TEMPORAL AND SPATIAL CHARACTERISTICS OF THE UPPER DISPLACEMENT LIMIT FOR MOTION IN RANDOM DOTS*

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Abstract—The upper displacement limit (D_{max}) or Braddick limit was measured in random dots. We then interposed a variable duration pause at half the distance jumped. Of interest was to see the shortest time (Δt) which would yield a value of two times D_{max}, thus indicating the time required to process one additional Braddick limit. A surprisingly short interval (as short as 10 msec under some conditions) was required. Furthermore for intermediate durations (20 to over 100 msec), the total limit was often more than doubled, indicating a nonlinear potentiation or sequential recruitment between successive displacements. Increasing field size had the following effects: (1) it increased D_{max}, (2) it decreased Δt (the processing time), (3) it increased V_{max} (the maximum velocity), (4) it increased the amount of sequential recruitment.

Random dots   Correspondence problem   Short-range process   Motion

INTRODUCTION

The use of random dots can isolate early motion processing from other visual mechanisms. As such, they are becoming increasingly popular as a psychophysical stimulus. With these dots it is possible to measure a minimum and a maximum displacement that can elicit a reliable sense of motion (Nakayama and Tyler, 1981; Braddick, 1974).

The maximum distance over which an observer can see coherent motion in random dots is often designated as D_{max} or the Braddick limit. In the original paradigm described by Braddick (1974), this upper limit was measured by setting up a central figure filled with random dots alternating with the same slightly displaced set of random dots surrounded by a noise background, which was uncorrelated from alternation-to-alternation. When the displacement of the central figure exceeded a small upper bound (15 arc min in the original experiments), the figure became unrecognizable. This suggested that there is an upper limit beyond which the motion mechanism cannot solve the "correspondence" problem and, as a consequence, displacements above this limit do not permit figural segregation. The results suggested that

experiments using random dots are able to distinguish an early short range motion process from a longer range process more conventionally associated with apparent movement (Wertheimer, 1912). Later investigation has revealed that this short range limit can vary with field size and retinal locus (Baker and Braddick, 1982).

In this context, we deal with a question that naturally arises when thinking of the time it takes to process moving stimuli. How long does it take for the motion system to encode such a displacement?

From an experimental point of view, the Braddick upper displacement limit is the maximum amount of positional shift (D_{max}) that can be seen as moving coherently. This can be measured by asking observers to increase the step size until coherent motion or figural segregation is no longer visible. Figure 1(a) schematizes this limit, indicating the largest step (D_{max}) that can be obtained with a single instantaneous jump. Suppose, however, that one were to interpose a pause, say 5 sec in duration, halfway between the total distance [Fig. 1(b)]. Since this is a long duration in terms of the integration time of the visual system, each individual shift at the beginning and end of such a pause would constitute an independent displacement stimulus. Because there are now two such shifts the total upper displacement limit (UDL) might be expected to increase from one Braddick unit to two.†

Of particular interest in this study were cases where the pause duration is much shorter. What is the minimum pause length necessary to encode an additional D_{max} [see Fig. 1(c)]? In this paper we show that this time interval (Δt) can be surprisingly short.

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†This figure of two times the Braddick limit assumes no probability summation, the absence of which is confirmed by the asymptotic value of the upper limit thresholds for longer duration pauses (see Figs 2, 3 and 6).

METHODS

We employed a random dot pattern similar to that used by Julesz (1971). The stimulus was generated on the face of a CRT (P31 phosphor) using shift register circuitry (see Nakayama and Tyler, 1981 and Nakayama, 1981 for details). Each pixel had a 50% probability of being light or dark, and unless noted was 4′ in size. An important technical feature of the display is the very fast screen refresh rate (400 Hz), especially as our experiments show large variation in thresholds for small changes in duration.

In all experiments horizontal differential motion was imposed, equivalent to a shearing motion where separate horizontal panels of the screen moved to the left while the others moved to the right. Each differentially moving panel moved as a rigid unit. The number and size of the differentially moving panels were varied within and between experiments (see below).

Between trials, the screen was blank. At the onset of a stimulus, the dots appeared and were stationary for 200 msec. Then the stimulus underwent a stepwise shearing motion, usually in two steps with a single variable pause Δt. After another 200 msec interval, the dots disappeared.

Mean luminance of the random dot array was approximately 15 cd/m². Contrast was about 60%.

For nearly all the experiments we found it most effective to use the method of adjustment. To confirm the key observations, however, we also used a forced-choice staircase technique (see Experiment VI).

For the adjustment procedure, the observer's task was to increase the displacement to the point where coherent motion broke down. In practice, the display underwent a rather predictable series of phenomenal changes as the step size was increased. At about 10 times the minimum motion threshold (as measured by Nakayama and Tyler, 1981), a sharp perceptual border was established between the separately moving areas much like that seen in regions of abrupt disparity change in random dot stereograms (Julesz, 1971). As the displacement increased beyond a certain point this border became less distinct, although the differential motion of the upper and lower portion of the screen remained very noticeable. With further increases, the obvious segregation of the upper and lower portion of the screen in terms of oppositely moving coherent areas broke down.

Because this last transition was most easily seen and was the most abruptly changing with increases in displacement, it represented a convenient and reproducible criterion for the method of adjustment procedure. It should be noted that beyond this transition point, some residual directionality could be seen over regions of the pattern such that one still sensed some difference in overall motion between adjacent parts of the screen, but the point where ths directionality disappears was more difficult to set reliably. For this reason the much easier criterion of figural segregation was adopted.

For the forced-choice staircase methods, the screen was divided into just two portions. The lower panel could either shear to the left or the right relative to the upper panel. The observer's task was to identify which direction of shear was presented. Three correct identifications incremented the movement amplitude by 0.125 log units and one incorrect identification decremented it by the same amount. The staircase series continued until 9 reversals occurred and we averaged the stimulus values after the second reversal. The procedure yielded on average, the amplitude where the observer was correct 79.4% of the time. As mentioned earlier, the criterion selected for the method of adjustment was chosen for its abruptness and as a consequence was somewhat lower than the forced-choice threshold obtained under comparable circumstances. Other than this difference, the results of the two methods were very similar (see below).

RESULTS

Experiment I: variable number of pauses

We started this research using a 2 × 2 deg square of random dots where each oppositely moving panel had a height of 13 arc min and pixel size was 1.9 arc min. In this experiment, we had three different conditions: two steps with one pause between them [Fig. 1(b, c)], three steps with two pauses between them [Fig. 1(d)], and essentially continuous motion consisting of 20 steps and 19 pauses [Fig. 1(e)].

The task of the observer was to increase the magnitude of the total displacement until the separately moving panels were no longer visible.
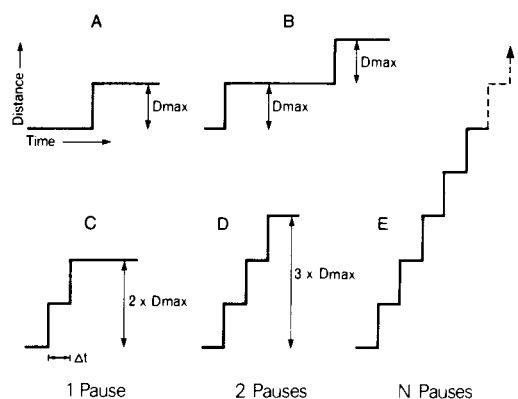

Fig. 1. Schematic representation of spatio-temporal displacements of random dots. Time is displayed along the x-axis and displacement is displayed along the y-axis. (A) For an instantaneous jump there is a maximum distance (D_{max}) over which a given random dot configuration can be seen as moving coherently. (B) If a long pause of time t is interposed at the half-way point of the distance jumped, we expect and also show that the largest distance will span one additional D_{max}. (C) Δt represents the shortest pause which will yield an addition D_{max}, bringing the total distance to $2 \times D_{max}$. (D) Situation where two pauses are expected to yield two addition D_{max}, bringing the total to $3 \times D_{max}$. (E) Representation of nearly continuous motion where there are N pauses.
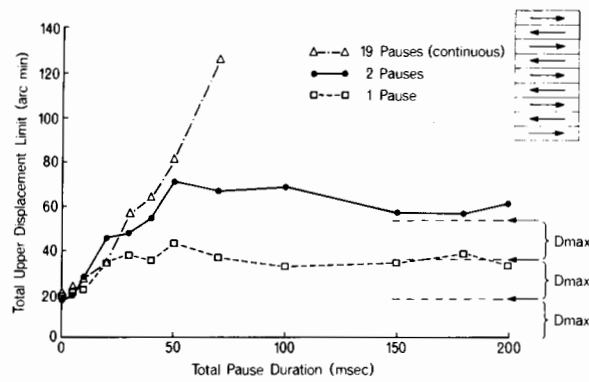
Fig. 2. Total upper displacement limit plotted as a function of total pause duration for three types of spatio-temporal displacements [as illustrated by Fig. 1(c)–(e)]. 1 pause is represented by the open squares, 2 pauses is represented by the solid circles, and essentially continuous motion (19 pauses) is represented by the open triangles. Stimulus is a 2×2 deg square of random dots moving as a series of rigid horizontal panels (see inset which is not to scale) each 13 arc min in height. D_{max} represents the maximum displacement that can be seen for a single isolated instantaneous displacement. Pixel size is 1.9 arc min. Subject is K.N.

Figure 2 shows the data for all three conditions by plotting the total upper limit threshold against total pause duration. Consider the case where there are just two steps with a single pause between the steps (open squares). With increasing pause duration, the upper Braddick thresholds double in a relatively short time (about 30 msec) and remain at this level for pause durations up to 200 msec. For three steps, one more Braddick limit is obtained with the final value being essentially triple at asymptote. A small overshoot at intermediate durations should be noted.

For the case of essentially continuous motion (19 steps), there is no leveling off of the upper displacement, rather there is a steady increase. Thus the upper displacement limit (UDL) falls along a constant velocity line (open triangles), approximating 16 deg/sec. Furthermore, increases in threshold for the one and two pause conditions lie close to this same constant velocity line, at least up to the point where they peel away and remain essentially constant at two and three times the Braddick limit, respectively.

To a first approximation, therefore, each additional pause enables the upper displacement limit to expand to a figure which is equivalent to $(n + 1)$ times the Braddick upper limit, where n equals the number of pauses. Furthermore, the results with many steps is consistent with the view that figural segregation based on velocity information is lost above an upper limiting velocity (V_{max}). In this case V_{max} is about $16°/sec$.

Experiment II: influence of stimulus area

As a further way to characterize the basic phenomenon, we chose 3 different field sizes (1.43 × 1.43 deg, 4.7 × 4.7 deg and 14 × 14 deg) and then measured the influence of pause duration on the UDL. In this and all other experiments to be described, we used only a single pause rather than multiple pauses. We also used only two moving panels rather than nine. The

upermost curve (Fig. 3) shows the influence of pause length for the largest field sizes (14 × 14 deg). The most prominent aspect of this curve is the very rapid rise of the UDL, increasing essentially instantaneously as the pause duration increased above zero msec. It reaches twice the Braddick upper limit value in only 10 msec overshooting this value and slowly falling to an asymptotic value of 2 times the Braddick limit in about 200 msec. For the smaller stimuli, the rise is progressively less rapid and the overshoot is progressively less noticeable.
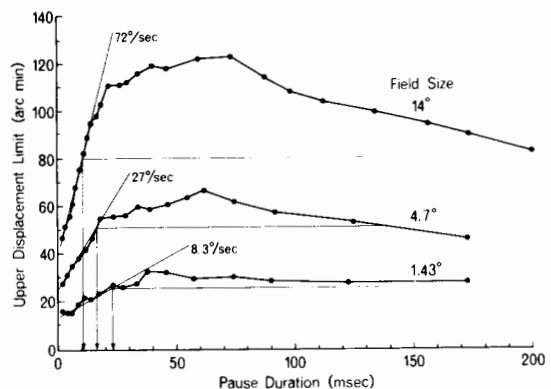

Fig. 3. Influence of field size for variable durations of a single pause. Total upper displacement limit plotted as a function of pause duration. Each curve represents the data taken for a different field size (as labeled). Differential motion consists of two horizontal panels moving rigidly and in opposite directions. Thin horizontal line adjacent to curve represents an amplitude of 2 times the Braddick upper limit. Thin vertical line associated with each function defines the time t where this $2x$ value intersects the function. This provides an estimate of the time required to process an additional Braddick jump (see arrows on the x axis). Note that t decreases for increasing field sizes, dropping from 23 to 11 msec. Diagonal lines labeled 8.3 deg/sec, 27 deg/sec, 72 deg/sec represent an upper velocity limit (V_{max}) for each field size. Note that it also increases with increasing field size. (Subject is K.N.)

Experiment III: influence of differentially moving panel size independent of area

The importance of stimulus area raises a number of questions. Most obvious is the confounding of individual panel size as field size is varied. Perhaps it is the size of these separately moving panels which dictates the results rather than the total field size itself. We addressed this question by keeping field size constant and varying the size of the panels.

For K.N. we used the stimulus size of 14 × 14 deg, for J.S. it was 4.7 × 4.7 deg. Figure 4 shows the influence of individual panel size. Note the extreme dependence of the results on panel size. Increasing panel size while keeping stimulus field size constant has essentially the same effect as increasing panel size by increasing field size.

Discussion: Experiments II and III

The foregoing results confirm and extend previous findings on upper displacement thresholds in random dots. First they show that the upper limit increases with panel size (Baker and Braddick, 1982). Second and most important, they show that the encoding of movement can be very rapid, also showing a dependence on the size of moving panels. To interpret these results in terms of the known properties of the visual system, we should consider what elements in the visual system may be responsible for the large differences in the results for the different panel sizes. To start let us assume that the motion detecting system is fed by receptive field units sensitive to either

blobs or lines of various sizes (Wilson and Bergen, 1979). Furthermore assume that the maximum distance over which such a unit can be directionally selective will depend on the size of this receptive field, with larger receptive fields having the ability to encode larger displacements. When the size of the oppositely moving panels is very small, then motion detecting units fed by large receptive fields will not generate directionally selective signals as each oppositely moving panel will tend to cancel adjacent panels within a receptive field. Only directionally selective units having small receptive fields will carry the motion signal for small panels but these units can only provide accurate direction of motion signals over a very short distance. Thus D_{max} will fall with decreasing panel size.

Experiment IV: spatial frequency content of the noise pattern

To explore this idea in somewhat greater detail, we kept panel size constant and varied the spatial frequency content of the noise pattern. To generate high pass noise we replaced the set of randomly light or dark pixels by an overlapping set of two-pixel dipoles, randomly polarized such that the right cell could be either light or dark and the left cell would be the opposite polarity. Because the two celled dipole was defined for each cell position in the display, the screen had three intensity levels. The three levels correspond to the summation of no bright components, one bright and one dark component, and two bright components. This pattern is high pass filtered in an orientation along the direction of motion. We also had a condition where we tripled the visual angle of the pixels to 12 arc min, thereby shifting the spectra for pixel limited noise to much lower spatial frequecies. The results are shown in Fig. 5.
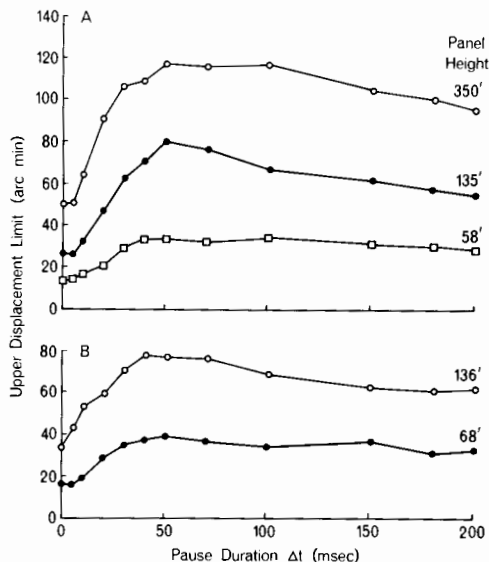

Fig. 4. Influence of moving panel size with a constant field size. Total upper displacement limit plotted as a function of pause duration for a constant field size. Each curve represents a different spatial frequency of shearing motion, also corresponding to a particular horizontal panel width. (A) Curves for subject K.N. Field size is 14 × 14 deg, pixel size is 6 arc min. (B) Curves for subject J.S. Field size is smaller, 4.7 × 4.7 deg. Pixel size is 6 arc min.
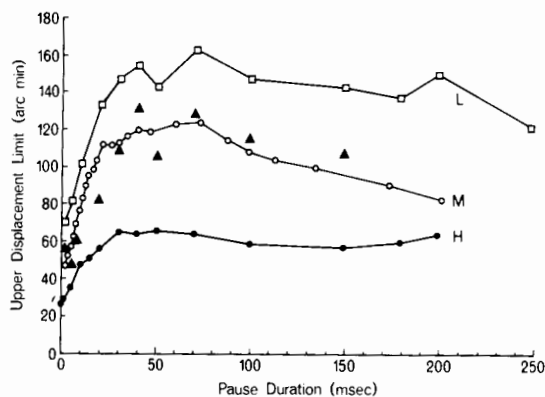

Fig. 5. Importance of spatial frequency content of the noise. Total upper displacement limit plotted as a function of pause duration for stimuli having different spectral composition. The two upper curves were obtained with different pixel size, 4′ labeled M for medium spatial frequency and 12′ labeled L for low spatial frequency. The lowest curve was obtained using high-pass dipole noise labeled H (see text), where pixels subtended 4′. All three curves are obtained with 14 × 14 deg field. Filled triangles represent data taken with 4′ pixel size but with 6.5 × 6.5 of the central field occluded.

Note that there is a progressive change as the spatial spectra are shifted from high, to medium, to low spatial frequency content. D_{max} increases with lower spatial frequencies, V_{max} increases, as well as the magnitude of the overshoot.

These results confirm our general hypothesis, namely, that it is the larger receptive fields that mediate the largest values of D_{max}. They also confirm Chang and Julesz (1983) who measured D_{max} using spatially filtered random dot patterns.

Experiment V: importance of peripheral retina

It is well known that receptive fields increase in size with increasing retinal eccentricity (Hubel and Wiesel, 1974). Thus a simple increase in moving panel size could have several effects. It increases the stimulation of larger receptive fields in any given region of retina but it also enables the larger peripherally placed receptive fields to participate. To examine these alternatives, we compared an annular stimulus that had 6.5×6.5 central square occluder with full field stimulaton described earlier. Despite the fact that the central 6.5 deg of the retina was unstimulated, the results were essentially the same as for the full field stimulus. The peripheral stimulation alone showed the same very high upper displacement limit as did the full field (see solid triangles in Fig. 5). In this regard, the present experiments are consistent with the recent paper by Baker and Braddick (1982) who concluded that an increased D_{max} for larger field size is mainly the result of an increasing stimulation of the peripheral retina.

Experiment VI: forced choice experiments

We confirmed the major findings of this paper using a forced-choice staircase procedure (see method section) in both subjects. In these experiments, the observer was required to determine whether the lower panel moved to the right or left. Figure 6 shows the results for K.N. using the same stimulus conditions used to obtain the top curve in Fig. 3. A very rapid increase in the upper limit is clear. Δt, for example,
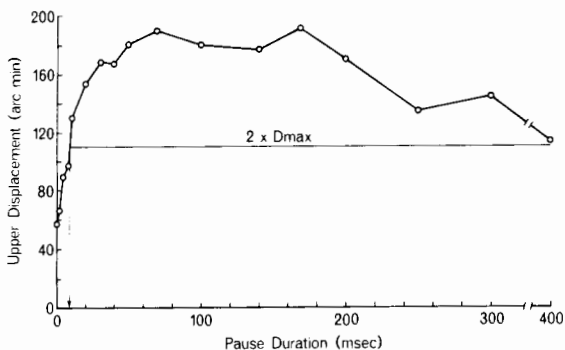

Fig. 6. Upper displacement limit as a function of pause duration using a forced-choice paradigm rather than the method of adjustment. Same stimulus conditions as those obtained for upper curve in Fig. 3. (Subject is K.N.)

is less than 10 msec, replicating the same result found using the method of adjustment (see top curve in Fig. 3). The overshoot is very pronounced, and settles to a value of twice the Braddick upper limit only at very long durations. The findings using forced choice methods confirm the basic observations of this paper, namely, that very short durations are needed to process an additional coherence displacement as well as demonstrating the existence of nonlinear potentiation (sequential recruitment).

DISCUSSION

The very small duration needed for the pause to bring the total upper displacement limit (UDL) to twice its normal value is one of the key observations of this paper. Depending on field size, this duration can vary between 10 and 40 msec. This indicates that the mechanisms mediating directional sensitivity can be very fast, especially for systems having large receptive fields.

This is somewhat surprising, considering the fact that the earliest hint of directional sensitivity occurs at the level of the visual cortex in the primate (Hubel and Wiesel, 1968) and that the earliest cortical evoked response in humans does not occur much before 80 msec (Spekreijse et al., 1973). Our present results suggest that the cortex can process directionally selective information within 10 msec of the receipt of afferent information, this despite a much larger conduction delay. It would seem that such rapid processing would require the precise synchronization of arriving signals in neighboring portions of the visual field. This needed property may be related to the existence of a fast conducting pathway now emerging from electrophysiological and anatomical studies of the primate geniculostriate system (Dow, 1974; Maunsell and van Essen, 1983). Very fast processing should also be contrasted with previous measurements of motion processing which indicate that it can be very slow. Tyler and Torres (1972), for example, found that motion sensitivity is distinctly low-pass, beginning to roll off above 1 Hz (Tyler and Torres, 1972). This is corroborated by similar experiments with random dots where one can be more certain that motion thresholds are not contaminated by positional sensitivity (Nakayama and Tyler, 1981). Furthermore independent evidence for very slow aspects of motion processing can be seen in present experiments, where it takes from 100 to 300 msec for the overshoot to fall to its resting value (see Figs 3–7).

The existence of both fast and slow temporal processes suggests several possibilities. Either it reflects the existence of more than one motion processing system, one fast and one slow; or it suggests different serial stages in a single motion system with different temporal properties. We favor the second view and propose a fast early stage which performs the task of sequence discrimination followed by a slower stage consisting of a neural integrator having
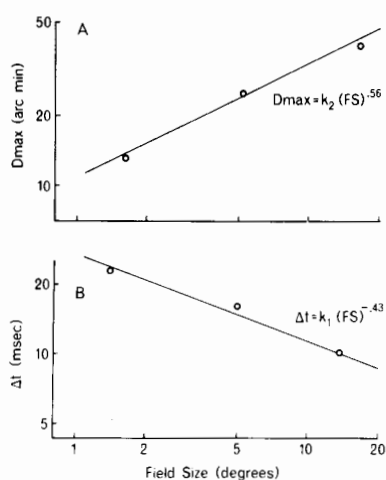
Fig. 7. (A) Relationship between D_{max} and field size (FS) as determined from data in Fig. 3. D_{max} increases less than proportionately with linear FS, having an exponent of 0.56. (B) Decrease of Δt with increasing field size has an exponent of approximately -0.43. Note that the fields are square and that FS represents the length of the sides, also note the double logarithmic coordinate axis. (Subject is K.N.)

a relatively long time constant. This latter view is consistent with previous models of motion sensitivity (Reichardt, 1961; Foster, 1971).

Sequential recruitment and its functional implications

For the larger field sizes, there is an obvious enhancement of motion processing in the range between 20 and 100 msec. With single pauses of this length, the visual system is able to encode a displacement that is much more than one additional D_{max}. Because the overshoot eventually falls to the lower asymptotic value at 2 times the Braddick limit, we interpret the overshoot in terms of physiological interaction, not probability summation. We suggest that it represents a nonlinear potentiation in the motion system, noting that two successive and relatively contiguous displacements provide more information about a moving stimulus, than two independent observations. McKee (1982) has coined the phrase "sequential recruitment" to explain similar findings obtained with velocity discriminations for successive displacements and it should be noted that sequential recruitment is also evident in the data of a number of previous workers (Sperling, 1976; Ramachandra and Anstis, 1982; Lappin and Fuqua, 1982). Because the result appears in such a wide range of experimental paradigms, we think that it reflects a fundamental property of the motion system, one that has not received wide enough attention, especially as it may provide an important distinction between binocular stereopsis and motion processing, systems that are often considered to have important similarities.

Each system must solve the "correspondence" problem (see Marr, 1982). The existence of nonlinear

recruitment in motion processing, however, indicates that the motion system may provide its own unique solution distinct from that developed for stereopsis. With smooth image motion, the motion system has the equivalent of many successive "looks" at the moving image, whereas the binocular system has just two views. Thus the motion system may make the correlation less on the basis of sophisticated spatial pattern matching of just two images (Nelson, 1975; Marr and Poggio, 1980) and more on cruder spatial correlations between many more successive images. The very fast time in which the motion process can make this early directionally selective decision is convenient as it enables information from a set of image pairs to be combined with other successive sets of image pairs during a short several hundred millisecond interval.

The results also tally with some important neurophysiological differences between motion and stereo systems in terms of receptive field types. Many classes of motion sensitive neurons are relatively unselective as to their shape requirements (Grusser and Grusser-Cornehls, 1973), whereas neurons thought to underly stereo discrimination are always tuned to orientation and this holds for species as different as cat, monkey and owl (Barlow et al.. 1967; Pettigrew and Konishi, 1976; Poggio and Fischer, 1977). Thus stereopsis, which has only two looks at a scene, has the requisite degree of spatial pattern matching machinery in the form of orientation and spatial frequency tuning. Motion which has the advantage of many views may not require such elaborate spatial matching.

Relationship of D_{max}, Δt, and V_{max}

We should also note a potentially interesting relationship between the Braddick upper limit, the processing time and the maximum velocity, each varying as field size or panel size is increased. Because we have the most detailed data in the case of increasing field size (Experiment II as shown in Fig. 3), we will summarize the relationship between these parameters graphically (see Fig. 7). For a given panel size, one can measure a D_{max}. Then given a D_{max}, one can measure the amount of pause required to obtain a second D_{max}, defining this as the processing time (Δt). From these two variables, one can define a V_{max}, where $V_{max} = D_{max}/\Delta t$. In addition, V_{max} can be easily measured from the slope of the line fitted to the curves in Fig. 3. How these various values change with increasing field size are of interest. D_{max} does not vary proportionally with linear field size, (FS), rather it falls roughly on a curve having a function of $D_{max} = k_2 (FS)^{0.56}$. Δt does not vary inversely with FS but decreases according to the relation $\Delta t = k_1(FS)^{-0.43}$. Together, however they jointly determine V_{max} and because $0.56 - (-0.43) \cong 1$, V_{max} rises linearly with field size

$$V_{max} = (k_1/k_2)(FS)^{0.56}(FS)^{-0.43} \cong (k_1/k_2)(FS).$$

We note this relationship because it is perhaps more

than fortuitously similar to a differently derived experimental finding between distance, time, and velocity obtained by van Doorn and Koenderink (1982). They found that by varying panel size and temporal frequency of random dot stimuli, the relationship of velocity with space and time was approximated by a power function having similar exponents of 0.6 and -0.4 respectively. The implication of both of these findings is that the coding of higher velocities, most probably by more peripherally placed receptive fields, is handled by two complementary approaches: increasing the receptive field size and decreasing the processing time.

Relation of D_{max} to D_{min}

At this point it is timely to discuss the relationship between D_{max} and D_{min} as well as other spatial parameters of motion sensitivity. Braddick (1974) has argued that the value of D_{max} obtained using random dots measures the properties of an early short range motion process in isolation from a long range more cognitive process (see also Anstis, 1982). Nakayama and Tyler (1981) argue that by measuring D_{min}, the minimum displacement to see motion in random dots, an early motion system can be isolated from static hyperacuity.

Are these measures unrelated or do they reflect some common property of early motion processing? Although no conclusive proof can be given, it is attractive to think of D_{min} and D_{max} in terms of directionally selective subunits suggested in neurophysiological models (Barlow and Levick, 1964) as well as mathematical models (Reichardt, 1961). We suggest that D_{min} and D_{max} represent the smallest and the largest displacement that can be faithfully encoded from the available classes of sequence detecting subunits. Because different size subunits are likely to co-exist at the same retinal locus, however, the span of distance between D_{min} and D_{max} cannot reflect the property of a single subunit type but merely the smallest encodable displacement from the smaller subunits and the largest encodable displacement from the larger subunits, respectively.

REFERENCES

Anstis S. M. (1980) The perception of apparent movement. *Phil. Trans. R. Soc. Lond. B* **290**, 153–168.
Baker C. L. and Braddick O. J. (1982) The basis of area and dot number effects in random dot motion perception. *Vision Res.* **22**, 1253–1260.
Barlow H. B. and Levick W. L. (1964) The mechanism of directionally selective units in rabbit's retina. *J. Physiol.* **178**, 477–504.
Barlow H. B., Blakemore C. B. and Pettigrew J. D. (1967) The neural mechanism of depth discrimination. *J. Physiol.* **193**, 327–342.
Braddick O. J. (1974) A short-range process in apparent motion. *Vision Res.* **14**, 519–527.
Chang J. J. and Julesz B. (1983) Displacement limits for spatial frequency filtered random-dot cinematograms in apparent motion. *Vision Res.* **23**, 1379–1385.
Dow B. M. (1974) Functional classes of cells and their laminor distribution in monkey visual cortex. *J. Neurophysiol.* **37**, 927–946.
Foster D. H. (1971) The response of the human visual system to moving spatially-periodic patterns: further analysis. *Vision Res.* **11**, 57–81.
Grusser O.-J. and Grusser-Cornehls U. (1973) Neuronal mechanisms of visual movement perception and some psychophysical and behavioral correlations. In *Handbook of Sensory Physiology*, Vol. VII/3A, *Central Processing of Visual Information* (Edited by Jung R. A.), Chap. 6. Springer, Berlin.
Hubel D. H. and Wiesel T. N. (1974) Uniformity of monkey striate cortex: a parallel relationship between field size, scatter and magnification factor. *J. comp. Neurol.* **158**, 295–306.
Julesz B. (1971) *Foundations of Cyclopean Perception.* Univ. of Chicago Press.
Lappin J. and Fuqua M. (1982) Non-linear recruitment in the visual detection of moving patterns. *Invest. Ophthal. visual Sci., Suppl.* **22**, 123.
MacLeod D. I. A., Nakayama K., Silverman G. H. and Mulligan J. B. (1983) Anisotropic spatial integration in the detection of movement. *Invest. Ophthal. visual Sci., Suppl.* **23**, 277.
Marr D. and Poggio T. (1974) A computational theory of human stereo vision. *Proc. R. Soc. Lond.* **200**, 301–328.
Maunsell J. H. and Essen D. C. van (1983) Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed, and orientation. *J. Neurophysiol.* **49**, 1127–1147.
McKee S. P. (1982) The coding of velocity in central and peripheral visual fields. *Perception* **11**, A5 (Abstract from *5th ECVP Meeting*).
Nakayama K. (1981) Differential motion hyperacuity under conditions of common image motion. *Vison Res.* **21**, 1475–1482.
Nakayama K. (1982) Fast processing in the perception of motion in random dots. *Invest. Ophthal. visual Sci., Suppl.* **22**, 144.
Nakayama K. and Tyler C. W. (1981) Psychophysical isolation of movement sensitivity by removal of familiar position cues. *Vision Res.* **21**, 427–433.
Nelson J. I. (1975) Globality and stereoscopic fusion in binocular vision. *J. theoret. Biol.* **49**, 1–88.
Pettigrew J. D. and Konishi M. (1976) Neuron selective for orientation and binocular disparity in the visual wulst of the barn owl (*Tyto alba*). *Science* **193**, 675–678.
Poggio G. F. and Fischer B. (1977) Binocular interaction and depth sensitivity in striate and prestriate cortex of behaving rhesus monkey. *J. Neurophysiol.* **40**, 1392–1405.
Ramachandran V. and Anstis S. (1983) Extrapolation of motion path in human visual perception. *Vision Res.* **23**, 83–86.
Reichardt W. (1961) Autocorrelation: a principle for the evaluation of sensory information by the central nervous system. In *Sensory Communication* (Edited by Rosenblith W. A.), pp. 303–317. MIT Press, Cambridge, MA.
Spekreijse H., van der Tweel L. H. and Zuidema T. H. (1973) Contract evoked responses in man. *Vision Res.* **13**, 1577–1601.
Sperling G. Movement perception on computer-driven visual displays. *Behav. Res. Meth. Instrum.* **8**, 144–151.
Tyler C. W. and Torres J. T. (1972) Frequency response characteristics for sinusoidal movement in the fovea and periphery. *Percept. Psychophys.* **12**, 232–236.
Van Doorn A. J. and Koenderink J. J. (1982) Spatial properties of the visual detectability of moving spatial white noise. *Expl Brain Res.* **45**, 189–195.
Wertheimer M. (1912) Experimentelle Studien uber das Sehen von Bewegungen. *Z. Psychol.* **61**, 161–265.
Wilson H. R. and Bergen J. R. (1979) A four mechanism model for threshold spatial vision. *Vision Res.* **19**, 19–32.