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# Collisions between moving visual targets: what controls alternative ways of seeing an ambiguous display?

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**Abstract.** When identical visual targets move directly toward and then past one another, they appear either to stream past one another or to bounce off each other. Bertenthal et al (1993 *Perception* **22** 193–207) accounted for the relative strengths of these two percepts by invoking a directional bias, arising from cooperative interactions within a network of motion detectors. We tested this explanation by devising conditions that would enhance or diminish the strength of such a directional bias. In separate experiments we varied (i) the presence or absence of temporal transients (pausing, disappearance, occlusion); (ii) the distances travelled by the targets; and (iii) their acceleration or deceleration before and after collision. The tendency to see the objects stream past one another was not related to the strength of an hypothesized directional bias, suggesting that the perception of this ambiguous motion display was not mediated by directional recruitment. Instead, the results suggest that perceived direction reflects the operation of neural constraints that mirror the constraints operating upon moving objects in the three-dimensional natural world.

## 1 Introduction

In two-dimensional displays, objects moving along intersecting trajectories can undergo illusory changes in speed and/or direction (Goldberg and Pomerantz 1982; Metzger 1934; Michotte 1946/1963). This general phenomenon becomes particularly interesting when the intersecting objects are indistinguishable from one another. When identical objects, say two discs, move toward one another, coincide, and then move apart, the retinal image underspecifies their post-coincidence trajectories. Here, the retinal image is equally consistent with two very different scenarios: after coincidence, the discs could have continued to move in their original directions, or they might have reversed their directions. In the first case, the discs would appear to stream past one another; in the second case, the discs would appear to repel or bounce off one another. Despite the total ambiguity of this stimulus, Bertenthal et al (1993) found that vision consistently settled on just one of the alternative percepts: streaming (the first case described above). To explain the massive bias in favor of streaming, Bertenthal et al proposed that the objects' initial motion toward one another biased activation within the visual system toward those directions of motion and toward a percept of streaming. Bertenthal et al attributed this perceptual bias to directionally selective recruitment via cooperative interactions among bilocal correlators tuned to a common temporal and spatial span (originally termed "homogeneous recruitment mechanisms" by Snowden and Braddick 1989a). Such inertial or hysteretic effects have been recognized since the earliest studies of motion perception (R Sekuler 1996; Wertheimer 1912), and may be quite widespread.

Bertenthal and his colleagues offered several experimental demonstrations consistent with the idea that streaming arose from directionally selective recruitment. In one demonstration, a brief pause was inserted into the objects' trajectories at the point of their coincidence. This pause was designed to reduce directionally selective recruitment.

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To see how this would work, consider a set of bilocal motion detectors tuned to a common spatial and temporal span. For ease of explication, imagine a target that moves across the retina in a series of steps that match the preferred spatial and temporal span of the bilocal detectors. Each step would increase the excitation within that single set of motion detectors, up to some limit. In this scheme, a pause introduced at the moment of overlap would permit the excitation to dissipate somewhat, or allow it to be reset by some active process. Empirically, the pause dramatically decreased the likelihood that the two moving objects were seen as streaming past one another, and increased the likelihood that they were seen as bouncing off one another.

In another demonstration, Bertenthal et al compared results when the objects approached one another at a constant speed (which should lead to a high degree of directional recruitment) with results when the objects slowed down as they approached one another (which should lead to diminished directional recruitment, because the objects do not activate a fixed set of bilocal detectors consistently). Again, the results were compatible with the predictions of directional recruitment: The speed change greatly decreased the likelihood of perceiving streaming, and increased the likelihood of perceiving bouncing.

The present experiments are motivated not only by an interest in the particulars of motion perception, but also by the chance to address a question of considerable generality in perception. In its clear ambiguity, Bertenthal et al's display is a reminder that all retinal stimulation underspecifies the distal stimulus. We look upon our experiments as a chance to explore, in a restricted relatively simple stimulus domain, factors that govern the perceptual resolution of retinal underspecification.

We report a series of experiments that explore the validity of Bertenthal et al's claim that the psychophysical bias toward streaming was the product of cooperative interactions among motion-selective mechanisms. In experiment 1 we introduced various temporal transients (occlusion, pausing, disappearance) into the targets' trajectory. Although any of these transients would disrupt the accumulation of information similarly within a set of bilocal detectors, each transient appeared to have a different effect on the perception of motion. In experiment 2 we varied the distances travelled by the objects. Although, in our experiment, directional recruitment should increase with the distance travelled, the distance had no consistent effect on the frequency with which observers perceived streaming or bouncing. Finally, in experiment 3 we varied the acceleration or deceleration of objects before and after collision. Although acceleration and deceleration should stimulate an equally large range of bilocal detectors, increased reports of bouncing occurred only when the objects decelerated as they approached one another. Our results suggest that the perceptual resolution of this particular ambiguous motion display is not primarily governed by directional recruitment.

## 2 Experiment 1

Before introducing theoretically motivated variations to the conditions tested by Bertenthal et al, we wanted to establish the replicability of some basic results. In our first experiment, observers saw a pair of white squares that continuously moved toward and past one another at constant speed from opposite sides of a computer screen. The observer reported whether the squares had appeared to stream through one another or to bounce off one another. In addition to the basic condition of constant uninterrupted movement, observers were also tested with pauses of varying duration introduced at the moment of coincidence between the squares. These Continuous and Pause conditions replicated Bertenthal et al's earlier work.

Because Bertenthal et al explained their results in terms of directional recruitment, we also tested two new conditions specifically designed to modulate directional recruitment. Previously, using a different paradigm, we had measured the rate at which the

precision of directional information builds up over time (A B Sekuler and R Sekuler 1993; A B Sekuler et al 1990). Those experiments showed that over as much as 500–600 ms, the representation of the direction of motion became increasingly precise. Most likely, given the frame duration of the stimulus, this growth in precision reflected directional recruitment within a relatively homogeneous set of motion mechanisms (cf Snowden and Braddick 1989a). We found that the accrual of directional information could be interrupted by any of a number of different transient events: a pause, a momentary disappearance, or even a brief occlusion. All three classes of temporal transients were equally effective in disrupting the accrual of directional information, as expected within the framework of directional recruitment. If the same processes were at work as in our own earlier measures, we would expect that, with Bertenthal et al's stimuli, disappearance, occlusion, and pause all would behave similarly. All of them would decrease the proportion of streaming percepts (increase the tendency to see bouncing relative to continuously moving stimuli). To test the hypothesis that various transients would be interchangeable in their effects, we created novel variants of Bertenthal et al's basic display in which the targets disappeared or were occluded when they coincided.

## 2.1 Method

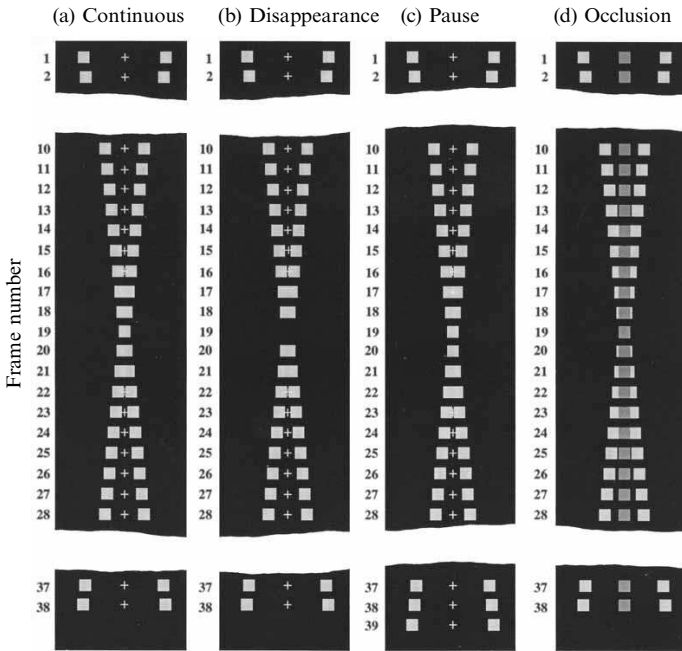
2.1.1 *Subjects.* Eight paid observers participated. All had normal or corrected-to-normal vision. None knew the aims of the study or had served previously as a psychophysical observer.

2.1.2 *Apparatus.* A Macintosh computer controlled the presentation of stimuli on an Apple 12-inch high-resolution monochrome monitor. Each observer viewed the display binocularly from a distance of 57 cm, with a chin-and-forehead rest steadying the observer's head, with the center of the display at eye level. A small fixation cross (0.6 deg) was present at all times in the center of the screen.

2.1.3 *Displays.* At the beginning of each trial two white squares appeared, one centered 6.7 deg to the left of the fixation cross and the other centered an equal distance to the right of fixation. Both squares were centered vertically within the display. The white squares were 1.07 deg on each side; their luminance was  $58.6 \text{ cd m}^{-2}$ , and they were presented against a steady, dark background of  $0.63 \text{ cd m}^{-2}$ . Immediately, the two squares began moving toward the center of the display in a series of small steps, each 21 min of arc. After reaching the center of the display, the squares continued to move, finally disappearing when each had reached the position originally occupied by its companion.

The complete sequence required 37 steps, each 60 ms, evenly distributed over 2.22 s; the combination of frame rate and displacement step size gave the squares an effective speed of  $5.83 \text{ deg s}^{-1}$ . Midway through the sequence, on the 19th frame, the two squares were perfectly superimposed. When the two squares overlapped, the computer set the area of overlap to a luminance of  $58.6 \text{ cd m}^{-2}$ , the luminance of either square alone. A portion of this sequence is illustrated in figure 1a. Details of this basic movement sequence, which constitute what we term the Continuous condition, were varied to create three other conditions: Disappearance, Pause, and Occlusion.

For the Disappearance condition (illustrated in figure 1b), the two squares disappeared from the screen on the 19th frame, when they would have been in perfect register. After a single frame (60 ms), the squares reappeared, shifted by one step (21 min of arc) left and right of center, and continued their journeys across the display. For the Pause condition (illustrated in figure 1c), when the squares were in register at the center of the display, they stood still momentarily, for either 1, 2, or 4 frames (60, 120, or 240 ms). For the Occlusion condition (shown in figure 1d), at the start of a trial a  $1.07 \text{ deg} \times 1.07 \text{ deg}$  gray square appeared in the center of the screen where it remained until the end of the trial. This static square completely occluded the moving squares



**Figure 1.** Schematic representation of the frames making up the four movement sequences used in experiment 1. Each frame shows the position of the target squares and the fixation cross. In each sequence, frames 3–9 and frames 29–36 are not represented explicitly. (a) Continuous motion: The target squares move toward one another at a steady pace from frames 1 to 18; they overlap on frame 19, and then move apart thereafter, from frame 20 to frame 38. (b) Disappearance: The target squares disappear on frame 19. (c) Pause: Note that the target squares do not change position between frames 19 and 20, indicating a pause for one frame. (d) Occlusion: A gray square is present at a fixed position in the center of the display throughout the sequence; on frame 19 the stationary gray square completely occludes the target squares.

when they reached its location. As the squares progressed towards the static occluder they were partially occluded on frames 17 and 18, and were completely occluded on frame 19; then as the squares emerged from behind the occluder they were again partially occluded on frames 20 and 21.

**2.1.4 Design.** The four conditions (Continuous, Disappearance, Pause, and Occlusion) were intermixed randomly in blocks of 100 trials, 25 trials for each condition. Observers were tested in six blocks (a total of 600 trials). The duration of the standstill in the Pause condition varied pseudo-randomly from block to block, with standstills of 1, 2, or 4 frames appearing in two blocks each.

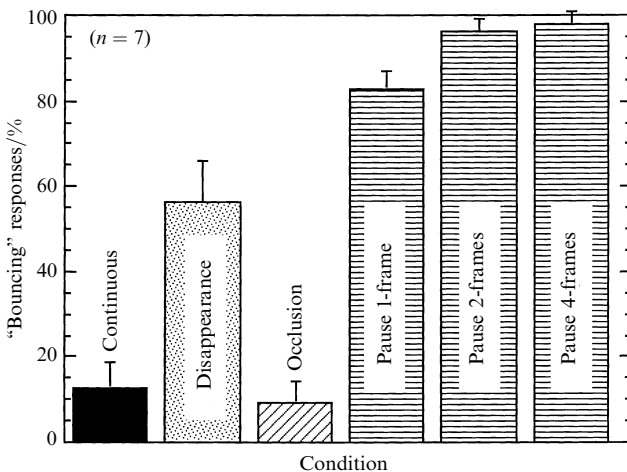
**2.1.5 Procedure.** Before the first trial, observers saw several sample stimuli, including some that, based on pretesting, should appear to stream, and others that should appear to bounce. Observers were instructed to fixate the small cross centered within the display screen. The observer ended a trial by using a computer keyboard to signal whether the two squares had appeared to stream or bounce; no other response alternatives were permitted. 500 ms after the response, the next trial's stimuli appeared.

## 2.2 Results

In this and subsequent experiments, although we tested eight observers, we present formal data analyses from only seven. After all of the experiments were completed, we discovered that one observer, GL, consistently made responses that were opposite those from the other observers. For example, whereas other observers in our study and in Bertenthal et al's (1993) responded that the Continuous stimuli appeared to stream and the Pause stimuli

appeared to bounce, GL reported the opposite (in this and subsequent experiments). Although this may in fact be a bona fide individual difference in observers' percepts, the consistent contrary nature of the responses suggests that GL may simply have mixed up the buttons corresponding "bounce" and "stream". Because we could not be certain that GL's responses reflected his percepts, the results are analyzed with his data excluded.

Figure 2 shows observers' average percentage of "bouncing" responses as a function of condition: Continuous, Disappearance, Occlusion, and Pause 1, Pause 2, Pause 4. Replicating one of Bertenthal et al's key findings, inserting a pause at the point of coincidence increased the tendency to see bouncing. In addition, the three types of temporal transients were distinct in their promotion of bouncing. An ANOVA confirmed that there were significant differences among the six conditions ( $F_{5,30} = 71.68, p < 0.0001$ ), and a posteriori analyses were made with Fisher's least-significant-difference tests. Continuous motion differed from each of the Pause conditions ( $p < 0.01$ ), but only Pause 1 versus Pause 4 differed from each other ( $p < 0.05$ ). Continuous also differed from Disappearance ( $p < 0.05$ ), but not from Occlusion. Occlusion differed from both the Pause conditions ( $p < 0.01$ ) and Disappearance ( $p < 0.05$ ), and, finally, the Pause and Disappearance conditions differed from each other ( $p < 0.05$ ).



**Figure 2.** Percentage of "bouncing" responses for various conditions: Continuous, Disappearance, Occlusion, and Pause 1, Pause 2, Pause 4, in experiment 1. Vertical lines indicate one standard error of the mean.

### 2.3 Discussion

Some of our results replicated Bertenthal et al's basic findings: The targets appeared to stream when motion was continuous and appeared to bounce when motion paused. The fact that more bouncing was seen with a 4-frame pause than with a 1-frame pause is consistent with the recruitment hypothesis, if one assumes that a longer pause leads to greater disruption of motion processing. However, relative to the effect of Continuous versus Pause, the duration of the pause—1, 2, or 4 frames—had only a minor effect. Even the briefest of our pause durations sufficed to shift the dominant percept from streaming to bouncing. Turning to the novel conditions tested, we see that not all transients caused the same perceptual shift. This variation in effect is not consistent with the recruitment hypothesis. Although "bouncing" responses did increase in the Disappearance condition, the effect of the disappearance of the squares was less potent than that of their pausing (for example, 56% "bouncing" with Disappearance versus 84% "bouncing" with the briefest Pause). In contrast to both Pause and Disappearance conditions, Occlusion failed to increase the proportion of "bouncing" responses, which remained at 10%.

Note that explicit motion information is temporarily disrupted by all three types of transients: pause, disappearance, and occlusion. Indeed, in both Disappearance and Occlusion conditions, the stimuli are momentarily absent from view. However, despite the fact that these three transient types all should have similar effects on directional recruitment, they led to strikingly different motion percepts.

#### 2.4 *Supplementary experiment*

To understand why the three transient conditions produced such divergent results, we homed in on the details of stimulation in those conditions. Normally, when one object moves in front of and then past another object, a characteristic set of deletion/accretion (cover/uncover) cues are generated (Gibson et al 1969). In our experiment, deletion/accretion cues were present in the Occlusion condition but were absent in the Disappearance condition. To see whether deletion/accretion cues alone could have accounted for the difference between Occlusion and Disappearance conditions, we re-tested five of our observers with a new condition, Gradual Disappearance, which omits an explicit visible occluder but nevertheless creates the accretion/deletion cues normally associated with an occluding object. The stimulus here was identical to that of the Occlusion condition except that the occluder was the same color and luminance as the background, and thus invisible.

Four of the five observers consistently perceived the objects as streaming past one another in the Gradual Disappearance condition, giving only 10% bouncing responses. However, one observer perceived bouncing 100% of the time. This same observer never perceived bouncing in the Continuous condition, and only 8% of the time in the Occlusion condition, so he clearly had not reversed his responses.

We asked observers to describe what they saw in the Occlusion and Gradual Disappearance conditions. The four observers who consistently perceived Gradual Disappearance as streaming used essentially the same words to describe both conditions. For example, observer WB described an Occlusion trial this way: "There was a box in the center that wasn't transparent, and blocks entering from the left and right simultaneously, which were mirror images of each other, at a nonconstant speed, which each passed through each other or superimposed behind the nontransparent box in the center." Of the Gradual Disappearance condition, this observer said: "I saw the same that I described before except when they meet in the center there was a black void with an x, but it leaves the impression that there is a square there and, like before, they either meet or superimpose and return where they came from." Observer DK, whose responses to the Gradual Disappearance condition were so different from those of the other observers, said of that condition: "It looks as if they bounce off the darkened part of the screen. They don't bounce off each other, they don't make it that close." An analogy to this sort of percept is the flip turn a swimmer might execute when she reaches the end of a pool: Her body compresses at the wall of the pool and then expands once she has turned about and is heading in the opposite direction, that is, she bounces off the wall of the pool.

When the squares appeared to move behind an occluder (real or illusory), subjects tended to see streaming; when gradual disappearance was not attributed to an illusory occluder, bouncing was seen. So accretion/deletion cues alone cannot predict the results of our first experiment. Instead, the perceptual outcome may be linked to the interpretation of the stimuli. The fact that, in our primary experiment, Disappearance led to a relatively balanced percept of "bouncing" and "streaming" also might be explained in terms of stimulus interpretation—specifically the degree to which the various conditions signal a continuation of object motion. In the Occlusion condition, observers perceived the object moving continuously while behind the occluder. In contrast, the Pause condition provided an explicit cue that motion had stopped. It may be that Disappearance is

the most ambiguous of the three conditions—sometimes being interpreted by the visual system as signalling motion continuation, and other times as motion stoppage.

The pattern of results in this single experiment clearly does not rule out the possibility that perceptual streaming stems from temporal recruitment. The next two experiments were designed to offer additional, converging evidence from more direct tests of the idea that the streaming bias results from cooperative interactions among directionally selective mechanisms.

### 3 Experiment 2

This experiment manipulated the strength of putative cooperative interactions by varying the pre-coincidence histories of the moving targets. Models of cooperative interaction among direction-selective mechanisms assume that longer trajectories produce stronger recruitment than do shorter trajectories. Experimental measurements suggest that cooperative interactions grow in strength with increasing trajectory lengths, up to 4–6 displacements (Snowden and Braddick 1989a, 1989b; Watamaniuk et al 1989). In experiment 2 we varied the starting positions of the squares so that, prior to their coincidence at the center of the display, they would have travelled greater or lesser distances. Some pre-coincidence trajectories in our experiment comprised fewer steps (3) than the recruitment limit; other trajectories comprised more steps (9 or 18) than the limit. According to current notions of recruitment, the 3-step condition should produce less effect than any of the longer sequences. Thus, if cooperative recruitment biases the visual system toward streaming, we would expect an increased proportion of “streaming” responses as the pre-coincidence trajectory lengthens, at least up to 6 displacements. This prediction reflects the fact that longer trajectories should produce increased recruitment.

#### 3.1 Method

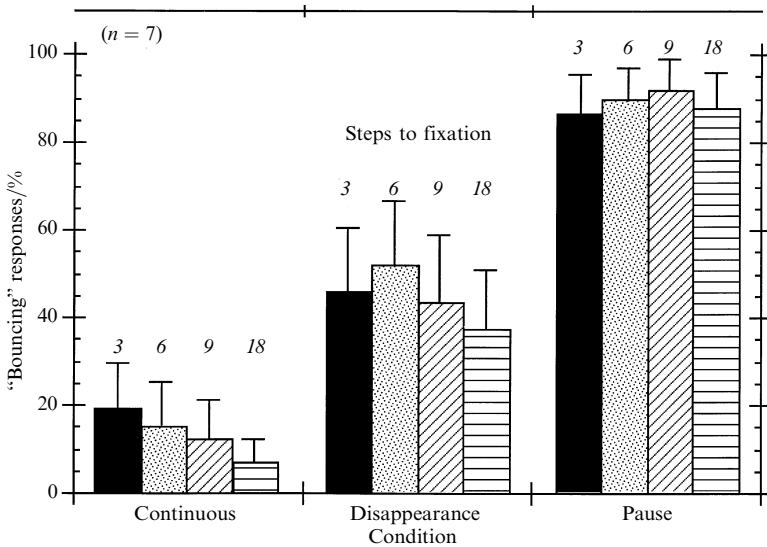
The eight observers from experiment 1 participated. Three of the movement sequences from experiment 1 were tested here: Continuous, Disappearance, and Pause (with a standstill of two frames). These conditions were identical to those of experiment 1, except that the starting and ending positions of the moving white squares varied randomly from trial to trial. At the start of each trial, the squares were centered either 1.4, 2.5, 3.4, or 6.7 deg from fixation (3, 6, 9, or 18 steps from coincidence, respectively). For all starting positions, when a square initially appeared  $x$  deg from fixation, it later disappeared  $x$  deg from fixation at the opposite side of the screen. Step size and frame duration were the same as in experiment 1.

The three movement conditions—Continuous, Disappearance, and Pause—were combined factorially with four starting–ending positions to yield a total of 12 conditions. Each of these 12 conditions was presented in random order six times per block; observers were tested in a total of four blocks. All other procedural details were as in experiment 1.

#### 3.2 Results

Figure 3 shows the mean percentage of “bouncing” responses for various conditions of motion—Continuous, Disappearance, and Pause. Within each condition, different bars show the results from 3, 6, 9, or 18 pre-coincidence steps. An ANOVA confirmed that there was a significant main effect of movement condition ( $F_{2,12} = 16.05$ ,  $p < 0.001$ ). However, neither the main effect of starting position nor the interaction between movement condition and starting position were significant ( $F_{3,18} = 2.037$ ,  $p > 0.14$ ;  $F_{6,36} = 0.740$ ,  $p > 0.5$ ; respectively).

Although results from the Continuous condition may suggest a tendency toward increased streaming with more pre-coincidence steps, this trend does not occur consistently in other conditions. In fact, in the Disappearance and Pause conditions, from 3 to 6 steps—the range of steps in which one would expect directional recruitment to increase most—the results suggest an opposite trend. Whereas the directional recruitment



**Figure 3.** Percentage of "bouncing" responses for Continuous, Disappearance, and Pause conditions in experiment 2. Within the data grouping for each condition, different bars show the results from 3, 6, 9, or 18 pre-coincidence steps. Vertical lines indicate one standard error of the mean.

hypothesis would predict an increased amount of "streaming" percepts from 3 to 6 steps, observers perceived slightly more "bouncing" with 6 steps than with 3 steps in both Disappearance and Pause conditions.

### 3.3 Discussion

Nearly fivefold variation in length and duration of pre-coincidence travel has no effect on the proportion of "streaming" reports. This result defies predictions based on the idea that streaming depends upon directional recruitment. The number of displacements in our trajectories spanned the range in which some variation in recruitment strength would be expected (Snowden and Braddick 1989a, 1989b; Watamaniuk et al 1989). Yet observers' tendencies to see streaming were unchanged. The impotence of trajectory length suggests that circumstances occurring well before coincidence are perceptually less consequential than circumstances at or near the moment of coincidence. In fact, the results of Anstis and Ramachandran (1987) suggest that recruitment effects are extremely local, and such a caveat to the recruitment hypothesis was suggested by Bertenthal et al (1993). Thus, the results from the present experiment and Bertenthal et al's results could be consistent with a nonlinear recruitment mechanism operating primarily over the first pair of frames prior to collision. Our third experiment pursued this possibility in more detail.

## 4 Experiment 3

Snowden and Braddick (1989a, 1989b) describe homogeneous recruitment processes as reflecting cooperative interactions among bilocal motion detectors that share a common spatial span,  $\Delta s$ , as well as a common temporal delay,  $\Delta t$ . Thus, such recruitment is both direction and speed selective.

Bertenthal et al (1993) exploited this property of directional recruitment to explain the result of speed variations as the targets approached one another. When the targets moved toward one another with fixed speed, as in the Continuous condition, after coinciding they appeared to continue moving in their original directions—to stream. However, when the targets decelerated as they approached one another and then accelerated after coincidence, the alternative percepts—streaming or bouncing—were



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reported with nearly equal frequency. The speed variation reduced the tendency to see streaming and therefore increased the tendency to see bouncing. Bertenthal et al related this finding to the strength of cooperative interactions among homogeneous motion detectors. They argued that pre-coincidence variation in target speed spreads neural activity over diverse motion detectors, thereby reducing the concentration of activity within detectors tuned to a single combination of target direction and speed. The result, according to this account, would be reduced homogeneous directional recruitment and a diminished bias toward seeing streaming.

Unfortunately, this result alone is not definitive with respect to the theory. If the phenomenon resulted from cooperative interactions among homogeneous motion detectors, then one would expect similar results regardless of whether the objects sped up or slowed down as they approached one another. Either situation, after all, would reduce homogeneous directional recruitment, but Bertenthal et al examined only the case of targets that slowed on approach.

In experiment 3, the movement sequence of targets was arranged so that targets either would speed up or slow down as they approached one another. In addition, we assessed the effect of circumstances (speed variation) that were proximate to or temporally remote from the targets' moment of coincidence.

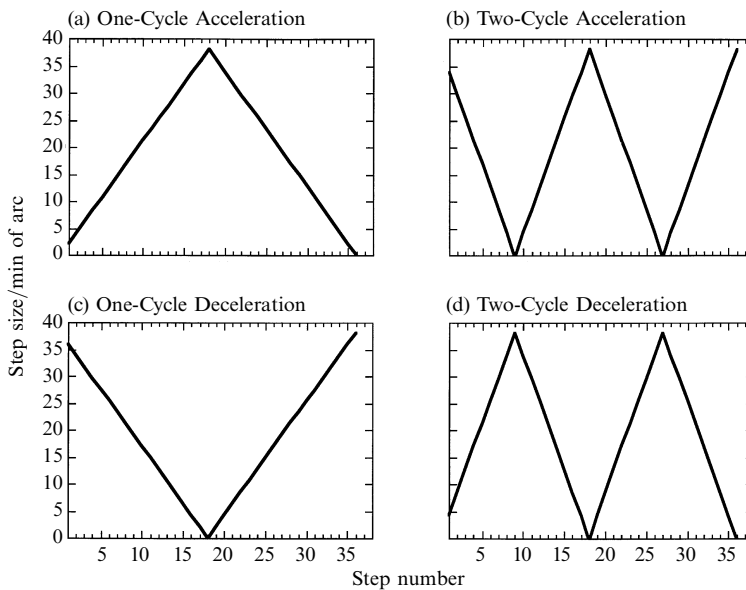
#### 4.1 Method

The same eight observers as in experiments 1 and 2 participated. At the beginning of each trial, the two white squares appeared at opposite sides of the screen, centered about fixation. They moved toward one another, reached superimposition on their 19th frame, and continued moving until they had travelled an equal distance beyond fixation. The squares then disappeared from the screen. Steps occurred every 60 ms, as in our preceding experiments. The starting and ending positions of the squares varied slightly among the four conditions illustrated in figure 4.<sup>(1)</sup> In two sequences (a and b), the squares accelerated as they approached the midpoint of their trajectories, when they overlapped and then began to decelerate; in the other two sequences (c and d), the squares decelerated as they neared superimposition and then began to accelerate. In all cases, object speed was governed by a triangular function of time, such that rates of acceleration and deceleration were constant.

The four sequences used in the experiment comprise factorial combinations of (i) the number of acceleration–deceleration cycles completed during a single trial (either one cycle or two), and (ii) whether the squares accelerated or decelerated as they approached coincidence. Therefore each movement sequence is denoted by a pair of terms in which the first term gives the number of acceleration–deceleration cycles, and the second term gives the direction of speed change just prior to coincidence.

At the start of a One-cycle Acceleration sequence, the squares were centered 6.04 deg left and right of fixation. Starting with a step size of 2.12 min of arc, the squares moved toward one another in successive steps that increased by 2.12 min of arc until they overlapped at the middle of the screen; thereafter successive steps decreased by 2.12 min of arc until the squares reached their terminal positions and disappeared. The maximum step size was 38.16 min of arc. This sequence is shown in figure 4a. For a One-cycle Deceleration sequence, the squares appeared 5.41 deg left and right of fixation, began moving with step size equal to 36.04 min of arc and, as they moved toward one another, successive steps decreased by 2.12 min of arc until the two squares were superimposed; thereafter successive steps increased by 2.12 min of arc until the squares reached their terminal positions and disappeared. As illustrated in figure 4c, the minimum step size in this sequence was 0 min of arc.

<sup>(1)</sup>This slight variation in starting and ending position is unlikely to have a material effect on our results because experiment 2 showed that far larger variations in these variables were without effect.



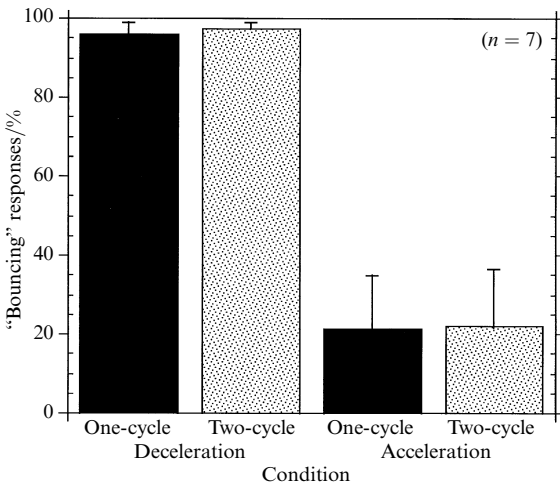
**Figure 4.** Schematic representation of movement sequences used in experiment 3. The sizes of steps taken by target squares are shown as a function of step number in the entire sequence. In all sequences, the target squares coincided on step 18 (frame 19). (a) and (b) Acceleration—conditions in which targets moved more rapidly as they approached coincidence. (c) and (d) Deceleration—conditions in which targets slowed down as they approached coincidence. (a) and (c) One-cycle—conditions in which targets went through just a single cycle of speed change, either speeding up and then slowing down (a) or slowing down and then speeding up (c). (b) and (d) Two-cycle—conditions in which targets went through two complete cycles of speed change on each trial. Steps occurred every 60 ms, as in our preceding experiments. Note that the starting and ending step sizes varied slightly among the four conditions.

The Two-cycle sequences were created by allowing successive steps to increase or decrease by 4.24 min of arc, twice the rate of change used for the One-cycle sequences. At the start of a Two-cycle Acceleration sequence, the squares were centered 5.72 deg left and right of fixation. Beginning with a step size of 33.92 min of arc, they moved toward one another in successive steps that decreased by 4.24 min of arc until the squares were one-quarter the way through their trajectories, when the step size had reached zero (see figure 4b). Successive steps then increased by 4.24 min of arc until both squares coincided at the center of the display. As seen in figure 4b, the maximum step size was 38.16 min of arc, as in the One-cycle Acceleration condition. Thereafter steps decreased during the third quarter of the trajectories and increased again until the squares reached their terminal positions and disappeared. For a Two-cycle Deceleration sequence the squares began 5.72 deg left and right of fixation. After an initial step of 4.24 min of arc, successive steps increased through the first quarter of the trajectory to a maximum of 38.16 min of arc, and then decreased by 4.24 min of arc until the two squares were superimposed (see figure 4d). As in the One-cycle Deceleration case, the step size reached zero at the point of coincidence. Thereafter, steps increased during the trajectory's third quarter, decreasing again until the squares reached their end positions, when they disappeared.

Each stimulus condition was presented in randomized order 25 times. All other procedural details were as in experiment 1.

#### 4.2 Results

Figure 5 shows observers' average percentage of "bouncing" responses as a function of number of cycles (One or Two) and direction of speed change (Acceleration or



**Figure 5.** Percentage of “bouncing” responses as a function of number of cycles (One or Two) and direction of speed change (Acceleration or Deceleration). Vertical lines indicate one standard error of the mean.

Deceleration). Compared to the results from Continuous conditions in experiments 1 and 2, Deceleration conditions increased the likelihood of perceiving bouncing, whereas Acceleration conditions had no effect whatsoever. An ANOVA confirmed that the direction of speed change, acceleration versus deceleration prior to coincidence, had a statistically significant effect ( $F_{1,6} = 23.623$ ,  $p < 0.005$ ). However, neither the number of cycles of speed change, nor the interaction between number of cycles and direction of speed change was significant ( $F_{1,6} = 0.117$ ,  $p > 0.50$ ;  $F_{1,6} = 0.017$ ,  $p > 0.50$ ; respectively).

#### 4.3 Discussion and supplementary experiments

Our results replicate Bertenthal et al’s finding that variation in speed can affect the way the display is seen: Decreasing speed as the targets approach coincidence increases the probability that they will appear to bounce. But Bertenthal et al’s explanation of this effect, as a product of directional recruitment, is not correct. Although both directions of change should produce the same dispersion of activation across speed-selective direction mechanisms, speed-up and slow-down behave differently. Only the condition of Deceleration produces increased reports of bouncing; Acceleration produces a preponderance of “streaming” responses, virtually identical in proportion to that of the Continuous conditions from our previous experiments. Because a condition with an 18-fold variation in speed produces the same tendency to see streaming as does a stimulus with no speed variation, we doubt that directional recruitment plays much role in controlling the percept.

For both deceleration and acceleration conditions, the two-cycle stimulus produced the same perceptual outcome as its one-cycle counterpart. This suggests that events early in the targets’ trajectories have little or no effect compared to events at or around the point of coincidence. This result is consistent with the finding, in experiment 2, that the length of trajectory prior to coincidence has no perceptual consequence.

Note that in both of our deceleration sequences—One-cycle Deceleration and Two-cycle Deceleration—velocity fell to zero at the moment of coincidence. This drop to zero velocity was designed to make our stimuli more consistent with those of Bertenthal et al, whose speed-varying stimuli also reached zero velocity at coincidence. However, the deceleration to zero introduced a momentary pause into the stimulus sequence. To ensure that the results from our Deceleration conditions—and from Bertenthal et al’s

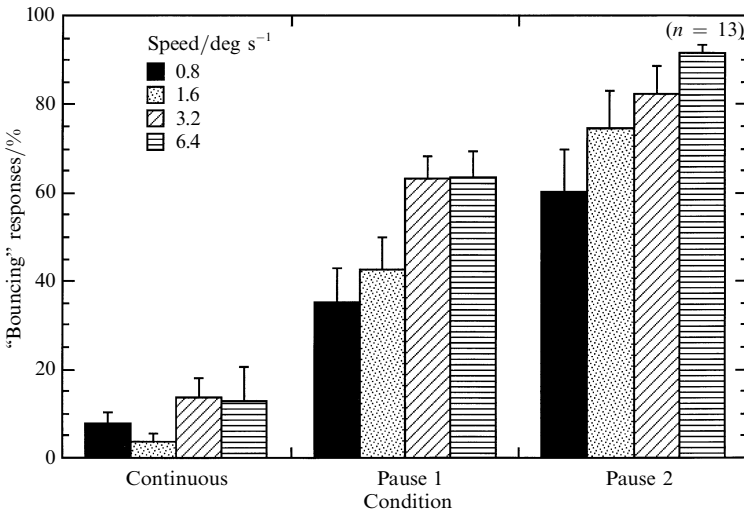
experiment—were not produced by the momentary pause, we re-tested five of our observers in another set of conditions: One-cycle Acceleration and Deceleration with the minimum step size set to 4.24 min of arc, rather than zero. We produced these conditions by adjusting the starting positions of the squares slightly, causing the squares to coincide on the 17th frame rather than the 19th. Because One-cycle and Two-cycle conditions produced virtually identical results in experiment 3, we tested only the One-cycle conditions here.

These conditions produced the same pattern of results as the comparable conditions in experiment 3, even though there was no pause in the present conditions. Observers mainly reported streaming for One-cycle Acceleration (73.6% “streaming”) and bouncing for One-cycle Deceleration (80.0% “bouncing”).

This control experiment showed that the inclusion of a pause was not necessary to invoke bouncing percepts in the deceleration conditions. However, there still remained a large difference in the speed around the point of contact in the two classes of conditions. In the Acceleration conditions, the average speed just before contact is relatively fast, and observers report mainly “streaming” percepts. In the Deceleration conditions, the average speed just before contact is relatively slow, and observers report mainly “bouncing” percepts. One possible explanation of our results, then, is that observers perceive more bouncing at slower contact speeds; we refer to this as the “speed-difference hypothesis”. The primary goal of our second control experiment was to test the speed-difference hypothesis; a secondary goal was to test the idea that extremely local recruitment, in just one or two steps before contact, drives the percept of streaming/bouncing. If that were the case, one would expect the speed-difference hypothesis to be supported. Thus, if only the one or two steps before contact are critical, we would expect to find more reports of “streaming” at faster speeds than at slower speeds.

In their original experiments, Bertenthal et al (1993) tested the effect of stimulus speed for stimuli moving at fixed speeds, and found essentially no effect of speed for Continuous stimuli. Although such a result is not consistent with the speed-difference hypothesis, Bertenthal et al varied speed by varying frame duration, whereas our stimuli held frame duration constant and varied step size. To determine whether the same results would hold under our conditions, we tested thirteen new observers in another control experiment. Here we tested the Continuous, Pause 1, and Pause 2 conditions for stimuli moving at fixed speeds of 0.8 to 6.4 deg s<sup>-1</sup> (step sizes 3.2, 6.4, 12.8, and 25.6 min of arc). Stimuli were presented at 15 frames s<sup>-1</sup>.

The percentage of “bouncing” responses is plotted as a function of condition and stimulus speed in figure 6. An overall ANOVA confirmed that there were significant main effects of speed ( $F_{3,26} = 8.3$ ,  $p < 0.001$ ), condition ( $F_{2,24} = 57.6$ ,  $p < 0.001$ ), as well as an interaction between speed and condition ( $F_{6,72} = 5.3$ ,  $p < 0.001$ ). The interaction resulted from the fact that whereas speed had no significant effect in Continuous conditions, faster speeds led to more “bouncing” responses in both the Pause 1 and Pause 2 conditions (as verified by an a posteriori Newman–Keuls test). Thus, the results stand in contrast to the predictions of the speed-difference hypothesis. When speed did have an effect, it was in the opposite direction than that predicted: faster contacts led to more perceived bouncing in the Pause conditions. We attribute this result to contextual determinants of the perceptual impact of a pause. Perhaps as a result of rapid neural gain control (Barlow 1997), any pause that follows fast motion may be more salient—and evoke stronger neural response—than the same pause following slow motion. Regardless of the underlying mechanism, however, the results of this second control experiment clearly show that speed at or just before contact does not account for the differences between our Acceleration and Deceleration conditions. What appears to be critical is not the speed at contact, but rather the way in which the stimuli change speed before making contact.



**Figure 6.** Percentage of "bouncing" responses as a function of condition and stimulus speed. Vertical lines indicate one standard error of the mean.

## 5 General discussion

Our experiments provide strong converging evidence that directional recruitment is not the main factor underlying the perception of motion in the displays with which we worked. In experiment 1, various transients, which should all have had similar negating effects on directional recruitment, led to dramatically different percepts. In experiment 2, increased activation caused by the addition of extra frames prior to coincidence should have increased directional recruitment, but the perception of streaming was uninfluenced by this manipulation. Finally, in experiment 3, although increases and decreases in speed should have disrupted homogeneous recruitment similarly, only decreases in speed led to increased bouncing percepts. Thus, none of the three predictions based on homogeneous directional recruitment was confirmed. We therefore can state with confidence that the perceptual resolution of our display's inherent ambiguity does not depend primarily upon directional recruitment. Clearly, one can never entirely eliminate the possibility that directional recruitment makes at least some contribution. One could posit that directional recruitment drives the perception of streaming/bouncing in some conditions (eg those used by Bertenthal et al), but not in others (those used in the current set of experiments). However, it is more parsimonious to suggest that a single, common mechanism underlies perception in all conditions. Because our set of results cannot be explained by directional recruitment, we argue that recruitment is not the critical mechanism that governs streaming/bouncing.

Unfortunately, we must be less confident in a statement about what *does* govern the resolution of the ambiguity, though, as shown below, our results do offer significant clues: the determining factor appears to be relatively local and it occurs after the processing of object completion. These issues, as well as the hypothesis that the results follow Newton's first law of motion, are discussed below.

### 5.1 The window of interaction

Results from experiments 2 and 3 suggest that visual resolution of the display's ambiguity depends only on events occurring close in time to the targets' coincidence. In experiment 2, viewing the stimuli moving at a constant velocity for over 1 s led to no more streaming than did viewing the stimuli for just one-fifth as long. Similarly, the One-cycle and Two-cycle speed variations in experiment 3 produced the same perceptual outcomes, even though the One-cycle condition contained half the speed variability of the Two-cycle

condition, and thus the latter might have been expected to lead to fewer streaming percepts. Perceptually, the determining factor in experiment 3 seemed to be the behavior of the targets at or around their rendezvous.

Although events temporally remote from the moment of coincidence have little or no effect on the balance of streaming and bouncing, we cannot now specify precisely the temporal window within which events are perceptually consequential. However, our results do not support the notion that recruitment in just the one or two steps preceding collision drives the percept of bouncing or streaming. If that were the case, then, as mentioned earlier, we would have expected to see a clear effect of the speed manipulation in our control experiment. Instead, what seems critical is the way in which an object's motion changes over time. Determination of the specific time frame during which such changes are perceptually most effective requires additional tests, involving systematic variation in asynchrony between temporal transients, such as a momentary pause, and the moment of coincidence.

### 5.2 *Psychoanatomy*

Consider the differential effects of the three types of transients introduced into the trajectories of experiment 1: Pause and Disappearance increased the proportion of "bouncing" responses, but Occlusion had no effect. The visual system treats the occluded targets as though they had moved continuously along complete, uninterrupted paths; much as in other circumstances, the visual system completes the representations of stationary partly occluded objects (A B Sekuler and Palmer 1992).

Julesz (1971) introduced the technique called psychoanatomy, which allows appropriate psychophysical observations to be translated into statements about the stages of human visual processing that produced those psychophysical observations. The result of experiment 1 with an occluding object provides some clues to the neural basis of the resolution by the visual system of the ambiguity present in our stimuli. Recall that, when an occluding square covered the point of coincidence between the moving targets, those moving targets were seen as streaming rather than bouncing. Research has shown that occlusion affects some motion phenomena (Shimojo et al 1989; Watamaniuk and McKee 1995; Yantis 1995), but not others (A B Sekuler and R Sekuler 1993). Such results can be used to specify whether the completion of partly occluded moving objects occurs before or after the processing of various types of motion information. For example, A B Sekuler and R Sekuler (1993) found that pause, disappearance, and occlusion all had the same effect on the precision with which direction information was extracted from a simple display with just one moving target. This suggests that the visual system takes completion into account *after* it has done some or all of the extraction of direction information. Because the extraction of direction information represents one of motion perception's most primitive components, it is not surprising that it takes place relatively early in the processing chain.

In contrast to those earlier results, in the present experiments various kinds of transients diverge in their effect on perceived motion. In particular, occlusion had no effect whatsoever on the tendency to see streaming, implying that the visual system takes completion into account *before* the generation of streaming or bouncing. If completion occurred afterwards, one would expect the effects of occlusion to mimic the effects of disappearance or pause. The motion phenomenon studied by A B Sekuler and R Sekuler (1993) and the motion phenomenon studied in the present paper undoubtedly depend upon different neural computations, and probably occur at different processing levels in the brain. In fact, Assad and Maunsell (1995) recently identified an area in primate cerebral cortex in which neurons complete the occluded portions of objects' trajectories. In the posterior parietal cortex, many neurons respond to partially occluded moving targets just as they respond to the same targets when

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they are not occluded. Assad and Maunsell's discovery does not rule out the possibility of comparable completion behavior by neurons in other cortical areas, earlier in the visual processing stream. Nevertheless, that occluded targets in our experiment appear to stream, just as their continuous counterparts do, suggests that the perceptual resolution of our display's inherent ambiguity takes place after the completion of occluded objects has occurred.

Note that the perceptual selection of streaming or bouncing requires not just the detection of motion or even the assessment of a single target's direction of motion. Instead, it requires the precise integration of information generated by two targets moving along quite different trajectories. Stoner and Albright (1993) proposed a theoretical framework that is generally consistent with the psychoanatomical statements made here. In their model, a first stage of motion detection precedes the computations that give rise to inferred figural relationships, including transparency and occlusion. These inferred figural relationships, in turn, precede the integration of signals produced by separate independently moving targets. Most likely, a full account of neural computations needed for many different motion tasks would require not just two stages of processing, but several. Additionally, a full account most certainly would include feedback as well as feedforward pathways to accommodate known state-dependent influences on motion perception (Maunsell 1995; R Sekuler 1995).

### 5.3 *Newton's first law of motion and satisfaction of natural-world constraints*

The behavior of two-dimensional stimuli traversing our computer display can be contrasted with the behavior of three-dimensional moving objects in the natural world. The structure of matter in the natural world constrains the behavior of objects that move about in that world. For example, the structure of matter makes it impossible for two objects to move into the same space at the same time. Coincidences in time and space between kinetic objects must give rise to inelastic collisions and some dissipation of kinetic energy, which can produce heat, sound, light, or other forms of energy. Such inelastic collisions also can cause physical deformation of the colliding objects. In contrast, our two-dimensional kinetic objects were not obliged to obey the constraints of the natural world. In the condition of continuous motion, our objects seemingly managed to coexist, happily occupying the same place at the same time. Their apparent collision produced neither any energy, such as a sound to herald the collision, nor a physical deformation. Our objects' constant velocity signified that no kinetic energy had been dissipated by their coincidence. Of course, with real objects the absence of a change in velocity would signify that the objects did not collide, but passed by one another, most likely in different depth planes.

Visual information associated with collisions in the natural world is so powerful that, by itself, it can create compelling illusory collisions with artificial two-dimensional stimuli. The best-known demonstrations of this phenomenon come from Michotte's studies of phenomenal causality, including his so-called launching and entraining demonstrations (1946/1963). In the natural world, immediate visual sequelae to collisions enable witnesses to appraise the magnitude of the collision and various attributes of the collision's participants. For example, a collision produces immediate changes in objects' velocities that reflect the objects' relative mass and hardness (Runeson and Vedeler 1993). Although ongoing argument surrounds the way in which such kinematic visual invariants might be processed, either directly or by means of an intermediate, heuristic representation (Hecht 1996), there is no argument about the perceptual power of such invariants.

The best-known generalization about motion in the natural world is Newton's first law of motion: When an object is moving in some direction, it will continue in that direction until acted upon by an outside force. Ramachandran and Anstis (1983) proposed that

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various phenomena of motion perception can be described as visual manifestations of Newton's first law. The argument hinges on two underlying ideas. First, that the human visual system operates in a world in which objects' movements are consistent with the characteristics captured in Newton's first law; second, that real-time analysis of objects' movements would be facilitated if the nervous system implicitly 'acknowledged' the validity of Newton's law. This acknowledgement, instantiated in neural circuits, would enable important, anticipatory responses to object movement. Note that we have not taken a position on the origin of nervous system's unspoken agreement with Newton's first law. That agreement could have developed during the course of evolution, perhaps as a result of advantages in natural selection; during the course of ontogeny, as a result of activity-dependent changes in an individual nervous system; or as a result of both phylogeny and ontogeny. Claims about neural mirroring of Newton's laws do not mean that such mirroring necessarily completely determines all perceptual and motor responses. Instead, such mirroring may be best understood as a strong persistent influence, but one that can be overridden. In fact, Kaiser et al (1992) found perceptual violations of physical laws when people made judgments about the actions depicted in computer animations.

We are aware that assertions about parallelism between vision and physics, which may be important in understanding our own empirical results, can be easily misinterpreted. The assertion of parallelism does not mean that an observer calls upon explicit knowledge of Newton's law when judging objects' motions. Rather it points to a set of rules that the visual system uses to resolve the underspecification of retinal information. Those rules, instantiated in neural activity and interactions, comprise the many constraints that neural computations must satisfy simultaneously. With many kinds of motion displays, perceptually important constraints are likely to include local smoothness and minimal distance. Caelli et al (1993) offer a good description of constraint-satisfying computations as they apply to motion correspondence, which is related to streaming and bouncing. Roughly speaking, streaming and bouncing can be described as alternative solutions to the correspondence problem created by our display's post-coincidence ambiguity. "Streaming" signifies one solution to that correspondence problem; "bouncing" signifies another.

For displays like ours and Bertenthal et al's, neural computations that derive objects' post-coincidence trajectories would likely operate on variables beyond the ones Caelli et al identified for the case of motion correspondence. These additional variables would include the depth planes occupied by the moving objects; the spatial and temporal details of visible trajectories at various times during a trial; the presence and position of other objects in the field, such as occluders; and other, nonvisual variables, such as sound and attentional modulation. In this view, retinal disparity information that the moving targets lay in widely separated planes would tip the computation strongly against "bouncing", because targets in different planes could not collide (see Bertenthal et al 1993, experiment 3). Post-coincidence perturbations in trajectory, which normally signal a loss of kinetic energy, would also contribute to the perception of collision, weighing in on the side of increased "bouncing". Even nonvisual information can promote increased "bouncing", if that nonvisual information signifies a collision. For example, R Sekuler et al (1997) found that "bouncing" responses increased when the onset of a sound was synchronized to the moment when the targets coincided. Finally, Watanabe and Shimojo (1998) have shown that when observers' attention was distracted from moving targets, either by exogenous or endogenous attentional cues, the proportion of "bouncing" responses increased. Thus, Watanabe and Shimojo suggest that attention modulates the tendency of the visual system to perceive an object as continuing to move in a constant direction.



In our experiments, and in Bertenthal et al's, "streaming" can be thought as the default *perceptual* outcome for continuous motion, which, not coincidentally, is the default *physical* condition described in Newton's first law of motion. Just as the absence of an outside physical force allows an object to continue in its motion, the absence of visual input that signals the action of an outside force allows neural computations to run to their default state. Unfortunately, such statements about default conditions lack disconfirmability, which reduces their usefulness as theoretical statements in their own right. However, such statements can serve as pointers to other, theory-valuable statements (Hecht 1996). For example, if one believes that perceptual streaming is a default condition, that belief points to variables that should have the power to undermine the default condition. Perturbations in attentional set and in target trajectories, such as momentary pauses, clearly are among the variables that are pointed to in this way.

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