Pergamon

PII: S0042-6989(97)00084-9

Vision Res., Vol. 37, No. 19, pp. 2725–2736, 1997

Printed in Great Britain
0042-6989/97 $17.00 + 0.00

Motion Interference: Perturbing Perceived Direction

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Received 3 November 1995; in revised form 2 January 1997

The minimum stimulus necessary to define motion is a change in position from one location to another in time, but past studies have provided evidence that the human motion system integrates motion over more than two positions. In this study we demonstrate strong sequential interactions affecting perceived direction in apparent-motion sequences; a perturbing dot can bias the perceived direction of motion between two test dots to which it is relatively close in space (up to 100 min arc) and time (up to 300 msec). These sequential interactions suggest a motion mechanism sensitive to the spatial characteristics of motion trajectories; the interactions are greatest for evenly spaced targets positioned along a single axis. The implications for motion-detection models and models based on attention as a mechanism to create apparent motion are discussed. © 1997 Elsevier Science Ltd

Apparent motion Direction Recruitment Psychophysics

INTRODUCTION

At some level of processing, the motion system appears to integrate multiple samples from an apparent motion sequence (Lappin & Bell, 1976; Nakayama & Silverman, 1984; McKee & Welch, 1985; Welch *et al.*, 1985; Anstis & Ramachandran, 1987; Casco & Morgan, 1987; Bowne *et al.*, 1989; Snowden & Braddick, 1989a,b, 1991; Zanker, 1992; Watamaniuk *et al.*, 1995). The successive presentation of two dots at nearby locations is logically sufficient for determining direction and apparent speed, but speed discrimination in apparent motion is greatly improved when more than two targets are included in the sequence (McKee & Welch, 1985; Snowden & Braddick, 1991). Speed discrimination for a test pair of dots can be drastically disrupted by embedding them in a longer motion sequence involving different velocities (Bowne *et al.*, 1989). The upper displacement limit for random dots (d_{max}) increases when the dots are displaced by two or more hops, rather than by just one hop (Nakayama & Silverman, 1984; Snowden & Braddick, 1989b).

This integration of multiple samples could arise from spatial summation of contrast or luminance within the receptive fields of large motion units. That is, longer sequences could be detected by cells with large receptive fields that simply sum the contrast or luminance energy of the long sequence. Cells with smaller receptive fields could not do this because the sequence would be too long to fit within their receptive fields. Alternatively, a network of interconnected units which sum signals along a motion trajectory might account for the observed integration. Bowne *et al.* (1989) suggest that motion detectors are small even when an apparent motion sequence is long, implying that there must be integration across small units to account for the improved performance with longer sequences. This postulated integration process across small motion detectors has been called sequential recruitment, temporal recruitment, visual inertia or grouping via a directionally selective process.

If the sequential recruitment hypothesis is correct for motion in general and not just for speed discrimination, then perceived direction in an apparent-motion sequence should also be modifiable by context. This idea is well supported in the literature from different kinds of experiments. The sequential effects mentioned thus far are examples of what has been called motion capture or motion assimilation (Ramachandran & Inada, 1985; Zhang *et al.*, 1993). These effects are distinct from motion induction or motion contrast (Duncker, 1938; Gogel & Sharkey, 1989; Zhang *et al.*, 1993), where the perceived motion is in the opposite direction to nearby motion. Zhang *et al.* (1993) base their discussion of both motion contrast and motion assimilation on low-level motion mechanisms. They argue that motion assimilation occurs when nearby objects are integrated together and motion contrast occurs when nearby objects are segregated from each other. When moving targets are segregated, i.e., interpreted as separate objects, the

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relative motion between them is generally preserved (Mack *et al.*, 1975), but their motion relative to the observer may be perceived incorrectly. In comparison, with motion assimilation, including the effects discussed in this paper, the object-relative motion (Duncker, 1938) is perceived incorrectly.

An alternative explanation for many misperceived motion effects invokes attention (Stelmach & Herdman, 1991; Hikosaka *et al.*, 1993a,b; Stelmach *et al.*, 1994), which is similar to the "Law of Prior Entry" of introspectionist psychology (Boring, 1950). According to this explanation, when an observer's attention is drawn by flashing a target or is voluntarily placed at a location, subsequent targets near the attended location are posited to be processed more quickly than farther targets. Because of the faster processing, the target nearest the attended location is interpreted as occurring earlier than farther targets, resulting in an apparent asynchrony between simultaneous stimuli. This means that in a three-frame apparent motion sequence, attention would be drawn to the target in the first frame and the perceived times of occurrence of the two later targets would be modified according to their relative spatial distances to the first target; the target closest to the attended location would then appear to occur sooner than the farther target.

In this study, we demonstrate strong sequential interactions affecting perceived direction in apparent-motion sequences; a perturbing dot can bias the perceived direction of motion between a test pair of dots to which it is relatively close in space and time. The spatial and temporal arrangements of the test dots and perturbing dots that give rise to changes in perceived test-dot direction suggest what characteristics the underlying mechanism(s) have. We argue that our results provide good evidence for a directionally selective network of small motion sensitive units and not for the effects of attention.

METHODS

The basic target configuration was an apparent motion stimulus: a pair of test dots separated by some horizontal distance, Δx, and some temporal asynchrony, Δt. A third, perturbing dot was located to one side of the test dots, either to the right or to the left. The observers were asked to judge which way the test dots appeared to move while ignoring the third, perturbing dot. The two test dots were always centered on the screen so the observers could tell which were the test dots, a discrimination aided in some experiments by fixed landmark dots vertically separated from the center of the test pair. The perturbing dot position and timing were varied between blocks of trials. The perturbing dot timing was measured from the temporal center of the test stimulus onset asynchrony (SOA); thus, when we refer to a perturbing dot occurring 100 msec before two test dots with a SOA of 20 msec, this means it was presented 90 msec before the first test dot and 110 msec before the second test dot. The perturbing dot was never presented between the test dots in time.

Data were collected in two different laboratories on similar equipment. The dots were displayed on Hewlett-Packard 1332A oscilloscopes equipped with a P4 phosphor. Dot display duration was 1 msec and dot diameter was 0.5 mm. The dot luminance was measured with a Pritchard Spectrophotometer in a completely dark room and calculated from the photometer's aperture area and the dot area. The luminance of the dot in the McKee lab was 1.73×10^{-3} cd; background luminance of the screen was 20 cd/m^2 in a dimly lit room. The viewing distance was 228 cm. The luminance of the dot in the MacLeod lab was 1.03×10^{-3} cd; background luminance of the screen was 27 cd/m^2. The viewing distance was 150 cm. Several control experiments were conducted with the dot and background luminances as much as one log unit different and similar effects were found; these effects do not depend critically on luminance. The observers were the three authors and three naïve observers, all of whose acuity, with correction if needed, was 20/20 for the viewing distances used in this study. Experiments were undertaken with the understanding and written consent of each observer.

Two different methods were used to measure the effect of the perturbing dot on the observers' perception of the test dots' timing characteristics. First, we used the method of single stimuli with a binary response on each trial. Observers were shown the test dots with the test asynchrony randomly chosen from a narrow range of asynchronies (e.g., −100, −50, 0, +50, +100 msec SOA), including left dot presented first (−100, −50 msec SOA), right dot first (+50, +100 msec SOA) and simultaneous presentation (0 msec SOA) of the test dots. The perturbing dot appeared randomly to the right or to the left of the test dots and the observers were asked to judge after each stimulus presentation in which direction the test dots moved by pressing one of two buttons. No feedback was given. The proportion of "leftward" responses as a function of test SOA formed a psychometric function which was fit by probit analysis with a cumulative normal curve to determine the test SOA that corresponded with the 50% point of the function, the point of subjective equality (PSE). The data plotted are the differences between the PSEs or means for the perturbing dot presented on the left vs on the right. Each data point represents at least 600 trials. Probit analysis also provided an estimate of the standard error of the mean (SEM) and the error bars indicate ±1 SEM. The SEM was calculated as the combination between two independent measures of variance (for the two perturbing dot positions):

$$\text{combined SEM} = \sqrt{(\text{SEM}_{\text{left}})^2 + (\text{SEM}_{\text{right}})^2}.$$

Our decision to present 0 msec test SOA on 20% of trials turned out to be unfortunate. Observers could sometimes tell when the test dots were simultaneous, even in conditions when the perturbing dot had a large effect. Ulrich (1987) has shown that observers may correctly discriminate asynchronous targets from simultaneous targets without being able to tell which asynchronous target came on first. With the displays used in this study, it was sometimes possible to discriminate simultaneous test targets from asynchronous targets but when a small test SOA was introduced, the test dots appeared to have the motion implied by the perturbing dot's motion, independent of which test dot came on first. Because the 0 msec test SOA was included in the method of single stimuli, this paradigm tended to underestimate the effect of the perturbing dot. As a result, we later used the method of adjustment to get a better measure of the motion interference. The motion interference measured with the binary task tended to be smaller in magnitude than with the method of adjustment, though they are in good qualitative agreement.

In our method of adjustment paradigm, observers were shown test dots with an asynchrony chosen randomly from the range −100 msec, +100 msec, and the location of the perturbing dot (to the right or left of the test dots) was varied from trial to trial. One stimulus was presented repeatedly, while observers adjusted the test SOA until the test dots appeared to be moving neither rightward nor leftward. The observers adjusted the asynchrony between the test dots with a trackball or by pressing one of two buttons and then pressed another button to record the asynchrony setting. The settings (10–25) for each perturbing dot position (right and left) were averaged and the SEM calculated. The differences between the settings for right and left positions are depicted on the graphs, with error bars showing the combination of the SEMs:

$$\text{combined SEM} = \surd(\text{SEM}_{\text{left}})^2 + (\text{SEM}_{\text{right}})^2.$$

One potential problem with the motion nulling technique is that, in general, the strength of perceived motion in apparent motion sequences depends non-monotonically on the temporal asynchrony between frames, with weak or no motion being perceived at very short SOAs and at long SOAs. In our experiments, strong motion was seen with perturbing dot SOAs between 15 and 100–200 msec, though some motion was also seen for 400 msec. Because the test SOA was generally 100 msec or less, the motion between the test dots in isolation was weak only for very short test SOAs (less than 5 msec). This means that a long perturbing dot SOA (e.g. 400 msec) could be nulled with a short test SOA (e.g. 5 msec). In other words, weak motion interference due to long perturbing dot SOAs was nulled with very short test SOAs. This way, the magnitude of the interference effect was positively correlated with the nulling test SOA.

For Experiment 4, both exponential and cosine functions were fit to the data. The best-fitting exponential function was found using a least-squares fit. The best-fitting cosine function was found using the same procedure with the restriction that the motion interference magnitude be zero for an angle of 90 deg. This angle corresponds with the perturbing dot being located directly above and between the test dots, and none of the possible hypotheses would predict a change in apparent test asynchrony in that configuration.

RESULTS

Experiment 1: perturbing dot asynchrony

The basic phenomenon in these experiments is that the introduction of a third dot into a two dot apparent motion sequence can drastically alter the perceived direction of motion between the two dots. The inset at the top of Fig. 1 shows an example stimulus arrangement. The dots labeled "T" are the two test dots and the dot labeled "P" is the perturbing dot. The perturbing dot could appear to the right of the test dots, as shown, or to the left. If the test dot on the right were shown, say, 15 msec before the left test dot, observers would see motion to the left. If the perturbing dot were displayed 60 msec after the same test pair (i.e. 15 msec SOA), the direction of motion between the test dots appears to reverse and observers see motion to the *right*. (The perturbing dot timing was measured from the temporal center of the test dots so in the example, the perturbing dot was displayed 52.5 msec after the second test dot, i.e. 60−(15/2) msec). This is the motion-interference effect we set out to investigate.

In the first experiment the temporal asynchrony between the test dots and the perturbing dot was varied systematically. The three dots were equally spaced (9 min arc for MDA and LW, 6 min arc for SPM). Within a block of trials, the time between test and perturbing dot presentations was held constant. Observers judged whether the test dots appeared to move to the right or to the left, while trying to ignore the perturbing dot in a binary judgment paradigm. Observer MDA was naïve as to the purpose of the experiment. The test dot SOA at which the dots appeared to have no net motion corresponds to the 50% response point on the psychometric functions. This point of subjective equality (PSE) or mean shift was determined for locating the perturbing dot on the right and on the left of the test dots. The two perturbing dot locations result in perceived test-dot motion in opposite directions. The data plotted in Fig. 1 show the differences between the PSEs for the perturbing dot on the right vs that on the left as a function of the time between presentation of test dots and perturbing dot. Negative perturbing dot SOAs indicate displays where the perturbing dot was shown before the test dots and positive SOAs indicate where the perturbing dot was shown after the test dots. The binary judgment data were confirmed using the method of adjustment (not shown). Motion interference is greatest for perturbing dot asynchronies between 30 and 100 msec and is seen for perturbing dot asynchronies up to 200 msec or more.

Experiment 2: perturbing dot relative spacing

In this experiment, the relative position of the perturbing dot was varied while keeping the spacing between the test-dots constant as a way to determine if the motion interference depends on the spatial proximity of the perturbing dot to the test dots. The perturbing dot

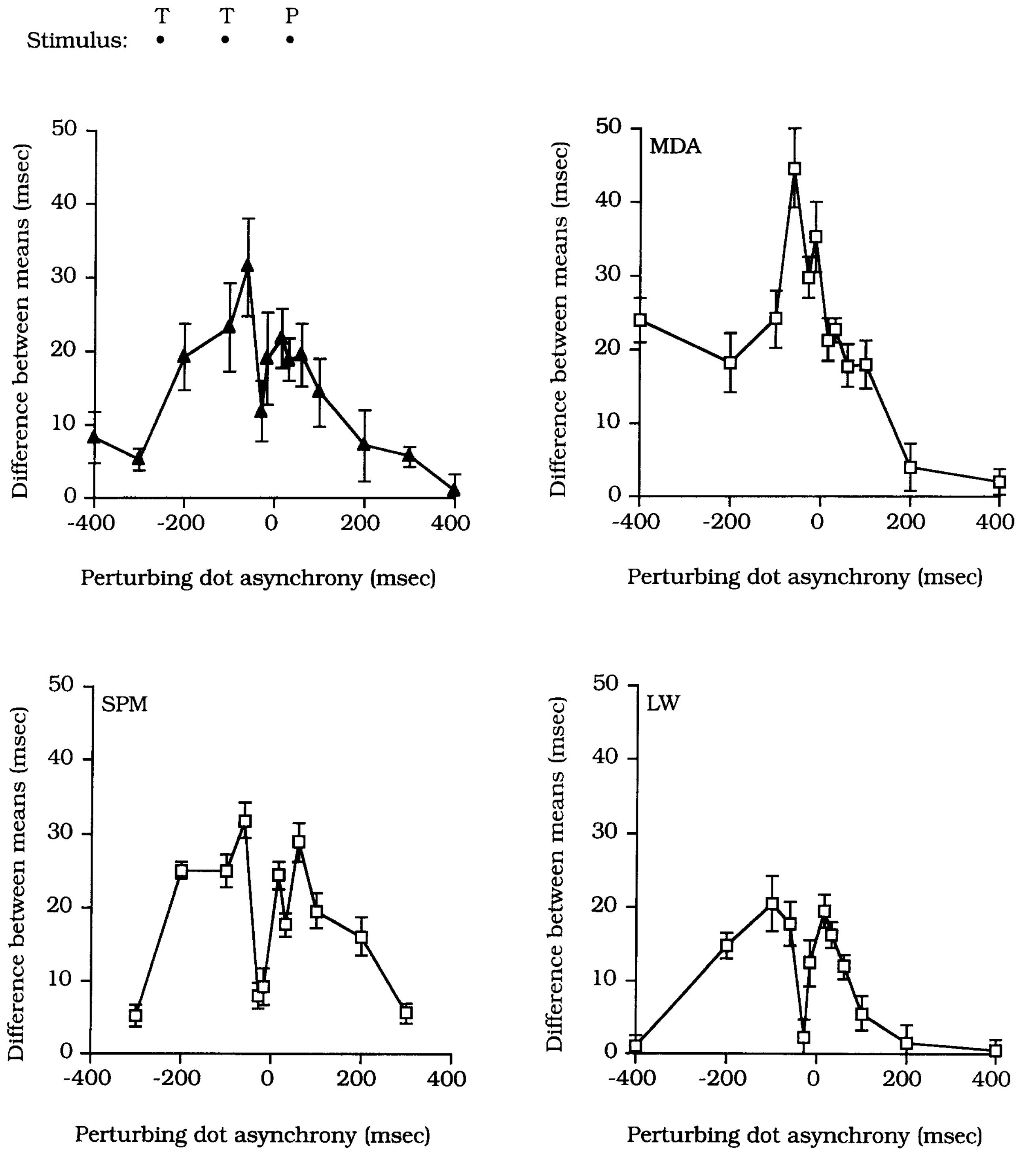
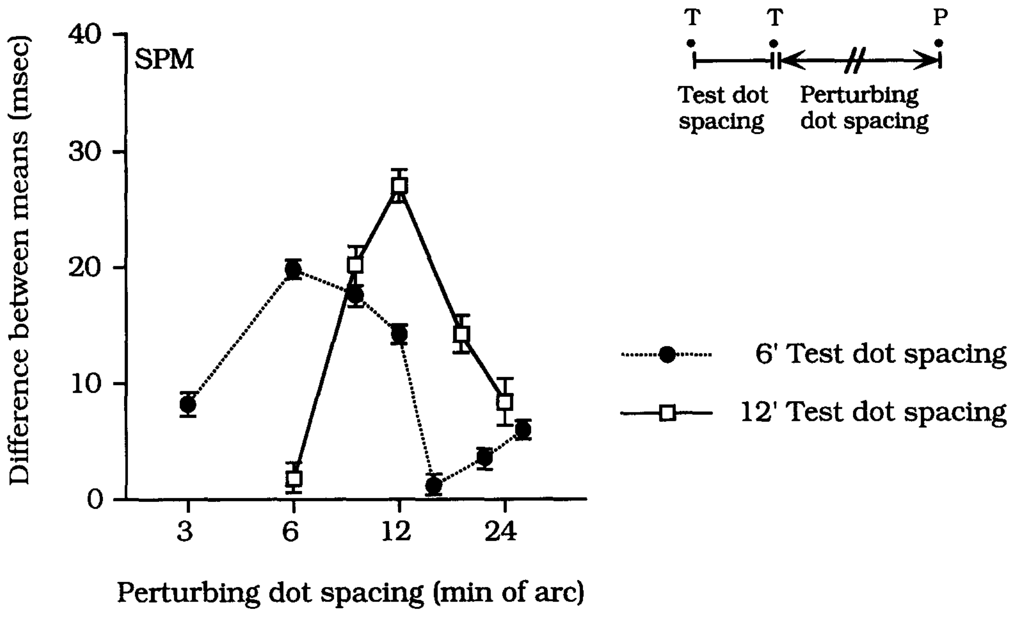


FIGURE 1. The effect of a perturbing dot on apparent motion order judgments. The stimulus arrangement for the perturbing dot on the right is shown in the inset at the top of the figure. The perturbing dot appeared randomly to the right or left of the test dots on each trial. The three dots were equally spaced 9 min arc apart for MDA and LW, and 6 min arc apart for SPM. The sign of the perturbing dot asynchrony indicates whether it appeared before or after the test dots; a negative sign indicates that the perturbing dot appeared before the test dots and a positive sign indicates that the perturbing dot appeared after the test dots. Observers indicated which direction of motion they saw between the test dots, while trying to ignore the perturbing dot. The top left graph shows the data averaged across the three observers. The data plotted are the differences between the PSEs or mean shifts for the perturbing dot on the right versus that on the left. The error bars show ±1 SEM.

was displayed 30 msec after the test dots. The distance between the perturbing dot and the nearest test dot was varied between blocks of trials. Observer SPM judged which direction the test dots appeared to move, while trying to ignore the perturbing dot in a binary judgment task. Observer LW adjusted the test-dot asynchrony until there was no net motion between the test dots. The perturbing dot was presented randomly to the right or left of the test dots and the difference between the mean shifts for the two positions was taken. Figure 2 plots the mean



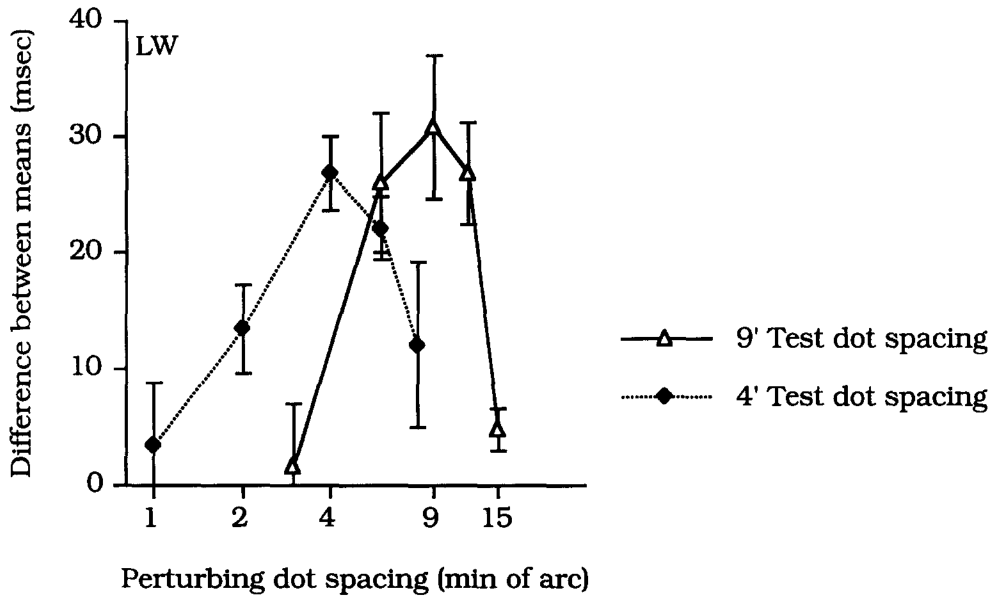


FIGURE 2. The effect of changing relative dot spacing. The inset at the top right of the figure depicts the stimulus configuration. Dot spacing is shown on the x-axis in logarithmic steps. The perturbing dot was displayed 30 msec after the test dots. Observer SPM used the binary judgment method and observer LW used the adjustment method. For each test-dot spacing, the greatest motion interference is found when the perturbing dot has the same spacing. Error bars show ±1 SEM.

shift difference as a function of the distance between the perturbing dot and the nearest test dot. The results for the two observers show that the position of the perturbing dot has a profound effect on the magnitude of the motion disturbance. The test-dot spacing is indicated in the figure legends. The maximal motion interference is found when the three dots are evenly spaced. The perturbing dot had less effect when placed either closer or further from the test dots. This result shows that perturbing-dot proximity does not determine the strength of the effect. Having the test and perturbing dots evenly spaced is more important.

Experiment 3: spatial scale limits, equally spaced dots

The previous experiment showed that equal spacing between the perturbing and test dots resulted in the greatest motion interference, but only in the case of small dot spacings. This experiment further examined the spatial-scale limits of the motion interference by varying the dot spacing over a larger range. The test and perturbing dots were always equally spaced, and the spacing was varied between blocks of trials in a method-of-adjustment task. The perturbing dot was presented 100 msec before the test dots. The observer adjusted the

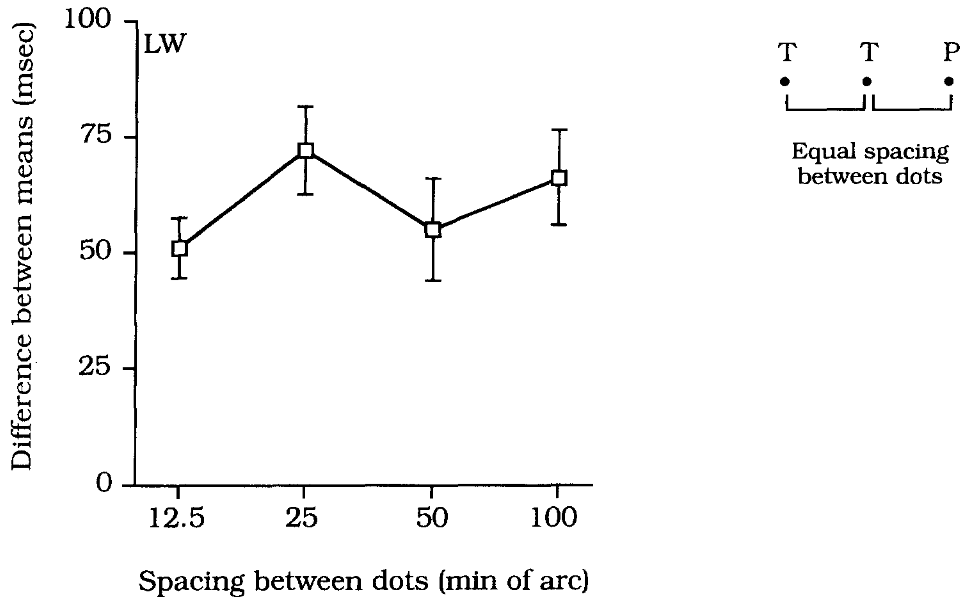


FIGURE 3. The effect of dot spacing when all three dots were equally spaced. Dot spacing is shown on the x-axis in logarithmic steps. The inset at the top right of the figure depicts the stimulus configuration. The perturbing dot was presented 100 msec before the test dots. The asynchrony of the test dots was adjusted until there was no apparent net rightward or leftward motion between the test dots. Error bars indicate ± 1 SEM. There is no systematic effect of dot spacing out to the largest separation tested, 100 min arc. The magnitude of the motion interference does not change as the dot spacing increases.

timing between the test dots until no net rightward or leftward motion could be seen. In Fig. 3, the difference between the right and left settings is shown as a function of dot spacing. The magnitude of the motion interference is not affected by stimulus scale over the tested range. For the largest dot spacing, the three dots spanned over 3 deg across the central fovea.

Experiment 4: directional specificity

In the previous experiments, the perturbing dot was placed on the same (imaginary) horizontal line with the test dots. A characteristic of motion detectors is their relatively sharp direction selectivity (e.g. Schiller *et al.*, 1976) which suggests that changes in the apparent-motion direction defined by the perturbing dot and the nearest test dot could affect the motion-interference magnitude. We investigated systematically the directional specificity of the motion interference by placing the perturbing dot at various positions away from the horizontal trajectory defined by the test dots. The perturbing dot was kept at a constant distance from the test pair by moving it around a circle centered on the midpoint between the two test dots (inset Fig. 4). We specified the position of the perturbing dot by its angular direction from the center of the circle relative to the line connecting the two test dots. The test dots were 9 min arc (MDA and LW) or 6 min arc (SPM) apart; the perturbing dot was 13.5 min arc or 9 min arc, respectively, from the center of the circle.

Observers judged the test-dot motion direction in a binary judgment task. The experimental results are plotted as the differences between the mean shifts for right and left perturbing-dot positions. These are plotted in Fig. 4 as a function of the perturbing-dot angle for three observers and for two perturbing-dot SOAs, 100 msec before the test dots (filled circles) and 30 msec after the test dots (open squares). Two SOAs were studied to show that the choice of perturbing-dot SOA is not critical. The average data for the three observers is shown in the lower right panel with two curve fits. The motion interference is greatly reduced if the perturbing dot is placed even a short distance away from the axis defined by the test dots. The results for the two different perturbing-dot asynchronies are similar, showing that this high degree of directional tuning is not specific to any one perturbing-dot asynchrony. The dependence on the angular placement of the perturbing dot is approximately exponential (solid line in figure), which, if considered a tuning function, has a half-width at half-height of about 10 deg.

This sharply tuned angular dependence shows that the bias in perceived direction of motion is not an interpreted perceptual asynchrony in the simplest and strictest sense; i.e., one in which the perturbing dot operates independently on the two test dots by influencing the times at which they are consciously registered. All such explanations (including the attention-based model of Hikosaka *et al.*, 1993a,b) incorrectly predict the cosine angular dependence illustrated by the dotted curve in Fig. 4, which has a half-width of 60 deg. This is because in such models the effect of the perturbing dot in biasing the perceived time of occurrence of each test dot will be some continuous function, $f(x)$, of the distance of the individual test dot from the perturbing dot. Any induced test asynchrony is due to the difference between the independent effects produced on the two test dots. For a small test-dot separation, that difference is approximately equal to the difference between the distances of the two

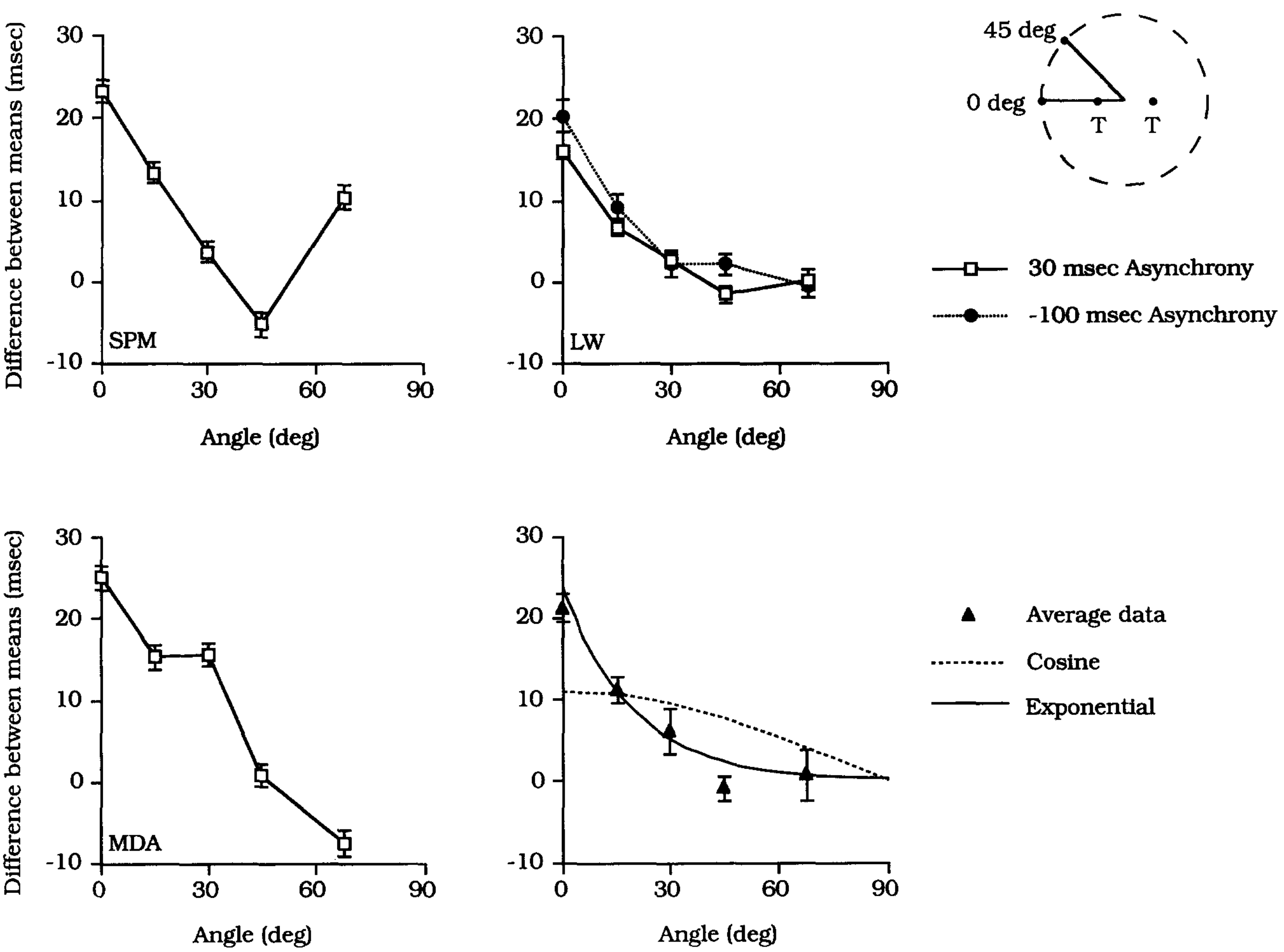


FIGURE 4. The position of the perturbing dot was specified by its position on a circle whose center was the midpoint between the two test dots as shown in the inset at the top right of the figure. For a perturbing-dot position of 0 deg, the three dots were evenly spaced (9 min arc for MDA and LW, 6 min arc for SPM) and placed along a straight (imaginary) line with the perturbing dot positioned either on the right or the left of the test dots. For a perturbing-dot position of 45 deg, a line from the perturbing dot to the midpoint between the test dots made an angle of 45 deg from horizontal. For each perturbing-dot position, its mirror image position was also shown randomly from trial to trial. Observer MDA was naïve as to the purpose of the experiment. Observer LW made judgments for two perturbing-dot asynchronies (open square: perturbing dot shown 30 msec after the test dots and filled circle: 100 msec before the test dots) showing that the perturbing-dot asynchrony is not critical. The difference between the mean shifts determined from the binary judgment method are plotted as a function of the perturbing-dot position. Error bars show ±1 SEM. In the lower right panel are the average data for all three observers (and both perturbing-dot asynchronies). The solid line shows the best-fitting exponential, and the dotted line shows the best fitting cosine. The exponential fits the data quite well ($r = 0.996$, $P < 0.01$) but the cosine function does not ($r = 0.762$, n.s.).

test dots from the perturbing dot (PT1–PT2), multiplied by $f'(x)$, the derivative of the distance function evaluated at $x = (\mathrm{PT1} + \mathrm{PT2})/2$, their average distance from the perturbing dot. This holds for any choice of $f(x)$, provided only that it is continuous.

In our experiments the distance between the two test spots, T1T2, was small relative to x, the constant distance from the center of the test pair to the perturbing dot. The distance difference, PT1–PT2, is then approximately equal to T1T2 cos(ϕ), where ϕ is the direction of the perturbing dot relative to the axis defined by the test dots. This yields a simple expression for the induced asynchrony:

$$\Delta t = f'(x)\mathrm{T1T2}\cos(\phi)$$

For the experiment of Fig. 4, $f'(x)$ is constant (since x is constant), and T1T2 is constant, so the asynchrony must, in this model, vary as cos(ϕ). Because the cosine does not fit the data well, to explain the observed sharp angular tuning we must instead suppose that the perturbing dot modifies, through some highly direction-specific interaction, a directional (motion) signal created by the test dots acting as a pair.

Experiment 5: motion interference in two directions simultaneously

Several papers which posit attention as the explanation for misperceived motion present data showing that motion can be created in two different directions simultaneously (e.g. Fisher *et al.*, 1993). These data are taken as evidence that attention can be divided to multiple locations simultaneously. Our data from the last experiment on directional specificity suggest that for the stimulus configurations we have chosen, low-level

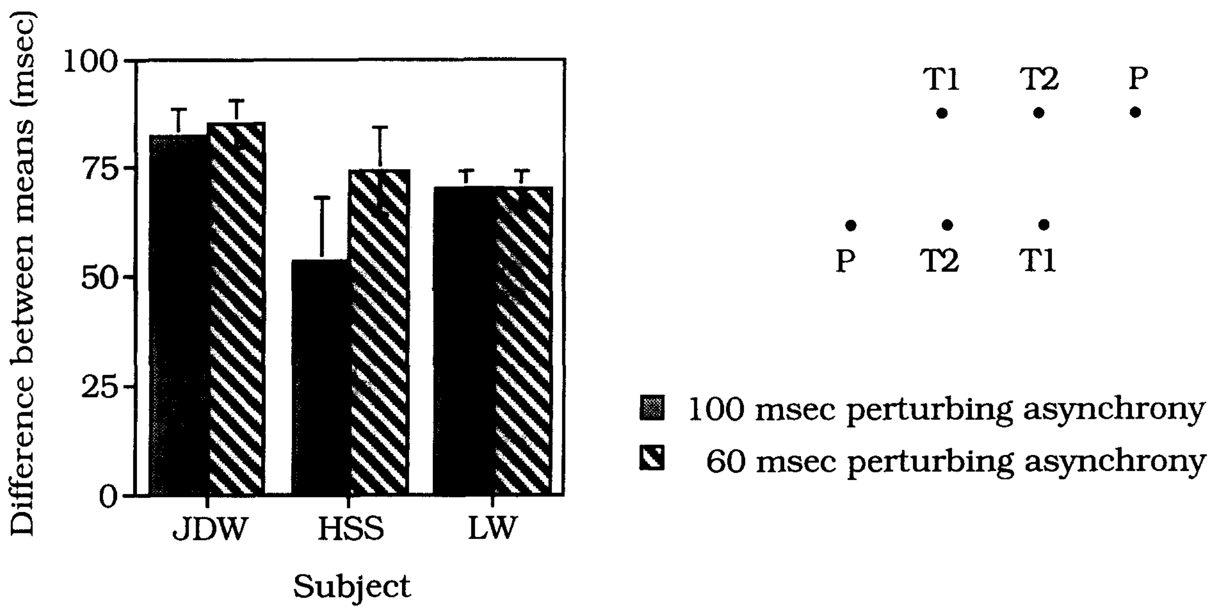


FIGURE 5. The inset shows the stimulus configuration to test if motion interference can occur in two directions at once. The dots were 30 min arc apart horizontally and 60 min arc apart vertically. The perturbing dots (labeled P) were presented simultaneously before the test dots (labeled T1 and T2). T1 test dots were presented simultaneously and T2 test were presented simultaneously. The depicted configuration and its mirror image were randomly displayed from trial to trial. The dots were not labeled in the experimental display. The asynchrony between the T1 and T2 test dots was adjusted by the observers until there was no net rightward or leftward motion between the test dots. Observers JDW and HSS were naïve as to the purpose of the experiment. The difference between the asynchrony settings for the top perturbing dot placed on the right minus the top perturbing dot placed on the left was the measure of motion interference. Three observers showed no systematic differences in motion interference for two perturbing-dot asynchronies. The error bars depict ±1 SEM. The magnitude of the motion interference is similar (though somewhat larger) to conditions with only one perturbing dot using the method of adjustment (see Figs 2 and 3). Motion interference can occur in two directions simultaneously.

motion mechanisms are more likely to be responsible for the motion-interference effects. Using a similar stimulus configuration, is it possible to show motion interference in two directions simultaneously? If so, this might weaken the argument based on the ability to split attention to multiple locations. In our next experiment we asked whether the direction of the motion bias can vary locally within the field of view by presenting two separated test stimulus pairs, each accompanied by a perturbing dot placed so that the biases would be opposite in direction. Two perturbing dots, labeled "P" in the inset of Fig. 5, were displayed at the same time followed by four test dots that were arranged so each test-dot pair had an associated perturbing dot along a horizontal axis. The horizontal spacing of the dots in each sequence was equal at 30 min arc, and the vertical separation between the test dots was 60 min arc. The test dots indicated by "T1" were displayed at the same time and the test dots indicated by "T2" were displayed at the same time. The asynchrony between the "T1" dots and the "T2" dots could be adjusted until rightward and leftward motions appeared equal in both (horizontal) test-dot pairs. Observers never perceived vertical motion between the test dots.

The perturbing dots were displayed either 60 or 100 msec before the test dots in separate blocks of trials; perturbing-dot SOA was not critical over the range tested. The data for this stimulus configuration are shown in Fig. 5. All three observers reported seeing two directions of motion and showed strong motion interference for the test dots at both perturbing-dot asynchronies. Motion interference was seen in two directions simultaneously (Khurana et al., 1996).

Experiment 6: no space–time interaction

Not all perturbing-dot SOAs have the same effect on the test dots' apparent timing (Fig. 1), and it is of interest to know if dot spacing interacts with dot asynchrony. If the motion interference were speed tuned across spatial scales, dot spacing would interact with dot asynchrony. The stimulus configuration was the same as shown in Fig. 5, with two perturbing dots and four test dots. This configuration was chosen because observers found that nulling the test-dot motion was easier with two directions than with one. In this experiment, the three dots were evenly spaced 10, 20, 30 or 60 min arc apart in separate blocks of trials. The vertical distance between the test dots was twice the horizontal distance between them (20, 40, 60 or 120 min arc, respectively). The perturbing-dot asynchrony was 30, 60, 100 or 300 msec in separate blocks of trials. The perturbing dots were always presented before the test dots. The differences between the settings for right and left perturbing-dot positions are plotted as a function of the perturbing-dot asynchrony at the top of Fig. 6, and as a function of perturbing-dot speed at the bottom of Fig. 6. The four different curves on each graph represent data for the four different dot spacings (10, 20, 30 and 60 min arc). There are only minor differences between the locations of the four

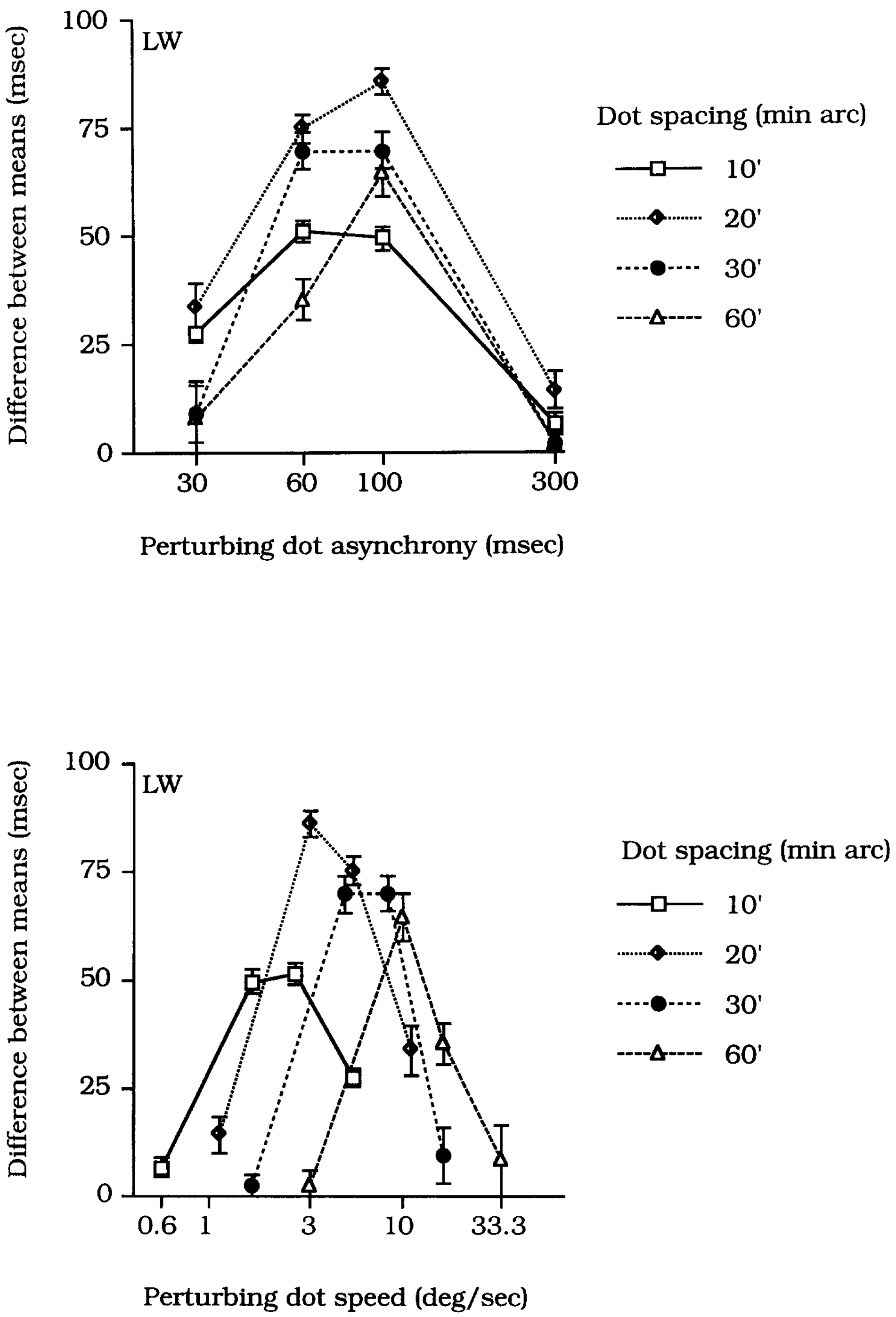


FIGURE 6. The effect of dot spacing (10, 20, 30 and 60 min arc) and perturbing-dot asynchrony (30, 60, 100 and 300 msec) on motion interference using the method of adjustment. All three dots were evenly spaced. The top panel shows the data as a function of perturbing dot asynchrony in logarithmic steps. The bottom panel shows the data as a function of perturbing dot speed in logarithmic steps. Error bars indicate ±1 SEM. The peaks of the functions overlap more closely when plotted across perturbing-dot asynchrony than across speed. For four perturbing-dot asynchronies there were no systematic differences in the interference effect at the different dot spacings. If the effect depended on the speed defined by the apparent motion between the perturbing dot and the nearest test dot, we would expect an interaction between dot spacing and perturbing-dot asynchrony. The motion-interference effect is not speed tuned across spatial scales.

curves' peaks plotted as a function of perturbing-dot asynchrony but there are significant, systematic differences for the curves plotted as a function of perturbing-dot speed. The curves are nearly superimposed in the top graph and not in the bottom. This suggests that the motion interference is not speed tuned across spatial scales, though it may be speed tuned at particular spatial scales. These data also show that the magnitude of the motion interference depends on the dot spacing with the weakest effect (50 msec) for the smallest spacing, 10 min arc. The effect magnitude may appear greater for this experiment than for some of the other experiments, but comparing these data with Fig. 2 (single perturbing dot) for the same observer and a 9 min arc dot spacing shows a not dissimilar effect size (30 msec). Two perturbing dots increased the interference effect somewhat (see Fig. 5).

DISCUSSION

We have presented data in support of a motion process that preconsciously and inevitably integrates multiple events to determine the direction of apparent motion. For the sequential presentation of a pair of dots, the identification of the right versus left direction is drastically disrupted by the presence of a third target, suggesting that motion information must be integrated over more than just one hop (or equally, more than two views). The disruption takes the form of a bias toward perception of a consistent motion direction for the three-dot sequence. We argue that the disruption is due to a motion mechanism that integrates all three dots into a single sequence even though observers were instructed to ignore the third, perturbing dot.

Numerous others have argued that motion is combined across more than two flashes and our data show some similarities to previous work. In Experiment 1, the data show that the integration time for the motion interference can be quite long, up to 200–300 msec for the perturbing dot presented either before or after the test dots (Fig. 1). Integration times of this magnitude have been found previously for other kinds of motion tasks. Bowne *et al.* (1989) found that speed discrimination between two test bars could be disrupted by additional bars along the same trajectory for asynchronies up to 250 msec between the additional bars and the test bars. Snowden & Braddick (1991) showed that integration time could be as high as 400 msec for a speed discrimination task when the signal dots were embedded in a sea of noise dots. Watamaniuk & Sekuler (1992) designed a direction discrimination task with random dots whose directions were taken from a distribution of directions. They found that direction discrimination (of the mean motion direction) improved for these displays with increasing stimulus duration up to 465 msec.

In our experiments, the dots must be approximately evenly spaced for the perturbing dot to be maximally effective (Fig. 2). If the effect were purely due to proximity, one might expect that the perturbing stimulus would have a greater effect the closer it was to the target pair, but the data show that this is not the case. The importance of spacing is somewhat surprising since, in the real world, moving stimuli are generally spatially and temporally continuous, and motion sensing mechanisms must be speed-selective to some degree. However, Snippe & Koenderink (1994) have suggested a scheme whereby motion detectors sensitive to different speeds have similar temporal characteristics and a detector's spatial scale determines which speed will stimulate the detector optimally. Support for such a scheme is found in Experiment 6, showing the lack of interaction between stimulus spatial and temporal characteristics on the motion interference. When all three targets are equally spaced and the spatial scale is varied, the motion interference as a function of perturbing-dot asynchrony is the same for all scales tested (Fig. 6).

The three dots must all be on the same axis for the effect to be obtained. The motion interference decreases sharply as the perturbing dot is moved off the horizontal axis showing sharp directional tuning (Fig. 4). As we have argued above, this critical importance of alignment demonstrates that these interactions involve motion signals. These interactions are not simply due to perturbations in the apparent position or timing of the test dots as a function of their distance from the perturbing dot, for in that case one would expect a more gradual cosine fall-off (dotted line, Fig. 4) in the effect as the perturbing dot is moved off the test pair trajectory.

Attention vs interaction within the motion sensing system

A similar stimulus configuration to our three-dot display was used by Hikosaka *et al.* (1993a) but their conclusions were couched in terms of attentional effects. They argued that the observers' attention was involuntarily drawn to a spot flashed in the location where one test line would be drawn later. Invoking a principle similar to the "Law of Prior Entry" of introspectionist psychology (Boring, 1950), they suggested that the apparent motion was due to the observers' attention causing the target at the cued location to be processed more quickly than the target at the uncued location. Because it was processed more quickly, the target in the cued location would be interpreted as occurring earlier than another target at a different location, and an apparent asynchrony would be created between simultaneous test targets.

Their effects are very similar to ours and we suggest, on several grounds, that their attentional effects are more simply explained by low-level motion processing that does not require attention (Tse & Cavanagh, 1995; Khurana *et al.*, 1996). (1) In Experiments 1 and 4, we find the motion interference comparable in strength when the perturbing dot is displayed *after* the test dots; it is not clear how the attentional process of Hikosaka *et al.* (1993a) could explain this. Attention would be drawn to the test dots because they are presented first, and the later presentation of the perturbing dot could not induce an apparent asynchrony between them. Alternatively, it is possible that the post-test stimulus could cause a response bias, but it is more parsimonious to postulate low-level motion mechanisms rather than adding yet another mechanism to create the bias. (2) As we have argued in discussing Experiment 4 (Fig. 4), the sharp directional tuning of the perturbing dot's interference calls for an explanation in terms of directional motion signals, rather than independent effects on the timing of the test dots. When the perturbing dot is moved away from the trajectory defined by the test dots, a process based on proximity would predict a cosine decrease in the interference effect, but we find a much sharper directional tuning. (3) Finally, the strong spatial tuning of the motion interference, i.e. the perturbing dot has its greatest effect when spaced the same as the test dots (Experiment 2; Fig. 2), has a natural interpretation in terms of velocity-sensitive motion-sensing mechanisms (Snippe & Koenderink, 1994), but is not obviously reconcilable with an attentional account.

There are, however, experiments that show induced motion between target pairs even without a third flashed target to set up a motion sequence (Gogel & Sharkey, 1989; Stelmach & Herdman, 1991; Stelmach *et al.*, 1994; Hikosaka *et al.*, 1993b). These experiments show that not all of the "attention induced motion" findings can be explained by our low-level motion ideas. However, since many of our findings strongly argue for a motion explanation rather than an attentional explanation, it is important to consider both possibilities when working with non-veridical motion perception. Indeed, most of the attention oriented studies do not consider low-level motion explanations for their results and the studies are often not designed to exclude sensory effects.

Modeling the interaction

Many contemporary models of human motion detection are, broadly speaking, variations of the classic correlator model proposed by Hassenstein & Reichardt (1956) for insect vision (Reichardt, 1961). Very briefly, these models postulate neural units with pairs of receptive fields which differ either in spatial position or in spatial phase, whose signals are correlated after one has been temporally delayed. The difference in spatial position, Δx, and temporal lag, Δt, define a unit's speed tuning. A single flashed dot produces weak motion signals in all directions, but after a second flashed dot, Reichardt correlators sensitive to the corresponding direction of motion would be the most active. Each pair of dots in our experiments would have an associated motion signal distribution, which would depend on the spacing and timing characteristics of the dot pair. If a dot pair were presented simultaneously, the motion signal distribution would be symmetrical and an observer making a right–left direction decision from Reichardt correlator signals would be expected to report right and left directions equally often.

However, if the motion detectors integrated information over more than two flashes, then the most active units would be the ones that respond to something like the average direction. In Barlow and Levick's (1965) study of rabbit retinal ganglion cells, they found evidence for multiple direction-selective subunits within one receptive field. Newsome *et al.* (1986) found similar motion subunits in macaque visual cortex. Each subunit could be modeled as a Reichardt correlator with many such subunits within a cell's receptive field. If the physiological correlate of Reichardt detectors were individual direction-selective cells like the rabbit retinal ganglion cell, then the detectors would have the ability to integrate over multiple flashes. Snippe & Koenderink (1994) have developed a motion extraction scheme using multi-input (more than two) Reichardt detectors that integrate motion information over more than two flashes.

The multi-input Reichardt detector idea is supported by the results shown in Figs 3 and 5 and by the results of Watamaniuk *et al.* (1995) demonstrating that a single dot moving in apparent motion along a fixed trajectory is easily detected amidst noise dots hopping in random directions. Indeed, Grzywacz *et al.* (1995) proposed a model in which trajectory detection is mediated by a network of small motion units. The activation of one unit in the network sends a facilitatory signal forward to units tuned to the same or similar directions, thereby enhancing responses to signals generated subsequently by motion in the same, consistent direction. This conjectured network consists of units tuned to the same spatial scale and the same or similar directions.

Another possibility is that the outputs of Reichardt detectors sensitive to only two flashes could be compared by units that can either integrate or not, depending on the stimulus characteristics. Anstis & Ramachandran (1987) made a similar argument, calling the effect "visual inertia". Snowden & Braddick (1989a) postulate a cooperative process that integrates among successive displacements along a trajectory of relatively constant velocity. The cooperative process consists of excitatory connections between motion detectors signaling similar directions and inhibitory connections for different directions. A two-dot stimulus would set up a bias in this type of network to "expect" a particular direction of motion from a third dot. Our data are consistent with all of these ideas.

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Acknowledgements—Parts of this work were presented at the 1985 ARVO meeting. Supported by NRSA grant EY06296 to LW, NIH grant EY01711 to UCSD, and AFO grant F49620-95-1-0265 to SPM.