Representational development of direction in motion perception: A fragile process

Allison B Sekuler
Department of Psychology, University of Toronto, Toronto, Ontario M5S 1A1, Canada

Robert Sekuler
Department of Psychology and Center for Complex Systems, Brandeis University, Waltham, MA 02254, USA and Department of Biomedical Engineering, Boston University, Boston, MA 02115, USA
Received 9 October 1982, in revised form 8 June 1993

Abstract. Response to a change in direction is more rapid if the target moves in a predictable direction before the change than if the pre-change direction is not predictable. However, if the target trajectory is viewed for approximately half a second before the change in direction, the effect of directional predictability disappears. Visual information gathered prior to change in direction is used to construct an increasingly more accurate representation of target trajectory. To study this process, we inject various temporal transients into the trajectory prior to the change in direction. We find that extraction of directional information is interrupted if: (i) motion continues along a constant trajectory, but the target disappears briefly behind an implicit or real occluder, (ii) the target pauses briefly, but remains visible, or (iii) the target changes speed briefly, while continuing to move in the same direction. The theoretical implications for motion perception are discussed. These implications include a framework for understanding interactions between stimulus-derived information and a priori information.

1 Introduction
Directional uncertainty impedes the detection of motion onset and retards the detection of directional change in moving targets. Specifically, when a target moves in a predictable direction, a change in that direction is easier to see than when the initial direction is unpredictable (A B Sekuler et al 1990). This effect of directional uncertainty can be neutralized, however, if the observer has a sufficiently long exposure to the initial motion before the directional change (A B Sekuler et al 1990). Presumably, this initial exposure yields sensory data that compensate for weak or unreliable cognitive information: cues derived from the stimulus itself reduce uncertainty and increase perceptibility. Such cues provide stimulus-derived information, which should be distinguished from any a priori information the observer might have about the stimulus. Of course, both types of information are instrumental in perception (eg Ball and R Sekuler 1981; Cohn and Lasley 1974; Davis and Graham 1981; R Sekuler and Ball 1977).

Although it has been little studied, coordination of stimulus-derived and a priori information is important in many real world situations. For example, in high-speed ball games such as baseball, a batter relies upon both types of information. Stimulus-derived information is derived from the current trajectory of the ball, whereas a priori information comes from having observed the pitcher’s delivery and subsequent flight of the ball during immediately preceding deliveries.

Our previous studies of directional uncertainty dissociated stimulus-derived information and a priori information. The dependent variable was the speed with which observers responded to an abrupt change in the trajectory of a moving target. If the initial direction was predictable, rather than random and therefore unpredictable, observers responded more quickly to a change in direction. The effect of uncertainty was indexed by the difference between (i) response time (RT) to change from an initial direction that was predictable, and (ii) RT to a similar change from an unpredictable
initial direction. When the duration of the initial trajectory was sufficiently long, the effect of uncertainty could be completely overcome. In particular, if the initial duration was as long as approximately 500 ms, response to change in direction was equally fast whether the initial direction had been predictable or not. Apparently, exposures on the order of 500 ms allow the visual system to extract stimulus-derived information about direction that is functionally equivalent to a priori information specifying a predictable initial trajectory (A B Sekuler et al 1990).\(^1\)

RT to change in motion enables one to examine the construction of a precise representation of a target trajectory. In the current study, we explore the fragility of this construction process. Our approach is to examine conditions that might interrupt or degrade the process of extracting directional information from the stimulus. Our main analytic tool is the brief disappearance of a moving target. The experiments described here address questions about the microgenesis of the directional representation of the target.

Why study target disappearance?

The perceptual completion of a partly occluded form requires several hundred milliseconds (A B Sekuler and Palmer 1992). Such completion is thought to occur relatively early in the visual processing stream, enabling its products to be used for object identification (Enns and Rensink to be published; Gerbino and Salmaso 1987; A B Sekuler and Palmer 1992), depth perception (Nakayama et al 1989), and some aspects of motion perception (Brown and Weisstein 1991; Shimojo et al 1989). Our aim was to make a similar assessment for the initial extraction of directional information.

As a first step towards understanding how perceptual completion relates to the extraction of directional information, we examined how much encoding of directional information takes place in the face of an analogue to occlusion—target disappearance. Also, by determining the conditions that interrupt motion processing, we sought better understanding of the mechanisms underlying the perception of directional change in particular, and motion perception in general.

In our experiments, brief disappearance of the target can be thought of as a surrogate for the momentary occlusion of a moving object as it passes behind some other object. In all but our final experiment, we opted against actually occluding our moving target because the continuous presence of an occluder would have narrowed our control over various spatiotemporal parameters that were of interest and would have introduced undesirable positional cues.

2 General methods

Stimuli were generated by, and presented on, Macintosh II or IIfx computers.\(^2\) A black fixation cross, 0.25 deg in diameter, was always present in the center of the screen (the location of target onset). At the beginning of a trial, a black disc (approximately 0.25 deg in diameter) appeared at the fixation cross, and immediately began to move. The initial direction of the disc was randomly chosen from a set of 24 different possibilities, spanning 360° in equal steps. The disc moved along its initial trajectory for a variable amount of time (the initial duration), and then suddenly changed direction by 30° counterclockwise (see figure 1). The frame duration was

\(^1\) The estimate of 500 ms reflects the time for essentially complete extraction of direction information, rather than just the time over which direction information is optimally integrated. The time to extract all the directional information may vary with direction uncertainty. For example, if the target trajectory was uncertain, but restricted to two, clearly different alternative directions (eg left or right), a far shorter exposure might be needed to extract all direction information.

\(^2\) Two computers were used because data were collected at different sites.
15 ms, with no interstimulus interval. In most experiments, target speed was constant at 1.25 deg s\(^{-1}\) (1.12 min arc per frame). Observers viewed the display binocularly from a distance of approximately 137 cm, and a chinrest stabilized the head.

Several naive volunteers (BB, NB, CF, MG, SM, PLP, PS, and JW) served as observers. All were paid for their participation, and all had normal or corrected-to-normal visual acuity. An observer began each trial with a button press, and responded as quickly as possible with another button press as soon as the directional change was detected. The observer was not asked to identify the direction of change, simply to respond as quickly as possible to any change in direction, while minimizing errors. RT was recorded to the nearest 5 ms and stored for later analysis.

There were two types of trials. In one, the moving target was visible throughout its entire trajectory. We will refer to this trial type as a 'Continuous trial'; it is schematically represented in the top sequence of figure 2. In the second type of trial, the moving target briefly disappeared for some portion of its initial trajectory, and then reappeared as though it had continued its motion invisibly. A random interval after reappearing, the target changed direction. We will refer to this type of trial as a 'Disappearance trial'; it is schematically represented in the bottom sequence of figure 2. Note that the starting time and duration of the disappearance were randomized, although this is not illustrated in the figure. For purposes of exposition and analysis, one can think of the total initial trajectory in Disappearance trials as comprising three phases: pre-disappearance, disappearance, and post-disappearance.

**Figure 1.** Schematic illustration of possible trajectories during the experiments. Stippled arrows represent the initial direction of motion; dark arrows represent the direction of motion after the 30\(^\circ\) counterclockwise change. The duration of the initial and post-change trajectories varied as described in the text.

**Figure 2.** The top panel illustrates the continuous trial type in which the moving target was always visible. The bottom panel illustrates the disappearance trial type in which the target disappeared briefly for some portion of the initial trajectory. The initial duration of Disappearance trials comprised three phases: pre-disappearance, disappearance, and post-disappearance.
3 Predictions

In the analyses below, RT to direction change is plotted against the duration of the initial trajectory (hereafter, such a plot is called an RT function). For Continuous trials, RTs are always plotted against the total duration of the initial trajectory. For Disappearance trials, one can define duration in more than one way, depending on whether or not processing is interrupted by the target disappearance. To determine how the visual system itself defines duration, we need to search for the definition that makes the RT functions from Disappearance and Continuous trials most similar. Consider now two alternative definitions of duration for Disappearance trials.

If processing were unaffected by target disappearance, RT functions for the two trial types could be made congruent by defining the duration of Disappearance trials as the sum of all three components of the initial trajectory: pre-disappearance + disappearance + post-disappearance phases. This sum is the total duration. Note that this definition of duration asserts that processing proceeds normally while the target is invisible; in other words, information about direction is 'filled in' during the absence of the target. This prediction is illustrated in figure 3a: RT decreases rapidly at first, and then becomes asymptotic. The estimated shape of this function was derived empirically from previous work (A B Sekuler et al 1990).

Suppose that processing were interrupted by target disappearance. If no processing occurred during disappearance, but all previously obtained information was retained, the RT functions for the trial types would be made congruent by defining the duration of Disappearance trials as the sum of pre-disappearance and post-disappearance phases. This would confirm that while the target was invisible all pre-disappearance processing was retained and built upon by post-disappearance processing, though no additional information was accrued in the absence of the target. This prediction is illustrated in figure 3b; the shape of this function is the same as in 3a, but the

**Figure 3.** Predictions associated with three definitions of initial duration for Disappearance trials. The Continuous RT function should be congruous with (a) the total duration RT function if processing is unaffected, (b) the pre + post duration RT function if processing is partially interrupted (suspended), or (c) the post duration RT function if processing is totally interrupted (disrupted).
function is shifted leftwards. It is also possible that pre-disappearance processing might be nullified in addition to processing being suspended by target disappearance. The prediction in this case would be a further leftward shift of the RT function because only the post-duration phase would be taken into account (figure 3c). Generally, our method cannot differentiate between (i) mere suspension of processing during disappearance and (ii) the destruction of previously obtained information. For this reason, although we will plot all three predictions, we will generally restrict our conclusions to whether or not processing is interrupted, where 'interruption' implies a break or discontinuity in perceptual processing, whether partial or complete.

4 Experiment 1: Exploration of temporal properties
4.1 Experiment 1a
In this experiment we sought to determine whether target disappearance interrupts the accumulation of direction information, and if so, whether some minimum disappearance duration is required for processing interruption.

4.1.1 Methods. For two subjects—JW and MG—the total duration ranged from 90 to 1000 ms, with the following possible phase durations: pre-disappearance, 30–100 ms; disappearance, 30–600 ms; and post-disappearance, 30–300 ms. For the third subject—SM—the total duration ranged from 90 to 1200 ms, with the range of times in the post-disappearance phase increased to 30–500 ms. Note that for all observers the duration of the disappearance phase covered a wide range, whereas the duration of the pre-disappearance phase was fairly constant and quite short. Each of 5 test blocks included 10 practice trials followed by 200 experimental trials per condition. Continuous and Disappearance conditions were block randomized. Results were analyzed separately for each disappearance duration in 100 ms bins.

4.1.2 Results and discussion. Figure 4 shows the results for observers MG and JW for the briefest disappearances—30–100 ms. For both observers, Continuous and Disappearance functions are most congruent for RT functions consistent with interruption (pre and post-disappearance, or post-disappearance duration functions). Seemingly, then, even a very brief disappearance interrupts the processing of direction information.

![Figure 4](image-url)

**Figure 4.** Results for two subjects with the shortest disappearance duration in experiment 1a. The solid line represents the Continuous RT function, and the symbols represent predictions from the three possible definitions of initial duration in Disappearance trials: circles represent the total duration prediction (no effect), triangles represent the pre+ post duration prediction (suspension), and squares represent the post duration prediction (disruption). The average standard error is 11.0 ms for MG, and 11.4 ms for JW.
To provide a clearer comparison, observer SM was tested over a larger range of post-disappearance durations. Figure 5 shows SM’s results.(3) Note that the critical

![Figure 5. SM's results for experiment 1a for all disappearance durations: (a) 100 ms, (b) 200 ms, (c) 300 ms, (d) 400 ms, (e) 500 ms, and (f) 600 ms. Symbol representations are as in figure 4. The average standard errors are 11.4, 9.3, 12.5, 10.3, 10.1, and 12.2 ms in panels (a)–(f), respectively.](image)

(3) In the interest of saving space, complete results will be given for only observer SM in experiments 1–3. This is because SM was the only observer to complete all of those experiments, and he was always run under conditions providing maximal comparison among the various predictions. Unless otherwise noted in the text, the results for all other observers were similar to those of SM.
portion of the curves are those in which RTs are changing as a function of duration; the asymptotic portion is less diagnostic because all functions should eventually overlap at asymptote. For all disappearance durations target disappearance clearly has an effect, although for the temporal parameters tested there is no systematic effect of disappearance duration. In other words, processing was interrupted for all disappearance durations tested, including those as brief as $30-100$ ms.

Figure 6. SM's results for experiment 1b for all pre-disappearance durations: (a) 100 ms, (b) 200 ms, (c) 300 ms, (d) 400 ms, (e) 500 ms, and (f) 600 ms. Symbol representations are as in figure 4. The average standard errors are 13.5, 13.1, 11.0, 12.0, 13.3, and 14.0 ms in panels (a)–(f), respectively.
4.2 Experiment 1b

In experiment 1a, pre-disappearance duration was limited to 30–100 ms—a relatively short time. Longer pre-disappearance durations might immunize against the interruption of processing for at least two reasons. First, accrual of stimulus-derived direction information is known to continue for up to 500–700 ms (A.B. Sekuler et al. 1990). Obviously, then, a very short pre-disappearance period permits just a fraction of the direction information to be extracted. Second, previous research has shown that the completion of partly occluded objects can take 200–400 ms (A.B. Sekuler and Palmer 1992). It may be that for the task at hand, occlusion cues can be taken into account only after several hundred milliseconds. If so, we would expect to find no effect of disappearance for pre-disappearance durations greater than 200–400 ms. In the present experiment, we ask: “Is the degree of processing interruption related to the pre-disappearance duration?”

4.2.1 Methods

The total duration ranged from 260 to 1400 ms, with the following combinations of durations: pre-disappearance, 30–600 ms; disappearance, 200–300 ms; post-disappearance, 30–500 ms. Note that, in contrast to experiment 1a, the pre-disappearance phase had the largest range of durations. Variation in disappearance phase duration was relatively small. CF and SM each completed 5 test blocks and PLP completed 6 test blocks, where each block included 10 practice trials followed by 200 experimental trials per condition. Continuous and Disappearance conditions were block randomized. Results were analyzed separately for 100 ms bins of pre-disappearance durations.

4.2.2 Results and discussion. For all observers, direction processing was interrupted even when the moving target had been viewed for 600 ms before it disappeared, although the observers differed in the extent to which processing was interrupted. Observer SM exhibited the largest effects of interruption, with the Continuous RT functions falling between pre+post-disappearance and post-disappearance RT functions (see figure 6). The general pattern of results was similar for the two other observers.

For all observers, pre+post-disappearance and post-disappearance functions were quite similar for the shortest pre-disappearance durations (30–100 ms), so we cannot determine whether interruption is partial or complete. More-sensitive measures are required to determine whether interruption is more severe for very short pre-disappearance durations. In any case, directional information is not ‘filled in’ during the absence of the target, even when the target motion is previewed for up to 600 ms.

5 Experiment 2: Effects of positional uncertainty

Might disruption in motion processing with target disappearance be due not to disappearance itself, but rather to an associated factor, positional uncertainty? On Disappearance trials, the observer could never be sure precisely where the target would reappear. Such uncertainty, of course, would not occur on Continuous trials. Previous researchers have shown that the detectability of static targets is greater when the observer has a priori information about the position in which a target will appear, than when the observer is uncertain about where the target will appear (Cohn and Lasley 1974; Greenhouse and Cohn 1991). To determine whether the disruption we observed was related to positional uncertainty, rather than to motion processing per se, we conducted an experiment in which a third condition was added where the target was always visible, but paused briefly instead of disappearing. We will refer to this condition as ‘Pause’.
5.1 Methods
The total duration ranged from 90 to 1200 ms, with the following phase durations: pre-disappearance (or pre-pause), 30–100 ms; disappearance (or pause), 30–600 ms; post-disappearance or (post-pause), 30–500 ms. As in experiment 1a, the disappearance phase had the largest range of possible durations, while the pre-disappearance phase durations were relatively constant and brief. Both observers (CF and SM) completed 5 blocks, where each block contained 10 practice trials followed by 200 experimental trials per condition. Continuous, Pause, and Disappearance conditions were block randomized.

5.2 Results and discussion
Figure 7 shows results from Disappearance, Pause, and Continuous conditions for observer SM. RTs have been averaged across all disappearance/pause durations.\(^{(4)}\) Regardless of whether the target disappeared or merely paused, some degree of interruption is evident. Even when the target remained continuously visible, a brief pause in its movement interrupted directional processing. Therefore, positional uncertainty alone cannot explain the results from experiment 1.

![Graph showing response time vs. initial duration for Pause and Disappearance conditions](image)

**Figure 7.** SM's results for experiment 2. The left panel shows results for the Pause condition, and the right panel for the Disappearance condition. Symbol representations are as in figure 4. The average standard error is 8.0 ms for Pause, and 10.6 ms for Disappearance.

6 Experiment 3: Effects of brief speed changes
Experiments 1 and 2 showed that if a moving target briefly disappeared or paused, the processing of direction information was altered. To put it another way: when the visual system is momentarily cut off from information about direction of an object, direction processing is interrupted. We wondered whether the interruption was limited to manipulations of direction per se, or whether other transients might interfere with the accrual of directional information. For example, a brief stimulus pause alters the information available about speed as well as direction; in this case, a pause can be considered an extreme change in speed without a change in direction. In this experiment we examined the effects of introducing a brief speed change into the initial trajectory. Note that a priori a change in speed need not necessarily interrupt direction processing. For example, if speed information were processed independently of direction information, or processed after direction (cf Driver et al 1992), a change in speed should have no effect on the accumulation of direction information.

\(^{(4)}\) We averaged across all durations here because, as results from experiment 1a showed, for these temporal parameters, increasing disappearance duration has no systematic effect on RT functions. The possibility remains that increasing disappearance duration might have a systematic effect if pre-disappearance durations were longer.
6.1 Methods
The trial structure illustrated in figure 2 was maintained with the addition of a new condition. Rather than disappearing, the target was visible but changed speed during what had been the disappearance phase in previous experiments. We refer to this phase of the initial duration as the speed-change phase, and we refer to this trial type as 'Speed-varying'. There were two subtypes of Speed-varying trials: 'Slow trials' and 'Fast trials'. On Slow trials the target moved at a third of the standard speed (approximately 0.42 deg s\(^{-1}\)) during the speed-change phase; on Fast trials the target moved at three times the standard speed (approximately 3.75 deg s\(^{-1}\)) during the speed-change phase. As before, frame rate was 67 Hz, and we varied the step size to manipulate speed. Note that the differences associated with these speed changes are well above speed difference thresholds (DeBruyn and Orban 1988; McKee 1981; McKee and Nakayama 1984).

The total duration of a trial ranged from 260 to 1000 ms, with the following phase durations: pre-disappearance (or pre-speed-change), 30–200 ms; disappearance (or speed-change), 200–300 ms; post-disappearance (or post-speed-change), 30–500 ms. Two observers—CF and SM—completed 5 blocks, where each block contained 10 practice trials followed by 200 experimental trials per condition. A third observer—PS—completed 3 blocks, where each block contained 10 practice trials followed by 100 experimental trials per condition. Continuous, Disappearance, Fast, and Slow conditions were block randomized.

6.2 Results and discussion
Results for SM are shown in figure 8; results for the other two observers follow the same general pattern. The solid line in each panel shows the RT pattern for Continuous trials. The right panel replicates SM's previous results for the Disappearance condition, and the central and left panels show RT patterns for Fast and Slow conditions, respectively. In every case, the Continuous and Disappearance functions are most similar when duration is defined as pre + post-disappearance or post-disappearance duration. As before, a relatively brief disappearance (200–300 ms) appears to interrupt the processing of directional information. In addition, these results suggest that a brief change in speed interrupts the accrual of stimulus-derived direction information. Further research is needed to specify precisely whether and how the interruption from a speed change compares with that from target disappearance.

What ought one make of the fact that a change in speed can interrupt the processing of directional information? Recall that in the Speed-varying conditions the target

![Figure 8](image-url)  
Figure 8. SM's results for experiment 3. The left panel shows results for the Speed-varying Slow trials condition, the central panel for the Fast trials condition, and the right panel for the Disappearance condition. Symbol representations are as in figure 4. The average standard errors are 14.6, 14.0, and 18.8 ms, for Slow trials, Fast trials, and Disappearance, respectively.
was always visible; it merely changed speed for some brief period of time while continuing to move in a constant direction. As stated earlier, one would not expect an effect of manipulating speed unless the mechanisms that encode direction were also sensitive to speed or received input from mechanisms that were. In this view, a change in speed interrupts processing of directional information because directional information is accumulated within mechanisms sensitive to different ranges of speed. When speed changes (despite direction remaining constant), information is integrated imperfectly over speed-tuned mechanisms. This notion is examined in more detail in section 8.

7 Experiment 4: Implicit versus explicit occlusion
One goal of our experiments was to determine how cognitive and sensory processes interact in motion perception. To this end, in our initial experiments we examined the effects of an analogue to occlusion—target disappearance—on the encoding of directional information. The results of our initial experiments show that directional information was not 'interpolated' or 'filled in' when the target disappeared. However, all subjects reported that the identity of the spot was preserved phenomennally across its disappearance. For the task at hand, processing of sensory information appears to dominate, while cognitive processes, including recognition of target identity, are relegated to a supporting role.

The question remains whether there exist conditions under which cognitive processes do influence the extraction of direction information. In our previous experiments target disappearance was meant to mimic occlusion, but the mimicry was not perfect. The target merely disappeared and then reappeared all at once, producing none of the deletion–accretion cues created when an object moves behind an occluder. Also, for methodological reasons explained before, no other object was present. Thus, the 'occluding object' in our experiments can be described as implicit, rather than explicit. This distinction is important because, under some circumstances, implicit and explicit occluders affect perception differentially, with explicit occluders—but not implicit occluders—supporting the continuation of perceptual processing (e.g. Enns and Rensink to be published; Shimojo et al 1989; Weisstein et al 1972).

This difference between explicit and implicit occluders raises the possibility that our previous experiments might have turned out differently if we had used an explicit, rather than an implicit, occluder. Recall that we initially chose an implicit occluder because the presence of an explicit occluder narrows control over various spatio-temporal parameters that are of interest, and the presence of an explicit occluder also introduces positional cues that can contaminate the results. However, direction information might have continued to accrue when an object was passed behind an explicit occluder, even though such information was certainly interrupted by an implicit one.

7.1 Methods
At the beginning of a block of trials, one of two transparent overlays was placed over the computer screen. One overlay, used for Continuous and Disappearance conditions, held only a fixation cross, which was aligned with the fixation cross on the screen. The other overlay, used for the Occlusion condition, held a fixation cross centered with a black, opaque annulus that occluded the disc when the disc moved behind the annulus. The width of the annulus was chosen so that it would occlude the disc, moving at 1.25 deg s⁻¹, for 300 ms (counting from the moment that half the disc was first occluded until half the disc had reemerged). The duration of this occlusion coincided exactly with the duration of the target disappearance with the fixation-only overlay.
The duration of each trial ranged from 530 to 1500 ms. The pre-disappearance or pre-occlusion duration was always 200 ms, the duration of disappearance or occlusion was always 300 ms, and the post-disappearance or post-occlusion duration ranged from 30 to 1000 ms. Two observers—BB and NB—completed 200 practice trials for each of the Continuous, Disappearance, and Occlusion conditions, followed by 2 test blocks, where each block contained 10 practice trials followed by 200 experimental trials. The three conditions were tested in block-randomized order.

7.2 Results and discussion
RT functions for the two observers are shown in figure 9. The post-disappearance and post-occlusion RT functions have been omitted for the sake of clarity. For both observers, the explicit occluder and the implicit occluder had similar effects on RT. For both definitions of initial duration, total duration and pre + post-duration, results from the Disappearance condition are congruent with results from the Occlusion condition at the shortest durations (the most diagnostic portion of the functions). Also, for both Disappearance and Occlusion, the results are consistent with a processing interruption. For both conditions, the Continuous RT functions are similar to the pre + post-duration RT functions. However, conclusions about the degree of interruption must be tentative for this experiment because the presence of an explicit occluder limits the number of comparison points at the shortest durations. In this experiment, the shortest possible Continuous duration was more than 500 ms because before changing direction the target had to move beyond the position where the outer edge of the occluder would have been; however, for both observers, the most diagnostic (nonasymptotic) points on the pre + post RT functions are at durations less than 500 ms. In any case, the fact that Disappearance and Occlusion RT functions overlap suggests that the accrual of direction information is affected similarly by implicit and explicit occlusion for the task at hand.

![Figure 9. NB and BB's results for experiment 4. The solid line represents the Continuous RT function, and the symbols represent predictions from two possible definitions of initial duration in Disappearance trials (filled symbols) and Occlusion trials (open symbols). Circles represent the total duration predictions, and triangles represent the pre + post duration predictions. The average standard error is 11.4 ms for NB and 7.2 ms for BB.](image_url)

8 General discussion and summary
Our experiments show that a variety of events can interrupt the processing of information about target direction. Processing is interrupted if: (i) motion continues along a constant trajectory but the target disappears behind an implicit or explicit occluder, (ii) motion ceases briefly but the target remains visible, or (iii) the target changes speed briefly while continuing to move in the same direction. In the face of these transient events, constructing an accurate representation of direction seems to be a fragile process, vulnerable to even the briefest transient.
Injection of diverse transients allowed us to explore the encoding of direction. Although one might imagine that transient events not related to direction per se would not be disruptive, we found that transient changes in speed did interrupt the accrual of direction information. We speculate, therefore, that direction encoding occurs within mechanisms tuned jointly for direction and speed. The idea of mechanisms tuned jointly for direction and speed draws support from two other studies in which procedures quite different from ours have been used. Driver et al (1992) examined the question of integrality using the visual search paradigm (e.g. Treisman 1988). Their results are consistent with jointly tuned detectors in the visual system. However, Driver et al suggest that whereas speed cannot be encoded independently of direction, direction can be encoded independently of speed. The implications of this latter conclusion are discussed further in section 8.3. Bertenthal et al (1993) studied the directional judgments made when two rectangles approached one another from opposite sides of a display, passed over one another, and then continued to move apart. After the momentary superimposition of the rectangles, their trajectories were equally consistent with two alternative percepts: the two rectangles could have continued to move in their initial directions, or the rectangles could have 'bounced off' one another, reversing directions. When the initial velocities of the rectangles were constant, observers almost always reported that the two rectangles appeared to continue their initial directions. However when the initial motions of the rectangles varied in speed (with the direction kept constant), observers reported the alternative, 'bouncing' percept with greater frequency. Just as our own experiment 3 showed, a change in speed affects a response that one might otherwise imagine would depend on direction alone.

Experiment 2 showed that a brief pause in the movement of the target could also affect the extraction of direction information. This result too has a counterpart in Bertenthal et al (1993). In one of their conditions, the criss-crossing rectangles ceased their steady movement momentarily, pausing for one frame while they were superimposed. This slight perturbation of the trajectory had an impact far out of proportion to its duration or saliency. The brief pause significantly diminished the tendency to see the rectangles continuing to move in the same direction, and increased the tendency to see their directions as having reversed. We turn now to a qualitative mechanistic model that can account for interruptions from stimuli disappearing, pausing, or changing speed.

8.1 A qualitative model: part one

In the present study and the earlier one by A.B. Sekuler et al (1990), we examined representation of target direction by the visual system, particularly the microgenesis of that representation. We construe the key features of that representational development as follows. The visual system samples directional information from the outputs of several stochastic directionally tuned channels. (For a discussion of noisiness of such channels see Wang et al 1990.) Over time, estimates from successive sampling epochs are combined in a running average, weighted non-linearly by the number of epochs. This nonlinear temporal integration is consistent with several results, including those of Snowden and Braddick (1989) and of Watamaniuk et al (1989). A notable feature of the nonlinearity is a heavy weighting for recency. By computing a nonlinearly weighted running average, successive samples result in an increasingly accurate representation of direction. After enough samples, the accuracy of the stimulus-derived representation matches the accuracy of a representation based on a priori information about a perfectly predictable trajectory.

The running average could reflect sequential stimulation of mechanisms having homogeneous spatial and temporal tuning, as described by Snowden and Braddick (1989).
This form of temporal recruitment, termed 'homogeneous recruitment', reflects cooperative interactions among bilocal detectors that share a common spatial span, $\Delta s$, and temporal delay, $\Delta t$. Because such detectors are speed selective (for a speed of $\Delta s/\Delta t$) any change in the target speed redefines the set of stimulated bilocal detectors. Because homogeneous recruitment involves activation of bilocal detectors tuned to a common direction, and having similar $\Delta s$ and $\Delta t$, the opportunity for recruitment is diminished by a change in motion that shifts activation from one set of bilocal detectors to another. From this perspective, then, it is not surprising that changing the speed of a target interferes with the extraction of direction information, as we found in experiment 3 and as Bertenthal et al. (1993) found when they introduced speed variation into their display.

The shift in activation from one set of bilocal detectors to another set can also occur when a target briefly disappears or pauses. In addition, if the target briefly disappears or pauses, many directionally tuned channels may respond to the transient in equal measure, adding noise to the current estimate of target trajectory. This noise would degrade the direction estimate. As mentioned earlier, we suppose that, like most sampling processes, the direction estimate improves with additional samples (frames). Thus, the disappearance or pause of a target visible for just a short time could be particularly disruptive because it introduces noise into a representation that is particularly vulnerable to even a few erroneous samples. This hypothesis requires additional research.

8.2 A qualitative model: an extension
As noted before, our experimental task encourages the combination of information from two sources: a priori information and stimulus-derived information. The former reflects observers' expectations about potential trajectories; the latter derives from observing the actual trajectory. A complete theory of our task and results must incorporate both sources of information. The statistical explanation sketched out in the preceding section incorporates only one of these sources of information—stimulus-derived information; in the present section we seek to flesh out the picture.

We believe that in our experiments the visual system constructs and continuously refines a mental template of a moving target. This template or representation can guide the extraction of additional directional information, which in turn further refines the template. In our experiments, some of the data used in this process probably come from velocity-tuned bilocal correlators, as suggested in the preceding section. How, though, might expectation about target trajectory make its mark on the mental template?

Ball and Sekuler (1981) showed that explicit attention to specific stimulus attributes boost the detectability of targets moving in particular directions and/or at particular speeds. They also demonstrated the converse, that wrong expectations about target movement can diminish detectability. Empirically, then, expectation strongly modulates the extraction of directional information. One way to conceptualize such effects is provided by adaptive resonance theory (ART), a family of neural network architectures that assign an important role to interactions between a priori and stimulus-derived information (e.g. Carpenter and Grossberg 1990).

Although a full discussion of ART networks is beyond the scope of this paper, comments about two of their attributes are in order. First, within the input layer of the network, each node combines three different influences: incoming sensory data, specific expectations about the sensory data, and a nonselective modulatory control signal. Successful activation of a node within the input layer requires that two of its three potential inputs be active. This two-thirds rule allows the ART system to be selectively primed by the expectation of some particular event or pattern. Second, the
input layer of the network and its output or classification layer are interconnected via feedforward and feedback vectors whose weights adjust or adapt over time. While the system attempts to recognize or classify some input, information filters back and forth between layers, leading to mutual reinforcement between layers. In this way, input data are processed adaptively rather than accumulated passively. As Carpenter and Grossberg (1992) put it, "... ART systems are 'intentional' or 'goal-oriented' systems in the sense that their expectations can be primed to selectively seek out data in which they are interested". Additional research is needed to determine whether an ART network, or networks with similar attributes, can capture the interactions between a priori and stimulus-derived information in motion perception.

8.3 Psychoanatomy

Psychoanatomical techniques, as defined by Julesz (1971), enable one to use interactions among different visual phenomena to illuminate the sequence of processing steps within the visual system. If the implications of occlusion were registered before the initial extraction of direction, the visual system should assume that our stimulus was 'hidden' but unchanged, and motion information should be extrapolated across the spatiotemporal gap. In other words, the development of a direction representation should be uninterrupted. Our results show that information about direction of motion is not extrapolated or 'filled in' across a spatiotemporal gap, or when the object moves behind an explicit occluder. Instead, accrued of directional information is interrupted when an object disappears or is occluded. This suggests that occlusion constraints are registered after the initial development of a directional representation.

Work with other forms of motion perception suggests a different sequence, namely that occlusion constraints are processed earlier than some aspects of motion. For example, Shimojo et al. (1989) showed that the visual system takes occlusion into account before it solves the aperture problem. In particular, the apparent direction of ambiguous motion depended on whether gaps in the motion field appeared to lie in front of and occlude the motion. Similarly, Brown and Weisstein (1991) found that the perception of Tyan-Sekuler moving phantoms (Tyan and Sekuler 1975) depends on how blank regions in the motion field were interpreted. When the blank regions were seen as lying in front of the moving grating, phantoms were seen moving right across these regions; however, when the same blank regions appeared to lie in the plane of the grating itself, phantoms were not seen. In both of these situations, then, information appears to be 'filled in' behind an occluder before motion processing is complete; the occluder affects the perceived motion of the occluded object.

These findings are not necessarily incompatible with our own conclusions. It is likely that the early analysis of direction information—the focus of our study—occurs at a different processing stage from either of the other motion phenomena just mentioned. For example, the aperture problem, examined in the experiments of Shimojo et al., is thought to be 'resolved' within the middle temporal area, MT (Movshon et al. 1985). Because occlusion appears to constrain the solution to the aperture problem, one suspects that occlusion is processed at some stage that feeds into MT. Our results, though, gave no evidence that occlusion constraints had been taken into consideration, as they were in the experiments of Shimojo et al. This suggests that early extraction of direction occurs before MT, and before the stage in which completion occurs. Furthermore, Driver et al. (1992) concluded that direction

---

(5) Recently, Carpenter and Grossberg (1992) extended ART to deal with nonstationary data: samples from a data stream whose statistics vary over time. This extension may be particularly applicable to various classes of moving targets.
is initially encoded independently of speed and only at some later stage are the two integrated. If this conclusion is correct, then it suggests that the extraction of directional information we are investigating occurs after the initial stage of encoding. However, we view this conclusion to be tentative because the discriminability and variability of direction and speed were not equated in the experiments of Driver et al.

The multistage framework for motion perception is consistent both with physiological investigations of motion processing and with psychophysical studies of motion [see Nakayama (1985) for a review]. Almost certainly, the perception of motion reflects contributions from several different specialized processing stages. To explore this notion further, we plan to identify other types of events that interrupt—or fail to interrupt—the extraction of direction information. For example, if motion and color (or motion and form) are functionally separate at the level of direction encoding, a transient equiluminant color change (or shape change) should not affect the accrual of direction information. In this way we could compare the level of processing at which initial direction extraction occurs with that of other processes, such as apparent motion (Kolers and Pomerantz 1971; Kolers and von Grünau 1976; Morgan and Cleary 1992), to determine further the loci of various aspects of motion processing.

Acknowledgements. This work was supported by grants to ABS from the University of Toronto and the National Sciences and Engineering Research Council of Canada OGP0105494, and to RS from United States Air Force Office of Scientific Research AFOSR 89-0243. Portions of this work were presented at the 1991 meeting of the Association for Research in Vision and Ophthalmology [Sekuler and Sekuler 1991]. Thanks to Patrick Bennett, Elizabeth Shannon, Tom Banton, Carol Flynn, and one anonymous reviewer for helpful comments.

References
Brown J M, Weisstein N, 1991 “Conflicting figure-ground and depth information reduces moving phantom visibility” Perception 20 155–166
McKee S P, 1981 “A local mechanism for differential velocity detection” Vision Research 21 491–500