement $d_{max}$ is on the order of 30 min arc, and increases by approx. 25% for a double displacement. $d_{max}$ is further increased with the number of displacements, but approaches an asymptotic figure, around 150% of the single displacement $d_{max}$, for around 4-6 displacements.

**Discussion**

Our data for two displacements can be compared with that of Nakayama and Silverman’s (1984) study, but the spatial and temporal parameters of the displays must be taken into account. Nakayama and Silverman found that the percentage increase in $d_{max}$ increased with field size and followed a U-shaped function with respect to the duration of middle frame (i.e. the interval between the displacements). If the present results can be equated to a middle
frame duration of 40 msec (10 msec frame duration and 30 msec inter-frame interval) then Nakayama and Silverman's data show an increase of around 20% for field sizes of 1.43 deg arc and 4.7 deg arc. The figure of 25% here, using a 3.7 deg arc field size, is in good agreement.

The finding of an asymptotic limit on $d_{\text{max}}$ raises the question of how the limit is determined. There are several possibilities consistent with exp 1:

(a) **Velocity limit.** The limit has been expressed spatially as around 48 min arc, but could also be expressed as a velocity—20 deg arc/sec.

If velocity is the critical variable manipulation of the stimulus onset asynchrony should lead to different asymptotic levels of $d_{\text{max}}$, with a larger stimulus onset asynchrony producing a higher level. This pattern of results is schematically displayed in Fig. 2a. Is the limiting factor spatial or spatio-temporal? Work on $d_{\text{max}}$ for a single displacement shows this to be a spatial limit which does not interact with temporal variables (Baker & Braddick, 1985b; Morgan & Ward, 1980). However, Nakayama and Silverman (1984) demonstrate that an upper velocity limit may also constrain the maximum displacement in double-step random dot kinematograms.

(b) **Integration time.** The asymptotic level for multiple-displacements was found to be reached in 4–6 displacements. This could also be expressed as a duration of 160–240 msec. The asymptotic limit might well be governed by the number of displacements taking place within some integration time. If so, a smaller stimulus onset asynchrony would produce higher asymptotic levels, since more displacements could be integrated within the time limit. Further, since the time taken to reach this asymptotic level would be the integration time, a larger number of steps would be required to reach asymptote. This pattern of results is depicted in Fig. 2b. Again the work of Nakayama and Silverman (1984) seems to add some support to an integration time hypothesis, since they show that recruitment in a double displacement stimulus only occurs if those displacements are separated by less than 300 msec.

(c) **A spatial limit.** If an asymptotic $d_{\text{max}}$ of 48 min arc per displacement is reached in, say, 5 displacements, then integration of information has occurred over motion through a total distance of 240 min arc. This distance might represent a limit on the spatial range over which motion information can be integrated. If the limit is spatial, then the form of the function relating $d_{\text{max}}$ to the number of displacements should not be influenced by the temporal parameters, except so far as non-optimal temporal parameters may degrade overall motion performance. This possibility is illustrated in Fig. 2c.

(d) **An n-step limit: the “knock-on” hypothesis.** A fourth hypothesis is that there is a genuinely limiting number of steps in the sequence over which information can be integrated. Such a limit might be determined by the properties of a process by which information was “knocked-on” from one displacement to the next. That is, $d_{\text{max}}$ for a single displacement is not an all-or-none threshold but comes from an arbitrarily selected level on the psychometric function. A “subthreshold” signal generated by a displacement beyond $d_{\text{max}}$ could be propagated to facilitate the directional response to a second displacement. Even if this latter response did

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Fig. 2. The expected pattern of results for manipulations of stimulus onset asynchrony for four possible hypotheses. (a) A velocity limit. If $d_{\text{max}}$ is limited by an upper velocity then larger stimulus onset asynchronies will produce greater $d_{\text{max}}$. (b) A limited temporal integration time. As all curves should asymptote after the same duration, when plotted as a function of the number of displacements the curve for a large stimulus onset asynchrony asymptotes in the least number of displacements. Note also that for small stimulus onset asynchronies more displacements could be combined therefore a greater $d_{\text{max}}$ is predicted. (c) Spatial limit or “knock-on effect”. Both these theories predict no change as the temporal parameters of the display are manipulated. See text for further details.
not reach the detection criterion, it would lead to a stronger signal being propagated to facilitate the next displacement, and so on. However, we may suppose that its effect would be lessened at each propagation and so would lead to measurable facilitation over a certain number of stages.

This idea must be distinguished from (1) probability summation of the detection of individual displacement, a possibility which is discussed below, and (2) linear summation of subthreshold signals in some kind of pool (for which we would expect the recruitment effect to be limited by the time and space constants of the summating mechanism).

Nakayama and Silverman (1984) found that the recruitment fell off at long and short stimulus onset asynchronies, but remained at a constant level for stimulus onset asynchronies from 20 to 140 msec. On the knock-on hypothesis we would therefore expect that within this range of stimulus onset asynchronies the propagated information would not depend on timing, giving the pattern of results shown in Fig. 2c. Experiment 2 manipulated the timing of multi-displacement sequences, to test between the possible results illustrated in Fig. 2.

EXPERIMENT 2—THE EFFECT OF VARYING STIMULUS ONSET ASYNCHRONY ON THE RECRUITMENT EFFECT

In this experiment stimulus onset asynchrony was varied between 20 and 100 msec and \( d_{\text{max}} \) per displacement measured for sequences of between 1 and 8 displacements. Stimulus onset asynchronies were simply equal to frame duration (i.e. inter-frame interval = 0) except in the case of 60 msec stimulus onset asynchrony where frame duration = 10 msec and inter-frame interval = 50 msec.

**Results**

Figure 3 shows data for two subjects, along with their data from experiment 1 (stimulus onset asynchrony = 40 msec, frame duration = 10 msec and inter-frame interval = 30 msec). The curves obtained at different stimulus onset asynchronies values follow the same shape, and asymptote at similar limiting values of \( d_{\text{max}} \). The data for 20 msec stimulus onset asynchrony are displaced a little downwards for all numbers of displacements. The presence of a blank inter-frame interval between exposures appears to have no effect upon \( d_{\text{max}} \) (compare the conditions stimulus onset asynchrony = 40 and 60 msec which include such an interval with those for the other values which did not).

**Discussion**

The basic findings can be summarized:

1. Asymptotic values of \( d_{\text{max}} \) are similar over a range of stimulus onset asynchronies (40–100 msec). This corresponds to more than a doubling the maximum velocity for which direction discrimination can be made.

2. When \( d_{\text{max}} \) is plotted against the number of displacements, the shape of the curves is very similar for all stimulus onset asynchronies. Asymptote is reached in 4–6 displacements regardless of the duration of this sequence.

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Fig. 3. The value \( d_{\text{max}} \) is plotted against the number of displacements in the sequence for a range of stimulus onset asynchronies. The two subjects data are plotted separately for clarity. In most cases stimulus onset asynchrony was equal to the frame duration, except for stimulus onset asynchronies 40 and 60 msec where frame duration = 10 msec and inter-frame interval = 30 or 50 msec respectively. Note the presence of a blank interval has little effect. All curves are of similar shape (asymptoting in around 5 displacements) and asymptote at similar levels, except for a stimulus onset asynchrony of 20 msec where the curve appears shifted down the ordinate.
The asymptotic value of $d_{\text{max}}$ appears to follow that for single displacements by the approximate relationship:

$$d_{\text{max}} \text{ (asymptote)} = 1.5 \times d_{\text{max}} \text{ (single)};$$

at least for this field size.

Clearly the results follow the pattern of Fig. 2c, and favour either the hypothesis of a “knock-on” facilitation or that of a spatial limit of integration.

Three other possible explanations must be considered. The first is that the enhanced processing might be a consequence of pursuit eye movements, initiated by the early displacements, which reduce the spatial interval on the retina for later displacements. To avoid the possibility of anticipatory eye movements the direction of movement was randomized from trial to trial. In considering the latency of pursuit eye movements we must take into account when the stimulus first actually provides directional information. No such information is available until the onset of the second exposure. Inspection of Fig. 3 shows there are cases when recruitment takes place in under 50 msec from this time, e.g. for two displacement sequences with a stimulus onset asynchrony of 20 or 40 msec. Latency for pursuit eye movements is normally quoted as around 150 msec (see Alpern, 1982), though recent elegant work has shown evidence that monkeys may initiate such tracking movements when presented with random dot kinematograms in as little as 60 msec (Miles & Kawano, 1987). Even so these times, which may not apply to humans, are not short enough to account for the current data.

A second alternative account is in terms of the spatio-temporal spectrum of sampled displays. A uniformly moving display can be regarded as containing spectral energy concentrated along a line through the origin in the spatio-temporal frequency domain. Apparent or sampled motion differs from continuous motion in that an infinite number of replicas of this energy are also present (Pearson, 1975). The higher the sampling rate (i.e. the smaller the intervals in space and time) the greater the spacing of these replicas in the frequency domain. If the replicas are so far apart that they fall outside the “window of visibility”, defined by the spatial and temporal frequency response of the visual system (Watson & Ahumada, 1985), they will not be detected and there will be no perceived difference between continuous and apparent motion (Burr, Ross & Morrone 1986a). However, this analysis assumes that the motion continues indefinitely. If the duration of the sequence is limited this energy is spread out from each replica, and may infringe more upon the fundamental component which is to be detected (Adelson & Bergen, 1985) making it less distinguishable from background noise. The fewer the samples the greater the spreading will be, and therefore greater the infringement. Hence we might expect poorer performance with fewer samples, the pattern of results obtained. However, it is worth noting that changing the sampling rate from 25 Hz (stimulus onset asynchrony = 40 msec) to 10 Hz (stimulus onset asynchrony = 100 msec) produces no change in the curves despite bringing the replicas of the spatio-temporal energy much closer to the region where directional energy is to be detected. If the smearing of energy in the replicas does affect motion detection we should expect it to do so more for low sampling rates. There is no evidence from the data to suggest that this is the case.

A related argument might be that the truncation of the stimulus in time would cause the fundamental component to spread, hence making its orientation in the spatio-temporal frequency domain less specific. Recent theories have emphasized the description of motion as spatio-temporal energy (Adelson & Bergen, 1985) and we might expect that the spreading of this energy would make the motion harder to detect. As the stimulus onset asynchrony is reduced the duration of the stimulus is also reduced, hence the spreading in the frequency domain will be increased, and performance should be impeded. It is clear from Fig. 3 that large changes in stimulus onset asynchrony bring about no changes in performance. For instance, stimuli containing four displacements range in duration from 500 msec (stimulus onset asynchrony = 100 msec) to 200 msec (stimulus onset asynchrony = 40 msec) and yet produce no differences in performance. The apparent vertical shift in the curve for stimulus onset asynchrony = 20 msec may, however, be explained by a similar argument. Here truncation in time may cause the first displacement to be poorly processed. The “knock-on” hypothesis then predicts that the curve will rise in a similar manner as the number of displacements in the sequence increases; the pattern of results found. It is, perhaps, worth noting that the two arguments arising from consideration of the
spatio-temporal frequency spectrum make predictions which would act against one another as stimulus onset asynchrony is changed, and it is therefore possible (though highly improbable) that they could cancel in such a way as to produce the pattern of results found.

Finally, though simple probability summation is ruled out by the data of Nakayama and Silverman (1984), a modified version which is perhaps more physiologically plausible, may be considered. If there is probability summation over a limited time (say 300 msec) this would account for the lack of recruitment found by Nakayama and Silverman when they separated the displacements by more than this interval. There is, however, no single time period that can account for the results of expt 2. When stimulus onset asynchrony was 100 msec recruitment takes place over at least 500 msec, yet when stimulus onset asynchrony was 20 msec recruitment was complete after 100 msec.

EXPERIMENT 3—THE SPECIFICITY OF RECRUITMENT TO INDIVIDUAL ELEMENTS

The temporal recruitment effect described in the earlier experiments may be dependent upon spatial as well as temporal factors. If a dot in exposure 1 is at a position $X - 10$ and at position $X$ in exposure 2, it may be predicted to be at position $X + 10$ in exposure 3. A system looking to detect and/or predict the movements of objects may well be biased to events occurring in this spatio-temporal position. A possible scheme uses a "delay and compare" model similar to that put forward by Reichardt (1961) and Barlow and Levick (1965) except that the single units are now coupled so as to form a chain parallel to the preferred direction. Figure 4 illustrates such a chain. Any element moving along this chain could be expected to excite each subunit in turn. Improved detection could now take place either by the improvement in signal to noise ratio at a unit which summates the signals from subunits in the chain, or by a facilitatory process in which a subunit which has just been stimulated primes the next subunit in the chain where the element is expected. Indeed such a priming phenomenon has been illustrated for single dots undergoing apparent motion (Ramachandran & Anstis, 1983). However, in relatively dense dot patterns like ours (or in the motion of real surfaces), effective recruitment might occur without being specific to the spatio-temporal sequence of an individual element so that movement of one element could aid the perception of movement in another nearby element with no history of movement.

This can be tested with a stimulus in which the pattern as a whole undergoes more than one displacement but any individual element makes only one displacement. Williams and Sekuler (1984) have used such a stimulus. They measured the percentage of coherently moving dots ("signal") embedded in incoherently moving dots ("noise") required for the perception of directional motion. In one condition the signal dots were the same from exposure to exposure whereas in another condition each dot was assigned to signal or noise independently of its previous history. They found no difference between the two conditions. Experiment 3 uses a similar type of display to observe any changes in the value $d_\text{max}$ due to recruitment of motion information.

In this display 50% of dots in exposure 1 had a displaced partner dot in exposure 2. The remaining 50% had no consistent displacement but were repositioned at some random point on the display in exposure 2. This process was then repeated from exposure 2 to exposure 3 under two conditions. In one (termed "same") the dots which had previously been displaced were again displaced. In the other (termed "different") the dots with no history of movement were the ones coherently displaced. Hence in the "different" case no dot in exposure 1 had a partner in exposure 3. The two types of sequence are represented in Fig. 5. In addition a single displacement case was also used consisting of two exposures from the above sequence. As there is no history of movement in this case there is no same/different distinction.

![Preferred direction of motion](image-url)

Fig. 4. An example of how "delay and compare" detectors may be combined into a chain. Recruitment may be due to improved signal to noise ratio at a cell receiving input from each element on the chain, or by a facilitatory signal being passed to each unit in turn along the chain.
Fig. 5. A diagrammatic representation of the stimuli used in expt 3. In the sequence marked "same" the elements labelled a are systematically shifted from exposure to exposure. The other elements are randomly repositioned each time. In the condition "different" the elements a are once again systematically shifted from exposure 1 to exposure 2, the others being randomly repositioned. However, from exposure 2 to exposure 3 it is these elements that have been randomly repositioned (c) that are systematically shifted. The elements that were marked a are randomly repositioned this time. The result being that no element in exposure 1 has a coherently displaced partner in exposure 3.

To obtain psychometric functions five displacements were presented 40 times for each of the three conditions. The resulting 600 trials were presented in random order. All other conditions were the same as experiment 1 (frame duration = 10 msec and inter-frame interval = 30 msec).

RESULTS

The number of errors is plotted as a function of displacement for the 3 conditions in Fig. 6. The result of reducing the percentage of dots coherently displaced from 100 to 50 can be assessed by comparing the displacement at which 29% errors (the point tracked by the staircase procedure) occur with the data for the relevant subject in Fig. 1. For both single and double displacements there is approximately a 25% decrease in $d_{\text{max}}$, hence overall the relationship between the single and double displacements $d_{\text{max}}$ is maintained. The double displacement $d_{\text{max}}$ is about 30% greater than the single (comparing 29% error rates). Note there is no obvious effect due to the history of
movement, the functions for "same" and "different" are very similar. These results show that the findings of Williams and Sekuler (1984), that the history of individual dots does not affect direction discrimination, extend to the determination of $d_{\text{max}}$ and to recruitment effects.

Discussion

It has been proposed that the perception of continuous motion and of motion in random dot kinematogram is subserved by Braddick's (1974) "short-range process". Apparent motion, however, may still be perceived over greater displacements (many degrees) if "simple" stimuli are used (Kolers, 1972). Braddick claims this apparent motion is subserved by a "long-range process" based on the occurrence of identifiable elements in different locations at successive times. Increasing the duration of a random dot kinematogram sequence might increase the possibility of the observer identifying any conspicuous clusters of dots whose direction of motion could be determined by this long range process or by conscious comparisons of position. In the "different" condition of exp 3 any such clusters would be destroyed as no dot in exposure 1 has a displaced partner in exposure 3. However, recruitment occurred equally in this condition. So recruitment does not depend on the "long-range process" responding to such clusters.

Ramachandran and Anstis (1983) have presented demonstrations of visual "inertia" in the perception of moving individual dots. They interpret this phenomena as the visual system taking advantage of Newton's first law of motion, that things normally move in straight lines. If this law is applied to the current paradigm we might expect the "same" condition to be more easily perceived as the dots here do obey the law, while the elements in the "different" condition magically appear and disappear. As, however, performance is equivalent in both conditions we conclude that the short-range motion system does not depend on the predictability of the specific motion path to enhance its ability to detect movement.

GENERAL DISCUSSION

$d_{\text{max}}$ has been shown to increase with increasing number of successive displacements up to 4–6 displacements, an enhancement not specific to individual dot paths in the display, but which applies equally to unrelated dots undergoing the same motion. The recruitment effect does not appear to be limited by the overall duration or velocity of the sequence, but by the number of displacements it contains. The experiments reported here do not distinguish whether this number itself is the limiting factor, or whether the limit reflects a maximum range of spatial interaction. However, in experiments to be reported elsewhere (Snowden & Braddick, 1988, 1989) we find a similar numerical limit determines performance even when individual displacements are much smaller than $d_{\text{max}}$, and therefore the asymptote is reached at a considerably smaller total displacement. The suggested reason for this dependency is that the processing of each displacement determines the enhancement of motion detection in the immediately following displacement—a "knock-on" effect which asymptotes after the cumulative effect of 4–6 displacements.

"Hetero" and "Homo" recruitment

Previous researchers have also found improved performance on motion perception with increasing numbers of displacements (e.g. McKee & Welch, 1985). However, these studies employed stimuli which contained correlations between non-adjacent frames. This means that detectors responding to the relation between frame N and frame N + 2 (or N + 3 etc) could contribute to performance in larger sequences. This improvement implies that the larger steps and delays are more nearly optimal for the detectors that responded to the 2-frame sequence, or that detectors with larger spans and delays, but tuned to similar velocities, are recruited (Van Doorn & Koenderink, 1983). We will call this recruitment "hetero" recruitment, and report fuller evidence for its contribution elsewhere (Snowden & Braddick, 1988, 1989). The temporal and spatial range of such recruitment should be limited by the limits of the short-range process (Braddick, 1974).

For a similar argument to explain the present results the recruited units would need to have spans on the order of twice $d_{\text{max}}$, which seems unlikely since such units should be able to signal a single displacement. It any case, this explanation is untenable, since all such recruitment would be destroyed in the "different" condition of exp 5. Instead we postulate a form of recruitment which we term "homo" recruitment as it involves detectors which have similar spatial and temporal properties. In this form of recruitment information is passed on over a limited time period; if another displacement
occurs within that time period it is subject to the influence of the information passed on from the previous displacement. These two types of recruitment fit with the results of Lappin and Fuqua (1982). They report a dramatic increase in performance with increasing number of displacements in a sequence if the stimulus onset asynchrony is small but a gentler increase if the stimulus onset asynchrony is large. Presumably when stimulus onset asynchrony is small, hetero recruitment is occurring, as well as homo recruitment. When stimulus onset asynchrony is large, so that temporally non-adjacent frames fall beyond the temporal limit of the short-range process, only homo recruitment is possible. In a second experiment Lappin and Fuqua (1982) had only one quadrant of the display coherently moving. This quadrant could be the “same” from displacement to displacement, or could by randomly chosen (therefore has a 1/4 chance of being same in successive displacements). They found little difference between these two conditions and suggest that the facilitation does not require consistency of the specific moving elements.

What type of neural organization would exhibit this type of behaviour? One possible organization is a network in which signals for similar directions are enhanced, whereas those for different directions are mutually inhibited. Hence when a displacement occurs it primes the system to be more sensitive to that direction of motion for a short time. If another displacement occurs within that time it will be influenced by the current state of the network and enhancement will accrue if this displacement is in the same direction as the first displacement. This type of structure resembles that of a co-operative network of the type proposed by Marr and Poggio (1976). Other researchers have recently reported evidence of co-operative type behaviour in the motion system (Chang & Julesz, 1984; Williams et al., 1986).

**Physiological correlates**

Finally it is of interest to look for physiological correlates of the current findings. Single cell recordings from the mid temporal (MT) area of macaque monkey by Mikami, Newsome and Wurtz (1986) suggest such a correlation. They note “... many neurons that were strongly directional in response to smooth motion or to multiple displacements of a stationary stimulus were poorly selective for single displacements of a stationary stimulus...”. It is therefore tempting to consider the present data in terms of the action of such cells. However, this enhanced performance may have resulted from the excitation of units tuned to twice (or even greater multiples) the size of a single displacement, as we have postulated to explain the data of McKee and Welch (1985) and Lappin and Fuqua (1982), i.e. the hetero recruitment, rather than homo recruitment, postulated for the present results. For more convincing proof of homo recruitment occurring in single cells we would need evidence that, even though detectors tuned to a given span are stimulated, performance improves with increasing number of displacements. Although this consideration should be kept in mind it is perhaps not coincidental that the maximum displacement for which a cell shows directional selectivity was found to be, on average, one sixth of the receptive field width, at least for cells with near-foveal receptive fields (Makami et al., 1986). In other words six maximum displacements could be fitted into the cell’s receptive field. While this figure is similar to the one suggested here for the number of displacements over which information is recruited, differences in the type of stimuli (slits and random patterns) and variability in the data from subject to subject, suggest caution in assigning the action of these cells as responsible for temporal recruitment. However, it has been suggested that area MT might well govern psychophysical performance for these large displacements. The finding that the psychophysically determined maximum displacement ($d_{max}$) in humans and the physiologically determined maximum displacement for single cells in MT vary in a similar manner with respect to eccentricity (Baker & Braddick, 1985a, Mikami et al., 1986) and differently from the cortical magnification factor (Rovamo & Virsu, 1979), or the maximum displacement limit for cells of area V1 (Mikami et al., 1986) lends weight to this argument.

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**REFERENCES**


