



Successive Episodes Produce Direction Contrast Effects in Motion Perception

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Motion coherence thresholds decline with an increase in the number of frames in a random dot kinematogram (RDK), indicating that motion information can be integrated across successive frames. We investigated whether such temporal integration would be disrupted by a brief interval (32–600 msec) inserted into a motion sequence, perceptually dividing it into two successive episodes. Both episodes consisted of only a few frames (between 3 and 15), with the first episode being 100% coherent and the coherence of the second episode being adjusted to determine threshold. In four experiments we observed that coherence threshold for motion in the second episode was elevated if the directions in the two episodes matched, was lowered if they were opposite, and was unaffected if they were orthogonal. This successive direction contrast effect did not vary with the duration of the interval, suggesting that it is not an adaptation effect. The result of varying the number of frames in the second episode suggests that these effects are not due to alterations in cooperative activity among motion detectors. We suggest that successive direction contrast effects may reflect activity of higher-order perceptual organization mechanisms. © 1998 Elsevier Science Ltd. All rights reserved.

Motion perception Visual adaptation Masking Coherence threshold

INTRODUCTION

One of the primary goals of the sensory processing systems is to parse the steady stream of incoming information into discrete meaningful units. In visual perception, we think of these units as objects or their surfaces and features. Effective parsing of visual information, as in figure-ground discriminations, depends on grouping mechanisms that are able to integrate or “smooth” across variations in local image information to form the perception of coherent surfaces. Equally as important to effective parsing are grouping mechanisms that are able to exploit local contrasts so as to define surface boundaries. Consider, for example, seeing a trout swimming in a shallow river. The various colours and markings making up the fish’s skin must be integrated and seen as single surface. Yet, if the trout is to be discriminated from the river bed, any local contrasts between the river pebbles, reflections in the water’s surface, and the fish’s marking must be made salient. In this paper we consider this classic segmentation vs integration problem within the domain of visual motion perception and ask specifically how grouping mechanisms operate over time rather than space. Our question

concerns how apparent motion information presented over successive frames may be segmented into discrete episodes, as opposed to being integrated into a single perceptual event. Characterizing temporal segmentation vs integration processes in motion may be useful in understanding more generally the episodic constraints on scene segmentation processes in other visual domains.

The capacity of the human visual system to integrate local motion information has been studied using “noisy” motion stimuli, i.e., partially coherent random dot kinematograms (RDKs). In these computer-generated, apparent motion stimuli, a percentage of dots is displaced on successive frames in a single (signal) direction, while remaining dots are displaced in random (noise) directions. Observers are able to accurately judge the signal direction with only a small percentage (about 10%) of dots moving in the signal direction and they tend to perceptually attribute this movement direction to the entire RDK. This ability is not based on monitoring the direction of a single signal dot, or on comparing any average speed differences between signal and noise dots (Scase, Braddick, & Raymond, 1996). Rather, this remarkable ability to judge global direction with such a small proportion of signal dots appears to reflect active integration of locally varying motion information. In contrast to this, there are ample data to indicate that visual motion mechanisms are able to exploit local differences in motion to enhance or create the perception of edges (e.g., Braddick, 1974). As Braddick (1993) has

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previously discussed, visual motion mechanisms appear to promote integration in some stimulus configurations and segmentation in others, perhaps by the use of cooperative and competitive mechanisms. Although a number of experiments have investigated the flexibility of the grouping mechanisms for motion as they might operate across space (e.g., Chang & Julesz, 1984; Nawrot & Sekuler, 1990; Ramachandran & Inada, 1985), there have been relatively few experiments to investigate integration vs segmentation of motion information over time.

There is evidence that active integration of information occurs within an episode of motion (e.g., within a series of frames in an apparent motion sequence such as an RDK). Many measures of motion sensitivity improve dramatically when the number of frames in a motion sequence is increased from two up to about ten. This temporal recruitment effect has been reported for measures of speed discrimination (McKee & Welch, 1985), D_{\max} (Snowden & Braddick, 1989; Todd & Norman, 1995) and for the minimum percentage of signal dots necessary for just accurate detection of the signal direction (referred to hereafter as coherence threshold) in noisy RDKs (Snowden & Braddick, 1990). Snowden (1989) suggested that temporal recruitment effects reflect the biasing of a network of direction detectors and proposed that such biases may persist in time for up to nearly a second.

In the experiments reported here, we investigated whether there may be mechanisms to limit integration over time so as to allow direction perception during one motion episode to be segmented from motion occurring at the same spatial location but at a later time. Considering segmentation vs integration processes as they occur across space, we reasoned that integration of motion within episodes and segmentation of motion information at temporal boundaries might occur.

We presented two brief RDKs successively at the same spatial location with a brief blank interval between them. Observers judged the direction of the second (test) RDK and the motion coherence of this stimulus was varied from trial to trial. If cooperative mechanisms that facilitate integration of motion information persist after stimulus offset, then presenting, say, coherent rightward motion in the first RDK should enhance sensitivity for rightward movement in the second RDK (relative to that produced with a static display in place of the first RDK) because of temporal recruitment. Alternatively, if grouping mechanisms respond to temporal boundaries like they do to spatial boundaries, then a direction contrast effect might be observed. That is to say, biasing with motion in one direction in the first RDK might produce desensitization for motion in the same direction in the second RDK coupled with sensitization for motion in the opposite direction.

In the first experiment, we report that brief prior exposure to motion produces direction contrast effects. In the second experiment, we measured the effect of the duration of the blank interval interposed between the two

RDKs. We observed the contrast effects to persist for at least a half a second with virtually no sign of decay, suggesting that they may be distinct from adaptation effects. We demonstrate in Experiment 3 that there are no alterations in sensitivity to movement in directions orthogonal to that seen in the first episode. In the fourth experiment we varied the number of frames in the second RDK to determine how temporal boundaries and pre-exposure to motion might affect temporal recruitment during the second episode. The results were that temporal recruitment functions are largely unaffected by pre-exposure to motion.

GENERAL METHODS

Apparatus

RDKs were generated by a Macintosh IIx computer using custom software written in C. They were displayed on a Monitorm 2000 19" monitor with a P20 phosphor, 72 dpi, and a vertical refresh rate of 62.5 Hz. Timing parameters were integral multiples of 16 msec. The monitor was operated in black-and-white mode. The luminance of the blackened areas of the screen seen by observers was 8 cd/m² and each white dot had a luminance of about 60 cd/m². To limit the presence of surround contours, observers viewed the display through a 2 cm aperture in a black card placed 10 cm in front of the observer's eye. In Experiments 1 and 2, a half-silvered mirror was positioned at a 45 deg angle between the aperture and the monitor so that the image of a red light emitting diode (LED) appeared superimposed on the centre of the motion display. The LED served as a circular (7.5 mm in diameter) fixation stimulus and was viewed from the same distance as the monitor face. In Experiment 4, the LED and half-silvered mirror were removed and a small, low power HeNe laser was used to provide a similar-sized fixation spot. No fixation spot was used in Experiment 3. In all experiments, a chin rest and forehead restrainer were used to stabilize head position and to maintain a constant viewing distance of 92 cm.

Stimuli

Motion stimuli consisted of successive RDK frames. Each frame was composed of 134 white dots randomly plotted within a borderless 2.5 deg square (dot density = 21.4 dot/deg²) stimulus area centered on the darkened face of the monitor. There was no blank interval between frames. On successive frames, some or all of the dots were randomly designated as signal dots; these were displaced in a single direction. The remaining dots (noise dots) were displaced by the same amount as the signal dots, but in a direction randomly chosen between 0 and 359 deg. Signal vs noise assignment was shuffled on each successive frame so that the motion of a single dot could not reliably provide a cue to signal direction. The percent coherence in the moving display was defined as the percentage of signal dots. A conventional wrap-around scheme was used for dots moving out of the display field.

The fixation stimulus was continuously visible throughout the experiment.

Observers

In all the experiments reported here, observers wore their own optical corrections as required. Testing was performed binocularly. All observers had some experience with the psychophysical task prior to testing. All observers in Experiments 1 and 2 and three of the five observers in Experiment 3 were naïve to the experiment's aim. Informed consent was obtained prior to the experiment.

Design and procedure

Each trial in each experiment comprised a first episode, followed in turn by a blank inter-episode interval (IEI) and a second (test) episode.

Each observer participated in both experimental and control sessions. From trial to trial within an experimental session, the motion in the first episode was randomly chosen by the computer to be either 100% coherent leftwards, 100% coherent rightwards, or 0% coherent (noise). Six motion coherence thresholds were assessed within a single session: one each for leftward and rightward motion in the test episode after each of the three types of motion in the first episode. In the control sessions, the first episode contained a static array of dots of the same size and density as the RDKs used in the experimental sessions.

For each test episode, the direction of signal motion was chosen randomly to be either left or right. The observer's task was to judge the global direction of motion in the test episode and to press the appropriate key on the keyboard. Observers were encouraged to guess if they were unsure of the correct response. No feedback was given. The per cent coherence in the test episode was adjusted from trial to trial according to an automated tracking procedure. Six interleaved staircases were presented, one for each combination of first episode direction (right, left, noise) and test direction (right, left). The staircases began at 100% coherence and required two successive correct responses to decrement and one incorrect response to increment the coherence value. The step size was 50% of the previous coherence value (or the next highest integer), regardless of whether the step amount was added to the previous coherence value (after an incorrect response) or subtracted from the previous value (after two correct responses). If the staircase required the motion to go below 0% coherence (i.e. when the nominal signal direction was correctly judged on two successive trials), the direction of signal motion was reversed. The staircase terminated after nine reversals. The mean of the per cent coherence values producing the final six reversals yielded the motion coherence threshold required for the observer to correctly identify the global test direction on 71% of the trials.

EXPERIMENT 1: IMPOSING A TEMPORAL BOUNDARY

The purpose of the first experiment was to determine if motion smoothing or motion contrast occurred when a brief disruption in the motion display caused the stimulus to be segmented perceptually into two episodes. To assess this we presented two brief RDKs successively at the same spatial location with a brief blank interval between them. Observers judged the direction of the second RDK. Motion sensitivity to this stimulus was assessed by measuring the minimum percentage of dots moving in the same (signal) direction required by the observer to just correctly identify the signal direction.

Method

Observers. Four healthy observers (one male and three females) ranging in age from 21 to 34 years (mean = 25 years) participated.

Stimuli. The first episode contained either three or six frames. Dots were always displaced by 10.6 minarc on successive frames. Two speed conditions were tested by manipulating the duration of each frame: a slow condition with an effective motion velocity of 1.83 deg/sec produced by a 96-msec frame duration, and a fast condition with an effective velocity of 5.52 deg/sec produced by a 32-msec frame duration. The frame duration was always the same in both episodes and there was no ISI. A 32-msec blank interval followed the first episode and was the only time in the stimulus sequence when the screen was completely darkened. The test episodes always contained two frames. An interval of 1500 msec elapsed between trials.

Design and procedure. Each observer participated in 16 experimental sessions. Half the sessions were conducted with the fast RDKs and half with the slow RDKs. For each speed, half the sessions were conducted with three frames in the first episode and half with six frames. In addition to these sessions, each observer participated in three control sessions, each containing a stationary random dot pattern in the first episode (one matched in duration to the 3-frame slow-, 3-frame fast- and 6-frame fast-moving RDKs used as the first episode in the experimental conditions). The order of all sessions tested was randomized.

Results and discussion

To measure the effect of coherent motion in the first episode, we compared motion coherence thresholds (measured for the second RDK) obtained in the experimental conditions (i.e., with coherent motion in the first episode) with those obtained in two different control conditions (stationary pattern or motion noise in the first episode). Both types of control stimuli produced the same luminance onsets and offsets as the coherently moving stimuli and both were featurally similar, i.e., they were similar in global shape, spatial location, dot size and density. Since the stationary stimulus did not provide any local or global motion information, threshold changes produced by coherent motion in the first stimulus can be

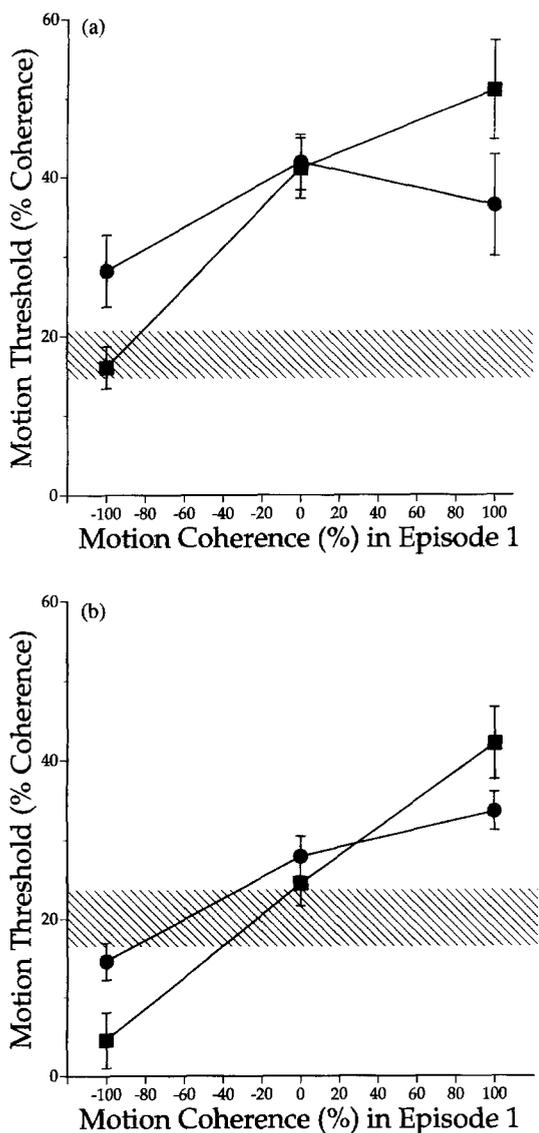


FIGURE 1. Group mean motion coherence threshold as a function of the percentage coherence in the first episode. Negative values indicate that the directions of global motion in the two episodes were opposite and positive values indicate that they were the same. The hatched areas represent the group mean threshold (± 1 SE) measured with a stationary random dot pattern present during the first episode. Circles and squares represent data obtained with three or six frames in the first episode, respectively. Vertical lines represent ± 1 SE of the mean. (a) Data obtained with 32-msec frames (fast speed). (b) Data obtained with 96-msec frames (slow speed).

attributed to either the local or global motion in the first RDK or to a combination of the two. Since motion noise provided an episode of local motion information with no concurrent global motion signal, this control may be used to determine the effect of global motion in the first episode.

Group mean coherence thresholds for all conditions are shown in Fig. 1. The hatched areas in both panels represent the mean of the thresholds obtained with a stationary pattern. For the slow stimuli, the stationary control condition yielded a group mean threshold of 20.1% ($SE = 3.7$). For the fast stimuli, group mean thresholds measured after a 3-frame stationary pattern (i.e., 96 msec in duration) and after a 6-frame stationary

pattern (i.e., 192 msec in duration) were 18.5% ($SE = 2.7$) and 16.5% ($SE = 3.1$), respectively and were non-significantly different.

Pre-exposure to motion noise. We first consider the effect of brief prior exposure to an episode of motion noise. For both speeds, motion noise acted to elevate group mean threshold above that measured with the stationary dot pattern. All observers showed this effect. However, statistical analysis (repeated measures ANOVA comparing stationary and noise conditions for both speeds and number of frames) revealed that noise-induced threshold elevations were only significant for the fast stimulus conditions, $F(1,3) = 119.4$, $P < 0.01$, and that, in these conditions, the magnitude of the elevations were non-significantly different for the 3- and 6-frame first episodes.

Do these data on the effects of pre-exposure to motion noise shed any light on the question of whether the motion system integrates motion information across the inter-episode interval or instead parses the motion information into two discrete episodes? Consider the fast stimulus condition with a brief (3-frame) first RDK which produced significant noise-induced threshold elevation. If the interval were *not* present, the RDK would be five frames (three in the first plus two in the test RDK) in total and, with 134 dots in each frame, would have consisted of 536 individual dot displacements. The mean threshold measured with the noise pre-stimulus was 42% ($SE = 2.7\%$) coherence. Thus, at threshold, only 54 dot displacements were in the signal direction. If integrated across all frames, this would be a percent coherence of 10.5%. This value is significantly higher than that we have measured in other experiments using highly similar RDKs (matched for frame duration, displacement size, density, etc.) consisting of a single 5-frame episode (mean for four observers = 6.1%, $SE = 0.3\%$; see Experiment 3). These data suggest that integration does not occur across the inter-episode interval and that noise in the first episode may have a detrimental effect on motion sensitivity (noise masking effect). An absence of cross-episode integration is further supported by the observation that coherence thresholds were the same after three or six frames of motion noise in the initial episode.

As can be seen in Fig. 1(b), for the slow speed conditions, motion noise had no effect on test RDK thresholds, even though the duration of the inter-episode interval was the same for both speeds. This also provides evidence that integration across episodes did not occur since if it had, thresholds would be expected to be higher in the noise conditions than in the stationary conditions.

Pre-exposure to directional motion. We next consider the effect of coherent motion in the first episode. For the slow speed, thresholds did not differ significantly between the same direction condition and the noise condition when the first episode consisted of only three frames. However, when six frames were presented, threshold was elevated significantly ($P < 0.05$) from 24.5% coherence after an episode of noise to 42.2% coherence after same-direction motion, a difference of

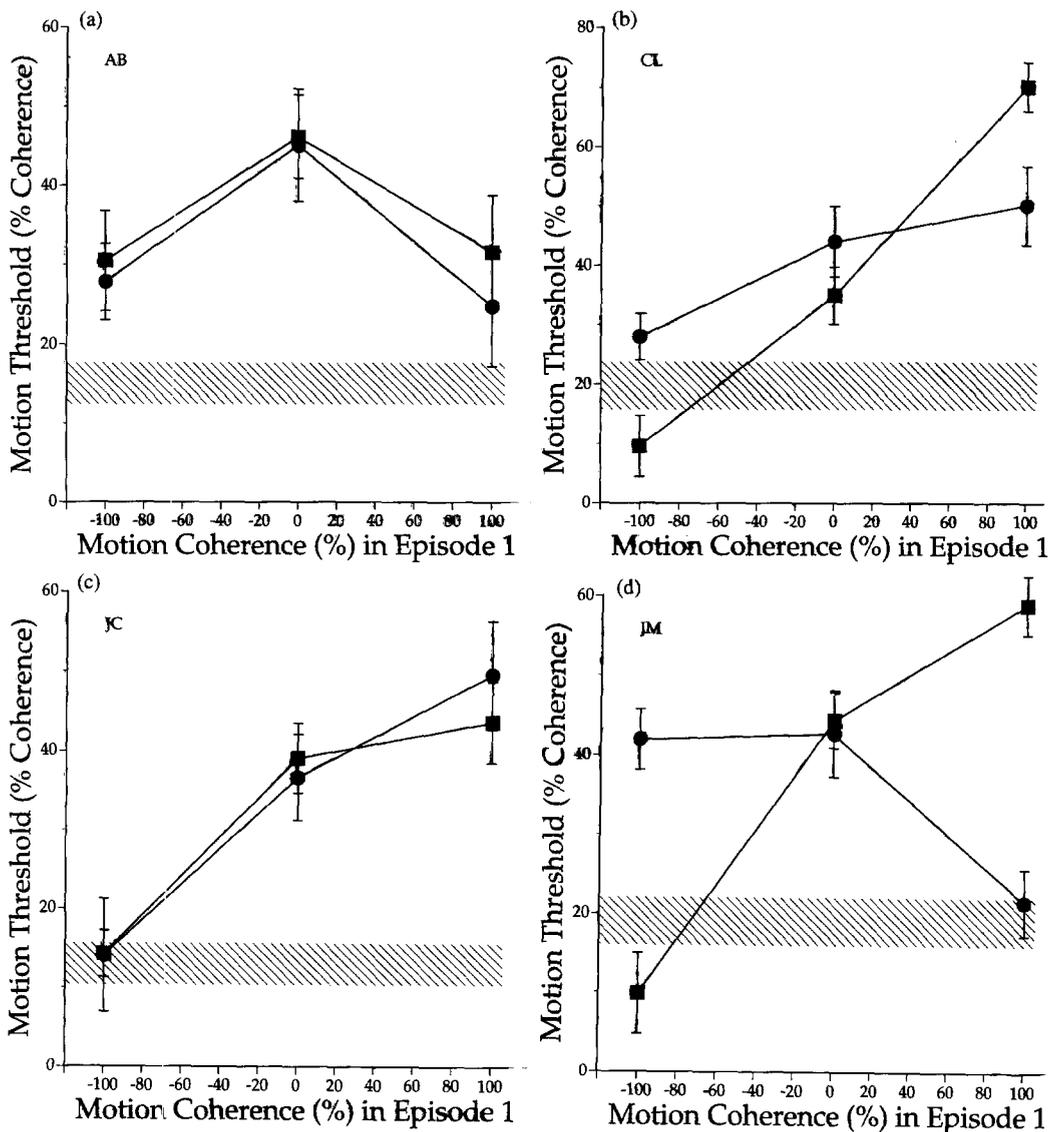


FIGURE 2. Motion coherence threshold as a function of the percentage coherence in the first episode for each observer. Data shown were obtained with 32-msec frames. See caption for Fig. 1 for details.

17.7 points. Motion in the opposite direction in the first episode acted to reduce threshold significantly ($P < 0.05$) for both 3- and 6-frame conditions. The magnitude of the threshold enhancement for the 3- and 6-frame conditions was 13.4 points and 19.9 points, respectively, compared with the noise conditions.

For the fast speed, these effects were more variable among observers (see Fig. 2). For the same direction conditions, neither the 3- nor the 6-frame conditions produced a significant elevation in the group mean threshold over that measured in the noise condition (an elevation of -5.4 and 10.0 points, respectively). Three observers showed threshold elevations and one did not. The opposite direction condition produced a significant reduction in group mean threshold (compared with noise) of 25.2 points for the 6-frame condition ($P < 0.05$) but a non-significant reduction of only 13.8 points was found in the 3-frame condition.

In summary, directional motion in the first episode generally produced an enhancement in motion sensitivity

in the second episode if the directions in the two stimuli were opposite. If the directions were the same, thresholds were generally elevated. This may be viewed as a temporally induced motion contrast effect. These data indicate that integration of motion information does not occur across an inter-episode interval and suggests that any cooperative recruitment processes initiated during the first episode are abruptly halted and, in some situations, reversed by an inter-episode interval.

EXPERIMENT 2: DURATION OF THE INTER-EPISODE INTERVAL

In this experiment we sought to investigate the temporally induced direction contrast effects further by varying the duration of the inter-episode interval (IEI). If the noise and directional effects seen in the first experiment were due to any type of motion adaptation during the pre-stimulus, then these effects would be expected to dissipate with longer intervals. To reduce

variability among observers we lengthened the second motion episode to three frames.

Method

Observers. Four healthy observers (four females) ranging in age from 22 to 26 years (mean = 24 years) participated. One observer (JC) had participated in the previous experiment.

Stimuli. The first episode always consisted of six frames and the test episode of three frames. Frame duration was 32 msec, producing an initial episode of 192 msec and a test episode of 96 msec. Dots were displaced by 10.6 minarc, giving them an effective velocity of 5.52 deg/sec. A blank IEI was imposed between the episodes; its duration was 32, 192, 320 or 608 msec. An interval of 1500 msec elapsed between trials.

Design and procedure. Each observer participated in 20 experimental sessions: five for each of the four IEI durations. IEI duration was constant within a session. In addition to these sessions, each observer participated in four control sessions, each containing a 3-frame static pattern during the first episode and one of the four IEI values used in the experimental sessions. The order of sessions tested was randomized.

Results and discussion

Group mean motion coherence thresholds are plotted in Fig. 3 as a function of the interval between first and second motion episode for each of the conditions. Since an ANOVA on the coherence thresholds obtained with a stationary dot pattern in the first episode showed that IEI duration had a non-significant effect on test threshold, $F(3, 9) = 1.91$, $P > 0.05$, the group mean value (9.9%,

$SE = 0.8$) is shown by the single dotted line in Fig. 3 for clarity.

The most striking aspect of these data is that successive direction contrast effects appear to be independent of the IEI duration, within the range studied here. An ANOVA of conditions and IEI durations found a significant main effect of condition, $F(3, 27) = 4.66$, $P < 0.01$, but a non-significant effect of IEI duration and a non-significant interaction effect. Collapsing across IEI duration, motion noise elevated thresholds significantly ($P < 0.01$) (compared with the stationary condition) to a group mean value of 14.5% ($SD = 1.7$). Motion in the same direction as the test elevated thresholds to a mean value of 25.8% ($SD = 10.0$), whereas motion in the opposite direction acted to reduce thresholds significantly ($P < 0.01$) to a value of 3.8% ($SD = 10.5$). Differences in threshold for the same direction condition (compared with the noise condition) seen in this experiment are similar in size (11.3 points) but more consistent than those observed in the condition of Experiment 1 using the same type of motion in the first episode.

The critical finding in this experiment is the lack of decay of changes in threshold produced by the first episode over the 32–608 msec intervals studied here. Such a result argues against a motion adaptation explanation. Although there are few data on the effects of brief adaptation stimuli, classical motion adaptation effects, i.e. motion aftereffects, have been reported to dissipate fully after an interval about half the duration of the adaptation stimulus (Hershenson, 1989), suggesting that for adaptation stimuli of only 192 msec duration, recovery from any adaptation effects should be complete by 96 msec. Clearly this was not observed. The absence of such decay in our data speaks strongly against an adaptation style, and particularly against a neural fatigue process.

However, there is a possibility that adaptation did occur and that “storage” effects observed by Spigel (1962) for the motion aftereffect contributed to the apparent lack of decay in the present data. This is unlikely, however, because storage effects have been reported to occur only in the complete absence of light (Thompson & Movshon, 1978), or in the absence of other visible contours (Spigel, 1962). The present experiment was conducted with a fixation spot and in dim ambient illumination. An alternative possibility (explored in the fourth experiment) is that the inter-episode interval may have disrupted the cooperative mechanisms that normally operate to facilitate global movement direction detection.

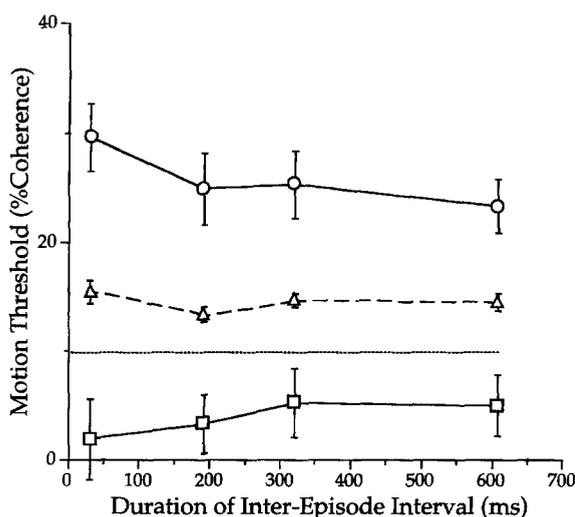


FIGURE 3. Group mean motion coherence threshold as a function of the duration of the interval between episodes of motion. Open circles represent data obtained when the movement direction in each episode was the same. Open squares represent data obtained when movement direction in each episode was opposite. Open triangles represent data obtained when the first episode consisted of motion noise. Vertical lines represent ± 1 SE of the mean.

EXPERIMENT 3: ARE MOTION CONTRAST EFFECTS AXIS-SPECIFIC?

In the previous two experiments the direction of motion in the test RDK was the same as or opposite to that in the first episode, i.e., in the same axis. To test whether the contrast effects are axis-specific or occurred simply because the direction of motion in the two episodes was the same or different, we performed a similar

experiment but included an orthogonal direction condition in the first episode.

Observers

Two female adults participated. One was an author and the other was naïve to the purpose of the experiment. Both had experience with the psychophysical task prior to testing.

Stimuli. The first episode always consisted of 15 frames (duration = 399 msec), whereas the second (test) episode consisted of three frames (duration = 80 msec). Frames were of 26.6 msec duration each. Motion in the first episode was either upwards, leftwards or rightwards and was always 100% coherent. Motion in the test episode was either leftwards or rightwards. The IEI was 266 msec. An interval of 1.15 sec elapsed between trials.

Design and procedure. The same procedure as described for the previous experiments was used, except that 100% coherent motion upwards replaced the previously used 0% coherent motion conditions. Thus, each observer participated in a single experimental session consisting of two staircases each for upwards, leftwards or rightwards motion in the first episode. This meant that two thresholds each were measured for conditions in which the direction in the two episodes was the same, opposite or orthogonal. Each observer participated in two additional sessions: one measuring six thresholds when the first episode was 0% coherent and the other measuring six thresholds when stationary random dots were presented in the first episode.

Results and discussion

The mean motion coherence thresholds for the two observers are plotted in Fig. 4. Data from each individual were highly similar and variability within each session was low. Compared with motion thresholds measured with stationary dots presented in the first episode, thresholds after motion in the same or opposite directions

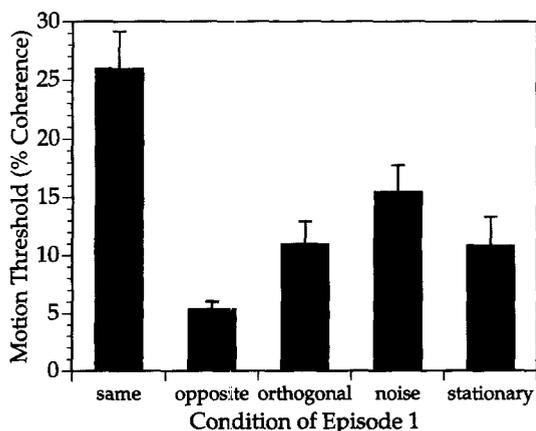


FIGURE 4. Mean motion coherence thresholds for two observers for five different conditions of the first episode, i.e., when the direction of motion in the first episode was the same as, opposite to, or orthogonal to that of motion in the second (test) episode, when there was no global motion (0% coherence) and when a stationary dot pattern was presented. Vertical lines represent ± 1 SE of the mean.

were significantly raised or lowered, respectively (as was found previously). As before, motion noise acted to elevate threshold by a small but consistent amount. However, thresholds measured after orthogonal (upwards) motion were highly similar to those measured in the stationary control condition. The observation that orthogonal motion in the first episode did not affect threshold for motion in the second episode suggests that the motion contrast effects are axis-specific. It should be noted that because observers were constrained into making leftward vs rightwards judgements, any repulsion effects (i.e., the perception of a downward component) would not be observable in this experiment.

EXPERIMENT 4: SEQUENTIAL RECRUITMENT AFTER A TEMPORAL BOUNDARY

In the previous experiments the test RDK was composed of only two or three frames. Data from temporal recruitment experiments have shown that global motion detection does not reach asymptotic levels of sensitivity until about ten frames are provided in the stimulus (Snowden & Braddick, 1989). Perhaps the successive direction contrast effects observed here occurred because global motion analysers were less than fully operational. To address this possibility, we varied the number of frames in the test stimulus, thereby producing temporal recruitment functions.

Method

Observers. Five healthy observers (one male and four females) ranging in age from 21 to 40 years (mean = 30 years) participated. All observers had some experience with the psychophysical task prior to testing; three were aware of the experiment's purpose (two being the authors) and two were naïve.

Stimuli. The first episode always consisted of 15 frames, whereas the second (test) consisted of 2, 3, 5, or 10 frames. Frames were of 32 msec duration. A 224-msec blank IEI was presented between episodes. An interval of 1.15 sec elapsed between trials.

Design and procedure. Each observer except SF participated in eight experimental sessions: two each for the 2, 3, 5, and 10-frame test episode conditions. The number of frames in the test episode was constant within a session. Observer SF participated in six sessions, two for each of the 2, 3, and 5-frame test conditions. In addition to these sessions, each observer participated in one static control session for each of the test episode conditions. Sessions were tested in a random order.

Results and discussion

Group mean motion coherence thresholds are plotted in Fig. 5 as a function of the number of frames in the test episode for each condition of the first episode. The expected sequential recruitment function was found for the static control condition and for the remaining conditions. It is readily apparent that sequential recruitment is largely unaffected by the nature of the motion or lack thereof in the first episode and cannot account for the

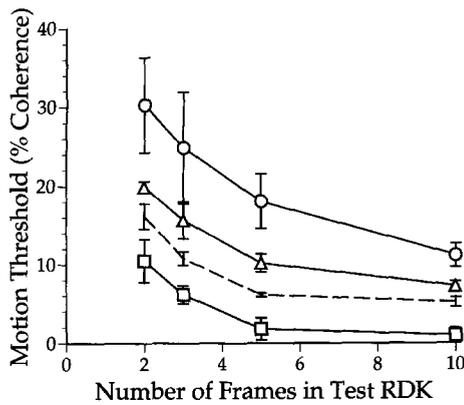


FIGURE 5. Group mean motion coherence threshold as a function of the number of frames in the test episode. The first episode consisted of 15 frames moving in either the same (open circles) or opposite (open squares) direction compared with the test stimulus, or was a static array of random dots (dashed line) or consisted of motion noise (open triangles).

successive direction contrast effects observed in these experiments. A 4×4 within-subjects ANOVA in which the factors and associated levels were condition (same, opposite, noise, static) and test frames (2, 3, 5, 10) revealed that the effect of condition on coherence threshold did not vary with the number of test frames, $F(9, 79) = 1.04$, ns.

As can be seen by the vertical positions of each curve in Fig. 5, successive direction contrast effects were found consistently in this experiment. To quantify these effects, we calculated the difference between each observer's threshold for the three motion conditions of the first episode (same, opposite or noise) and their threshold for the static control condition. An ANOVA conducted on these differences revealed, predictably, that the type of motion in the first episode had a significant effect on test thresholds relative to thresholds measured in the static condition, $F(2, 59) = 14.75$, $P < 0.01$.

Same-direction motion in the first episode elevated test thresholds by a mean of 11.5 percentage points. This threshold elevation appeared to decline with an increasing number of test frames, dropping from 14.1 points when there were two test frames to 6.0 points when there were ten test frames. However, the decrease approached significance only when the number of test frames was increased from five (mean threshold elevation 11.9 points) to ten (mean = 6.0 points), $F(1, 59) = 3.71$, $P = 0.06$. When the test contains ten frames, the offset asynchrony between the pretest and the test is 544 msec; some decay might be expected by this point, although the results from Experiment 2 do not support this.

As in Experiments 1 and 2, motion in the opposite direction in the two episodes induced a modest but reliable enhancement effect, decreasing test thresholds by 4.7 points on average. The sensitization effect was unaffected by the number of frames in the test, ranging only from a mean decrease of 5.7 percentage points when test RDKs contained two frames to a mean of 4.2 points when there were ten test frames, $F(1, 59) < 1$.

Finally, dynamic noise in the first episode produced a

small but reliable and significant loss in sensitivity, increasing coherence thresholds by a mean of 3.7 percentage points over thresholds obtained in the static condition. (One-tailed t -tests indicated that the threshold elevations produced by noise pretests were greater than zero when test RDKs contained two, three, five, or ten frames, $t(4) = 2.77, 2.46, 3.28$, and 4.40 , respectively, all $P < 0.05$.) The magnitude of this noise masking effect did not vary significantly with the number of frames in the test episode, indicating that sequential recruitment effects are unlikely to contribute to noise masking effects.

GENERAL DISCUSSION

In three experiments, sensitivity to global motion direction was measured with and without prior exposure to a brief episode of coherent motion. The main finding is a successive direction contrast effect. Prior exposure to a brief episode of motion in one direction causes significant, direction-specific alterations in sensitivity to motion in a second, temporally distinct episode. When the direction is the same in both episodes, sensitivity is reduced, when the directions are opposite, sensitivity is enhanced, and when the directions are orthogonal (Experiment 3), sensitivity is unchanged. Experiment 1 showed that these effects can be observed with fast or slow stimuli and are somewhat more robust with six rather than three frames in the first episode. Experiment 2 demonstrated that direction contrast effects do not deteriorate appreciably when the blank interval between motion episodes is lengthened up to 600 msec. Although the first three experiments used very brief 2- or 3-frame test stimuli, Experiment 4 demonstrated that direction contrast effects can be observed with longer test stimuli and that sequential recruitment functions appear unaltered by prior exposure to motion. In all four experiments, a noise masking effect was observed in which pre-exposure to an episode of motion noise decreased sensitivity.

Capture vs contrast effects: the role of episode boundaries

Why was a direction contrast rather than a motion "capture" effect seen with successive episodes? To probe this issue we consider such effects for two spatially contiguous areas of moving random dots. If areas of coherently moving dots are interdigitated by narrow areas of motion noise, then capture effects are seen, i.e., the areas of motion noise appear to move in the same overall direction as their coherent surrounds (Chang & Julesz, 1984;). This observation with *spatially* adjacent stimuli suggests that capture effects should be seen with *temporally* contiguous stimuli like those used here, in which one episode (the first episode) is high in coherence and the other is low (the test episode). Moreover, reports of sequential recruitment effects in motion (e.g., Snowden & Braddick, 1989; Snowden & Braddick, 1990; Todd & Norman, 1995) and theories suggesting that they reflect cooperative and competitive biases among direction detector networks (Snowden, 1989)

predict that prior exposure to motion should capture or facilitate rather than hinder detection of motion in the same direction.

However, we observed contrast, not capture, effects. Perhaps the dark, blank temporal interval separating the two bright random dot episodes provided a salient temporal boundary, defining each episode in time in much the same way that luminance, colour, depth, motion or texture contrasts might delimit spatial areas. The idea that object borders and the surfaces they define may play a key role in capture vs contrast effects has been suggested previously (Culham & Cavanagh, 1994; Ramachandran, 1987). If we view two perceptually distinct episodes as analogous to two distinct objects, then the observation of contrast effects is more consistent with the simultaneous direction contrast effects observed when a central area of dots moving coherently in one direction is surrounded by an annulus of dots moving coherently in an orthogonal direction (Mather & Moulden, 1980) or when two random dot patterns, each moving in different directions, are seen in transparency (Marshak & Sekuler, 1979). The notion that boundaries are critical in producing contrast effects is supported by Nawrot and Sekuler's (Nawrot & Sekuler, 1990) experiments, in which capture effects were observed when the borders between coherent and incoherent patches of dots were imperceptible.

Before conducting the present experiments, we tested pilot conditions with no blank interval between the so-called first and second episodes. When the first six frames in an RDK were 100% coherent and the last two or three frames had low coherence in either the same or opposite directions, observers were unable to detect the presence of the latter test frames, even when they moved in the opposite direction, presumably because of successive motion capture. A blank interval of only 32 msec was sufficient to render a percept of two episodes rather than one and to produce the direction contrast effects we report. Most current models of temporal cooperativity among motion detectors do not incorporate the idea that temporally "global" information, such as that concerning the onset and offset of motion episodes, must modify the activity of motion networks.

How might episode boundaries be defined?

In the present experiments, the perceptual salience of the temporal boundary most likely arises from the luminance offset and onset associated with the blank inter-episode interval rather than from information relating its duration to that of the frames within the RDKs themselves. In Experiment 1, the 32 msec blank interval segmented the RDK into two episodes, both when the frames themselves were equally short (32 msec) and, in other conditions, when they were three times as long (96 msec). In all the experiments reported here, the interval between frames within an episode was 0 msec, making the inter-episode interval the only time within the trial when no dots were present. In other temporal recruitment studies (e.g., Todd & Norman, 1995) there is

typically no ISI between successive frames or, if there is one, it is of a constant duration. Perhaps this is the key as to why other studies show temporal integration across intervals even longer than the inter-episode interval we used here. In addition to the simple luminance contrast which defined our episodes temporally, the rhythm of successive stimulus presentations may determine perceptual organization of temporal information. To test this idea we created a multiple frame RDK using 32-msec frames with 32-msec blank intervals placed between each frame. The perception produced is one of a single episode containing coherent, albeit jittery, apparent motion with an obvious global direction. Thus, motion information may be smoothed across regularly presented 32-msec blank intervals but, as in the experiments reported here, a novel 32-msec blank interval may serve as an episode boundary. Such demonstrations of temporally global organization of motion processing pose interesting questions for theories of motion perception. For example, Todd & Norman (1995) model temporal motion integration largely on changes to signal-to-noise ratios afforded by multiple frame stimuli. Although the inter-episode interval we used may have introduced spatiotemporal "noise" which could reduce sensitivity, this cannot explain why sensitivity was elevated for opposite directions, unaffected for orthogonal directions or why the effects persisted over very long inter-episode intervals. Clearly when stimuli are temporally complex other, perhaps global, factors constrain temporal integration of motion information.

Motion offsets and onsets may mark episode boundaries in the absence of luminance contrasts. Snowden's (Snowden, 1989) observers judged the horizontal motion of an array of random dots that were viewed transparently with a second "background" array of vertically moving random dots. The test dots were moved either before, during, or after a 100 msec episode of background motion. There was no luminance offset to signal the termination of the background episode, merely the cessation of motion. D_{max} for the test motion was reduced when the background motion was concurrent with the test motion and, of particular relevance here, when the background motion preceded the test motion by as much as 700 msec. No changes to D_{max} were observed when the background motion followed the test motion. The background motion is analogous to the first episode in our experiments and although it was orthogonal in direction to the test motion, it had a suppressive effect similar to that induced by same-direction motion in our experiments. That the time course of Snowden's effect is consistent with Experiment 2's results suggests the possibility of a common basis. However, his result conflicts with our findings in Experiment 3 wherein we fail to observe any changes in sensitivity for motion in directions orthogonal to motion in the first episode.

Snowden (1989) suggested that the long-lasting stimulus interactions he observed reflected continued cooperative and/or competitive activity initiated by the background motion. To the extent that sequential

recruitment functions reflect cooperative interactions among direction detector networks, Experiment 4's results do not support this idea. Although test thresholds were raised or lowered overall depending on whether the direction in the two episodes was the same or different, the rate of sequential recruitment was unaffected. This suggests that direction contrast effects are not caused by either unusually poor or unusually efficient cooperativity among direction detectors.

The relationship between direction contrast effects and motion adaptation

Successive contrast effects seem to resemble adaptation effects. In previous work one of us demonstrated that 90-sec adaptation to coherent motion in one direction caused large, robust elevations of coherence thresholds for same-direction motion, but little or no alterations in sensitivity for motion in orthogonal or opposite directions (Raymond, 1993; Raymond & Braddick, 1996). These effects on coherence thresholds are similar in direction and are only modestly larger than those observed here with the much briefer "adaptation" (i.e., first episode) stimuli. In the previous adaptation experiments using RDKs with the same frame durations and dot displacements as those used in the fast- and slow-speed conditions of the present experiments, 90 sec of adaptation combined with 5 sec top-up intervals and 2-frame test stimuli produced threshold elevations of 49 percentage points for the slow (Raymond, 1993) and 40 points for the fast condition (Raymond, 1994). In Experiment 1, the analogous threshold elevations were 25 and 32 percentage points after only six frames of motion in the first episode.

The current experiments cast doubt on the idea that bonafide adaptation is responsible for the difference in the magnitude of these effects. First, the magnitude of successive direction contrast effects is largely unaffected by the duration of the first episode. Examining Experiments 1 and 2 conditions with comparable inter-episode intervals and test episode durations, the threshold elevation induced by same-direction motion (relative to static first episodes) was 15.0 and 14.1 percentage points for 6- and 15-frame first episodes, respectively. For opposite-direction motions, thresholds were decremented by 6.6 and 4.6 percentage points for the 6- and 15-frame conditions. Second, direction contrast effects did not decay as the duration of the inter-episode interval increased. These results imply that direction contrast effects are themselves not due to the neural fatigue widely thought to underlie motion adaptation. Instead, they suggest the intriguing possibility that successive contrast effects may have contributed substantially to the adaptation effects observed previously.

Concluding remarks

We lastly consider what purpose successive direction contrast effects might serve. Perhaps they reflect the activity of mechanisms that normally assist us to preferentially process novelty and change in the visual

array over "old" information that has already been coded. Recent theories of "object-oriented" perception emphasize the importance of attention and selection mechanisms that respond to both local and global information in the scene to speed perceptual organization around objects, particularly new ones and those affording responses (Duncan, 1996; Houghton & Tipper, 1994). Research in this area has demonstrated that selecting objects in briefly, successively presented stimuli can lead to temporary but relatively long-lasting (in the order of a half a second) deficits in visual detection and identification. A number of different but possibly related phenomena, such as repetition blindness (Kanwisher, 1987), the attentional blink (Raymond *et al.*, 1992), inhibition of return (Posner & Cohen, 1984), and negative priming (Tipper, 1985) all indicate that perceptually organizing visual information in order to select or respond to an object is episodic in nature and that selection of one visual object can have a significant impact on the efficiency with which subsequent objects may be processed. Successive direction contrast effects and noise masking effects may reflect such visual selection processes. Although further research remains to be done to address this possibility, our data leave little doubt that motion perception is constrained by episodic information. Understanding this may be useful in characterizing more generally how episodic factors may determine scene segmentation in other visual domains.

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