

Vision Research 40 (2000) 3651-3664

Vision Research

www.elsevier.com/locate/visres

# Limits of attentive tracking reveal temporal properties of attention

Frans A.J. Verstraten <sup>a,\*</sup>, Patrick Cavanagh <sup>b</sup>, Angela T. Labianca <sup>b</sup>

<sup>a</sup> Division of Psychonomics, Helmholtz Research Institute, Universiteit Utrecht, Heidelberglaan 2., NL-3584 CS Utrecht, The Netherlands <sup>b</sup> Department of Psychology, Vision Sciences Laboratory, Harvard University, 33 Kirkland Street. Cambridge, MA 02138, USA

Received 28 September 1999; received in revised form 18 May 2000

#### Abstract

The maximum speed for attentive tracking of targets was measured in three types of (radial) motion displays: ambiguous motion where only attentive tracking produced an impression of direction, apparent motion, and continuous motion. The upper limit for tracking (about 50 deg s<sup>-1</sup>) was an order of magnitude lower than the maximum speed at which motion can be perceived for some of these stimuli. In all cases but one, the ultimate limit appeared to be one of temporal frequency, 4–8 Hz, not retinal speed or rotation rate. It was argued that this rate reflects the temporal resolution of attention, the maximum rate at which events can be individuated from those that precede or follow them. In one condition, evidence was also found for a speed limit to attentive tracking, a maximum rate at which attention could follow a path around the display. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Attention; Apparent motion; Tracking; Temporal limits

### 1. Introduction

In 1912 Max Wertheimer reported a percept of motion that can not be explained in terms of current models of low-level motion analysis (e.g. Reichardt, 1961; Schouten, 1967; Morgan, 1979; Watson, Ahumada, & Farell, 1982; Adelson & Bergen, 1985; Sperling, van Santen, & Burt, 1985; van Santen & Sperling, 1985; Watson & Ahumada, 1985; Borst & Egelhaaf, 1989; Zanker, 1994; see Mather, 1994, for an overview). Wertheimer's stimulus is shown in Fig. 1A. Using a tachistoscope, he presented a configuration of two intersecting lines and alternated this stimulus (a cross) with one that was rotated 45 deg. In space/time, the lines of the cross have correlations of equal strength in both the clockwise and the counterclockwise direction. This results in an ambiguous percept where back and forth motion between the lines is often the initial impression. However, Wertheimer (1912) also noticed that this was not always true. In the case where

"the lines stand normal to one another, and the distances are objectively equally favored, then it is *set and posture of attention* [...] that proved decisive in determining whether the rotation was seen towards the right or towards the left." (our italics, translated in Shipley, 1961; p. 1070).

This observation clearly points out the importance of attentional mechanisms in perceiving motion under ambiguous stimulus conditions. This motion percept can be called *attention-based motion perception*.

Despite its early discovery, the interest in this phenomenon has revived only recently (e.g. Ramachandran & Anstis, 1983; Cavanagh, 1991, 1992). None of the relatively recent monographs on motion, Kolers (1972), Nakayama (1985), Sekuler (1996), mentions this particular attention-based motion percept. So far, not much is known about the nature of the phenomenon or its underlying mechanisms although it is clearly part of a high-level motion system.

The notion of a second motion system was suggested originally by Wertheimer (1912) and restated by Julesz (1971). Julesz claimed that the low-level movement detectors found by Hubel and Wiesel (1968) were dif-

<sup>\*</sup> Corresponding author. Tel.: + 31-30-2533371; fax: + 31-30-2534511.

*E-mail addresses:* f.verstraten@fss.uu.nl (F.A.J. Verstraten), patrick@wjh.harvard.edu (P. Cavanagh).

ferent from higher-level movement analyzers that operate following shape identification. This idea was elaborated by Braddick (1974, 1980) and Anstis (1980). Low-level motion extraction has been described as energy-based (van Santen & Sperling, 1985; Adelson & Bergen, 1985; Watson & Ahumada, 1985), or passive (Cavanagh, 1991) where the motion computations rely on spatiotemporal filters. Since the filters are extracting components of the image in various spatiotemporal frequency bands, the motion is not linked to particular discrete features in the image (e.g. edges, or corners). Indeed, in the missing-fundamental illusion (Adelson & Bergen), the motion is seen in one direction while the discrete features of the pattern move in the opposite direction. In comparison, high-level motion extraction is tied to discrete spatial features that must be seen and then tracked.

Julesz (1971) suggested that when cues for both motion streams are present, the low-level stream usually dominates and the operation of the higher-order mechanism is concealed. He claimed that using cyclopean stimuli avoided engaging the low-level process, allowing the higher-level one to be isolated (although see Patterson, Bowd, Phinney, Pohndorf, Barton-Howard, & Angilletta, 1994). In this case, a directionally ambiguous stimulus (a counterphasing set of dots) with balanced low-level signals was used so that only higher-order mechanisms can determine the perceived direction.

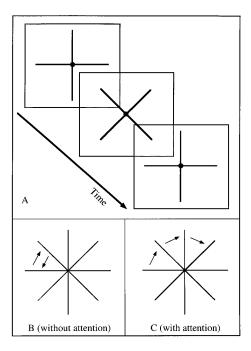


Fig. 1. (A) Stimulus configuration as used by Wertheimer (1912). One cross is alternated in time with a second cross that is rotated 45 deg. Passive viewing will lead to the impression of back and forth motion (B). However attentive tracking will make the configuration rotate in the chosen direction (C).

It has already been shown that attention-based motion can operate even in the face of some degree of opposing low-level signals (Cavanagh, 1992; Ashida & Verstraten, 1998). For example, in one experiment (Cavanagh, 1992), a luminance and a color grating were superimposed and set in motion in opposite directions. The contrast of the luminance grating was adjusted until its motion dominated. The bars of the color grating were still visible but were not seen to move unless the observer attentively tracked a specific color bar. The tracking could not rely on low-level motion signals because the low-level response was driven by the oppositely moving, luminance grating. This result suggests that tracking can be accomplished even with a dominant low-level signal coding for movement in the opposite direction. However, it also suggests that a dominant low level signal is not sufficient for attentive tracking as well. In particular, if low-level signals alone were sufficient for tracking, observers should have been able to track the luminance bars in the same display described above; but observers in this experiment could not track these bars at all — they were masked by the color grating and could not be seen despite producing the dominant motion percept. The tracking process appears to be an independent, effortful, feature-based motion system.

When the color bars were being tracked in this composite stimulus, observers reported that they appeared to be moving, not merely changing position. These motion impressions may be derived from some process that monitors the change in the position of the attended target. Alternatively, as Wertheimer (1912) suggested, motion impressions could be based on information about the focus of attention itself, either its position or its displacement. This is analogous to the efference copy theory of motion during smooth-pursuit eye movements.

Attention-based motion has at least one common characteristic with other proposed higher level motion systems, such as the long-range process (Braddick, 1980; Petersik, 1989) or Anstis's System 2 (Anstis, 1980), namely, it is based on feature identification. Thus, when feature localization is not possible, attention-based motion perception breaks down as shown by the inability to track the luminance grating whose motion was visible but whose features were not (Cavanagh, 1992). As will be demonstrated here, tracking requires localization not only in the spatial domain but in the temporal domain as well.

Attentive tracking also shares a common characteristic, attention, with another very different model of high-level motion: the feature-salience motion of Lu and Sperling (1995b). These authors demonstrated a striking phenomenon where an extremely brief display with no intrinsic motion could be seen to move in either direction depending on attention to one feature or

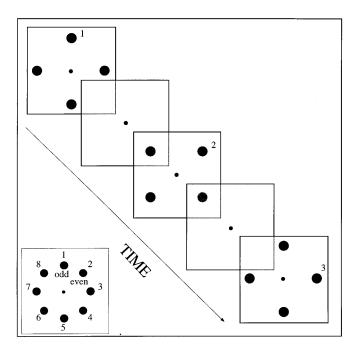


Fig. 2. An example of the circular stimulus configuration for four discs. Two arrays of four discs are alternated in time and space (see inset: even and odd sets on alternate frames, separated by a blank ISI) so that 8 'steps' are needed to complete a full revolution. As is true for the configuration in Fig. 1, passive viewing will lead to the impression of back and forth motion (e.g. motion alternating between positions 1 and 2 in the inset as in  $1-2-1-\ldots$ , the numerals were not present in the display), or random motions, or, at higher rates, just flicker of each disc in place. Attentive tracking, however, makes a selected disc appear to follow a path around the display in a direction that is under the voluntary control of the subject as in  $1-2-3-\ldots$ , as shown by the numbers on the arrays, or  $1-8-7-\ldots$ .

another. For example, if a stereo-defined grating with near and far bars is exchanged with a color-defined grating of red and green bars offset by 1/4 cycle, motion is seen in one direction when the observer attends to red but in the opposite direction when the observer attends to green. To explain their result, Lu and Sperling proposed that Reichardt-like motion detectors operate on a salience map of the visual field where salience is determined by the observer's selection of figure as opposed to ground. The motion of any salient object is then signaled by the response of these detectors. In the example above, the near bars of the stereo-defined grating are assumed to be naturally more salient than the far bars whereas the salience of the red and green is set by the observer's voluntary attention. Bars of highest salience then translate in one direction from frame to frame when red is attended and in the other when green is attended. This model and the phenomenon it deals with differ in two fundamental ways from the attentive tracking which are being addressed in this article.

First, feature-salience motion can be seen with brief presentations. Lu and Sperling themselves claim that

their stimuli were 'much too brief for conscious tracking' (Lu & Sperling, 1995b). Even though they do not feel that their motion phenomenon is mediated by conscious tracking, they do suggest that the reverse might be true, that tracking may be mediated by their feature-salience motion mechanism.

However, it is felt this is unlikely because the second difference between the two motion phenomena appears to preclude any role of their feature-salience mechanism in tracking. Specifically, little or no training is required to see motion and reverse its direction at will in Wertheimer's stimulus (Fig. 1) or in the authors' ambiguous motion stimulus (Fig. 2). In contrast, Lu and Sperling (1996) write that, in their task, once the observer is able to give a correct response to one feature direction and subsequently is asked to attend to the other feature, it takes 'an hour or so of practice' [italics added] before the observer reaches a statistically significant motion percept again. With no evidence of this extremely sluggish response in the conscious tracking task, it is hard to imagine that the feature-salience motion mechanism is involved.

In the current paper, the limits of attention-based motion will be examined for ambiguous stimuli and then compared to the limits for tracking two unambiguous motion stimuli. Since the ambiguous stimulus is spatially discrete, the upper bound on its speed could be set by any of three different factors: the speed, the spatial step size, or the temporal flicker rate. Each of these implies different constraints on attentive tracking. The speed itself may impose a limit if there is a maximum speed with which attention can move through space. Independently of the speed, the spatial step size might be too large if there is a limit to the spatial range over which items can be selected to participate in the motion. Finally, the timing might be too rapid for the events at each location to be individuated (He, Intriligator, Verstraten, & Cavanagh, 1998; Rogers-Ramachandran & Ramachandran, 1998). Using the method explained below it is possible to discriminate among these possibilities.

In the first experiment, observers track targets in the absence of any net, low-level motion energy. In the last two experiments, observers track targets undergoing apparent motion and also a target bar in a continuously moving sinewave. The spacing of the targets in the apparent motion displays is varied from wide enough to appear as discrete motion steps which one assumed do not drive low-level detectors, to close enough to appear more continuous and capable, as was demonstrated, of driving low-level motion. Thus both the apparent motion and continuous motion stimuli have the potential for generating low-level motion signals that might aid the observer in tracking the targets. If tracking of an unambiguously moving target (with low-level motion signals present) is no better than the tracking of ambiguously moving targets (in the absence of net lowlevel motion), it can be concluded that attentive tracking may operate independently of low-level motion and that it relies ultimately on visible, local features.

### 2. Experiment 1: tracking ambiguous stimuli

In this experiment, the goal is to find the maximum speeds which support attention-based tracking of ambiguous stimuli. The number of discs in the array is manipulated to uncover whether the limiting factor is spatial, temporal, or spatio-temporal.

An example of the stimulus configuration, in this particular case for four discs (8 steps per complete rotation), is shown in Fig. 2. There are two sets of discs constructed so that the discs of one set fall exactly midway between the discs of the other set. Because of the balanced spatial positions, there is no net motion energy in either direction. And yet, if an observer pays attention to a particular disc and imagines that it is moving in, say, the clockwise direction, that disc then appears to be moving in steps around the array in that direction. The stimulus supports tracking in either direction and it is the observer's intent which determines the direction and trajectory, not the stimulus. The number of discs that are present in the display is manipulated between conditions (from 4 [= 8 steps] to 16 discs [= 32 steps]).

Both a *method of constant stimuli* and a *method of adjustment* were used as described below. In the first procedure the accuracy of tracking at each speed was determined and a criterion of 75% correct tracking was set to estimate the threshold speed for each density. In the adjustment procedure, subjects directly controlled the flicker frequency of the discs and therefore the required tracking speed. Their task was to find the highest rate at which they could track a disc for at least two revolutions.

# 2.1. Methods

### 2.1.1. Observers

Three observers participated in the experiment in the Method of Adjustment procedure. Two of these also completed the experiment in the Method of Constant Stimuli procedure. All observers had normal or corrected to normal vision and were experienced observers.

# 2.1.2. Stimulus

One of the stimulus configurations used is shown in Fig. 2. Two circular arrays of discs are alternating in time and space. The diameter of the circular array was 11.5 deg of visual angle at a fixed viewing distance of 70 cm. The discs had a diameter of 1.5 deg of visual angle.

The number of discs on this circular array was varied across conditions. The discs were always evenly spaced around this array, had a luminance of 65 cd m<sup>-2</sup>, and were presented on a 10 cd m<sup>-2</sup> background. The temporal onset and offset of the individual discs was a step function. The fixation mark was a bull's-eye at the center of the display (approximately 1 deg of visual angle in diameter).

It is important to understand the consequences of the manipulation of the rotation rate — the tracking speed required if the observer is to maintain accurate pursuit of the target — and the number of discs along the circular array:

- *Rate (in revolutions per second, rps):* The *rate* is the speed with which a target disc moves around the circular display in revolutions per second. The target disc and the direction in which it is to be tracked are initially indicated either by a small marker presented within the disc during its first few steps (method of constant stimuli) or by the choice of the observer (method of adjustment). The rate is the speed that has to be maintained by the observer in order to accurately track the target. Since the spacing is fixed for a given number of discs, an increase in rate is established by an increase in the temporal frequency of the flickering discs.
- *Number of discs:* The number of discs along the circular array is also varied between conditions. As the number of discs is increased, the space between the discs decreases and more 'steps' or displacements are needed for one disc to complete a revolution around the display. As a result, in order to have the same rate in terms of revolutions per second of a target disc, the temporal frequency of the individual discs has to be increased as the number of discs increases.
- The *inter stimulus interval* (ISI) was fixed at 60% of the interval from the onset of one array to the onset of the next, subject to limitations of the monitor refresh rate. The duty cycle of the discs, the proportion of each interval during which the disc array was present, was 40%. The actual duration of the ISI in ms varied as a function of the rotation rate tested in each condition. The effect of varying ISI and duty cycle is tested in a separate control experiment described later.

# 2.1.3. Apparatus

The stimulus configuration is programmed in Vision Shell and presented on a calibrated 14 in. 67 Hz Macintosh display driven by a 7100/80 Power Macintosh.

### 2.1.4. Procedure. Method of constant stimuli

Observers fixated a 'bull's-eye' in the center of the display. The trial started with a little marker disc

presented in the centre of one of the flickering discs. This marker disc made successive steps in a defined direction on each alternation of disc sets. The observers attentively tracked the disc in which the marker appeared. After 2 s the marker disappeared and observers tried to attentively track the disc along the path that was indicated by the marker disc. After a 1.5 s the marker appeared again for 240 ms, either in the correct location for accurate tracking, or one step before or after the correct location. The observers had to indicate whether the test disc appeared in the disc they were tracking or not. A range of rates (0.1-1.8 rps) was presented for a range of disc numbers (4, 6, 8, 10, 12, 14, and 16) with eight trials at each rate. The maximum tracking rate was taken as the fastest rate which generated 75% correct tracking responses. Two subjects completed the experiment using this method and the results derived from a Weibul fit of the psychometric curves were basically the same as for the much faster method of adjustment.

#### 2.1.5. Method of adjustment

Observers again fixated the central bull's-eye but now they selected a target disc and the direction in which to follow it at will. They then attempted to follow that target for two full revolutions. If they were successful, they increased the rate of rotation, if not they decreased it. The flicker rate for which two full circuits of tracking was just possible was recorded. Settings were made for a range of disc numbers (4, 6, 8, 12, and 16) with at least three settings for each condition. This method does not monitor whether the

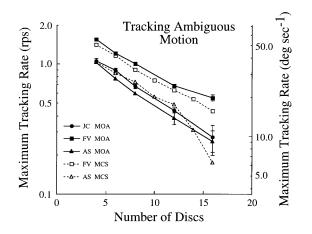


Fig. 3. Maximum tracking rate as a function of the number of discs in the array for two observers with the method of constant stimuli (MCS, dashed lines, outline symbols) and for three observers with the method of (MOA, solid lines, filled symbols). The left vertical axis shows the tracking rate in revolutions per second (rps); the right vertical axis shows the rate in degrees of visual angle per second. Standard errors ( $\pm 1$  S.E.) are shown for the MOA data where the value is larger than the data symbols.

subject is tracking the disc accurately. However, the results with this method were basically the same as those for the *method of constant stimuli* where accuracy of tracking was known.

# 2.2. Results and discussion

The results are shown in Fig. 3. The maximum rotation rate for 75% correct responses (method of constant stimuli, outline symbols) and for two successful rotations (method of adjustment, filled symbols) decreases with increasing number of displayed discs in all cases. For the two observers who were tested with both methods, the results are very similar across methods.

In Fig. 3, the right hand scale shows the rotation rate in degrees of visual angle per second. Surprisingly, the maximum rate (about 50 deg s<sup>-1</sup>, for FV) is quite low compared to the fastest speed for which motion direction can be judged (10 000 deg s<sup>-1</sup>, Burr & Ross, 1982). Burr and Ross found this highest value only for extremely low spatial frequency gratings (0.01 cycles deg<sup>-1</sup> visual angle), however, an informal test was run with a display more similar to that here. A mechanical display of a single disc moving in a circular path around a fixation point was used. The display was viewed under natural outdoor light from an adjacent window to allow continuous motion of any speed. With approximately the same luminance, size and eccentricity for the single disc as in the computer generated tracking display, four observers were able to achieve rotation rates of around 25 rps (900 deg s<sup>-1</sup>) and still judge whether rotation was clockwise or counterclockwise. This is an order of magnitude higher than the maximum rates that supported attentive tracking.

Clearly in Fig. 3 the speed at which tracking could be maintained decreased with the increasing number of discs even though only one disc was tracked in each condition. The real limit may not be in terms of speed, however. Fig. 4 replots the results for the three observers in terms of the temporal frequency with which the discs flickered at each location.

The figure shows that, across the range from four to 16 discs, the maximum flicker rate that supports tracking varies less than the maximum speed (Fig. 3). However, the maximum frequency is not exactly constant either — it does vary for one observer by about a factor of two (AS, method of constant stimuli). Over the same range, however, the maximum speed changes by a factor of three (FV) to six (AS). It appears that temporal frequency of the discs is a major variable limiting the speed of tracking.

This upper limit of 5–7 Hz is very similar to the upper limits reported for apparent motion between widely separated discs (phi motion, Neuhaus, 1930;

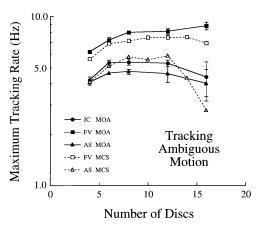


Fig. 4. Temporal frequency in Hz at maximum tracking rate as a function of the number of discs in the array for two observers with the method of constant stimuli (MCS, dashed lines and outline symbols) and for three observers with the method of adjustment (MOA, solid lines and filled symbols). This temporal frequency is the flicker rate of an individual disc at a fixed location. Standard errors ( $\pm 1$  S.E.) are shown for the MOA data where the value is larger than the data symbols.

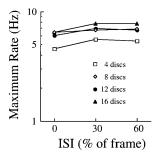


Fig. 5. The effect of inter stimulus interval (ISI) on the maximum tracking rate in Hz for one observer, FV. The duration of the ISI was fixed at 0, 30 or 60% of the SOA. Maximum tracking rate was measured with the method of adjustment for displays of four, eight, 12, and 16 discs.

Caelli & Finlay, 1979, 1981; Tyler, 1973). It is also similar to the upper limit reported for the discriminating the direction of moving stereo-defined gratings (Patterson, Ricker, McGary, & Rose, 1992; Lu & Sperling, 1995a) and motion-defined gratings (Lu & Sperling, 1995a; Zanker, 1996).

Motion is not the only percept with a maximum rate of about 4–8 Hz. Phase discrimination for flicker shows a similar limit (He & MacLeod, 1993; He et al., 1998; Rogers-Ramachandran & Ramachandran, 1998). For example, if a field of several discs is modulated on and off in synchrony and one of the discs is modulated in counterphase, it can only be detected for flicker rates lower than about 7 Hz. A phenomenon called *Gestalt Fusion* also shows the same limit of about 7 Hz (see van de Grind, Grüsser, & Lunkenheimer, 1973; Grüsser & Landis, 1991). In this case, a single light is turned on and off. Below about 5–7 Hz the light appears to alternate between on and off states. At higher rates, the light never appears to turn off but stays on and flickers. Also, Morgan and Turnbull (1978) showed that smooth pursuit for sampled motion begins to break down at about 7 Hz. This limitation is therefore seen across a broad range of phenomena. It may reveal a fundamental limit to the processing of temporal events in the sense that onsets and offset of events can be accurately judged only for rates lower than, say 7 Hz. Above that rate, the rapid sequence of changes becomes a temporal texture rather than a series of individually addressable events.

Whether this temporal limit is a property of attention or of a stage preceding attentive processing is not addressed by the experiment. To better characterize the limits of attentive tracking, subsequent experiments will examine: (a) whether unambiguous apparent motion can be tracked at higher rates than the ambiguous motion stimuli of this first experiment; and (b) whether faster tracking is possible for continuously moving stimuli. Before dealing with these issues, a study was conducted that examined the effect of the ISIs used in the first tracking study.

### 2.3. ISI/duty cycle control experiment

There are reports that ISI and duty cycle influence the perception of motion. For example, Giaschi and Anstis (1989) have shown that increasing the ISI and reducing the duty cycle of the discs at a fixed alternation rate results in an increase of the perceived speed for apparent motion. Although their stimulus and task were different from those here, it was decided to run a short control experiment for one observer to investigate the role of ISI and duty cycle in these stimuli.

ISI was investigated by setting the blank field duration to one of three fixed fractions (0, 30 or 60%) of the interval from the onset of one array to the onset of the next (SOA) at each alternation rate. In this case, the duty cycle, the proportion of the SOA during which the discs are present, is fixed as well in that ISI + DC =100%. Because both were set as proportions of the SOA, both ISI and the duration of the discs become shorter at higher alternation rates.

Ambiguous motion displays of 4, 8, 12, and 16 discs were presented with the same tracking instructions used in the method of adjustment procedure of Experiment 1. Each condition was tested once.

The results are presented in Fig. 5. The maximum rate at which the observer could attentively track the target for two rotations is shown as a function of the ISI with the number of discs as a parameter. The results indicate that there is little or no effect of the ISI and duty cycle on maximum tracking rate.

### 3. Experiment 2: tracking apparent motion

The relatively low speed of attentive tracking may be due to the attentive load of the task. It is effortful to select a target disc and to 'will' it to move in the indicated direction. No stimulus information maintains this direction over the opposite direction. Perhaps if there were no ambiguity, the maximum rate could be higher. To examine this possibility, an apparent motion stimulus with targets jumping through discrete, nonoverlapping positions was used. Observers still tracked one of the discs in the stimulus but the direction of motion was inherent to the stimulus. The spacing of the discrete steps of the display was also varied from close enough to appear relatively smooth (driving low-level detectors, we assume), to far enough to appear as distinct jumps (and not driving low-level detectors). The participation of low-level motion responses was also examined as a function of the step size.

The test has been limited to a display of four discs in all conditions so one cannot distinguish between speed and temporal frequency as limiting factors. While the number of visible discs was held constant at four, the spacing of the steps was varied as mentioned above. This allowed one to test a number of hypothe-

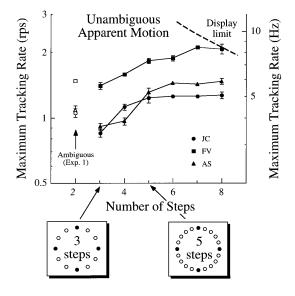


Fig. 6. Maximum rate for tracking one of four discs in apparent motion. Rate is shown as revolutions per second (rps) on the left vertical axis and as flicker rate of individual locations (Hz) on the right axis. The number of steps taken to move to the position of the adjacent disc (1/4 of the circumference) is shown along the horizontal axis. The data for tracking one of four discs in the 2-step, ambiguous stimulus of Experiment 1 (method of adjustment) are shown as outline data points on the left. Standard errors ( $\pm 1$  S.E.) are shown where the value is larger than the data symbols. In one condition, one observer's settings, shown in gray, were at or above the 2.08 rps limit for 8 steps, a limit imposed by the 67 Hz refresh rate of the monitor and shown as the stippled area at the top right.

ses concerning the essential factors which limit tracking. The smallest number of steps (widest spacing) which evenly divides the space between two adjacent discs is two but this is the ambiguous case examined in the previous experiment. The range therefore extended from 3 to 8 steps per quadrant (see Fig. 6). For the 3-step condition, for example, it takes three steps to reach the location originally occupied by the adjacent disc and four times that number of steps, 12 in this case, to make one complete trip around the display. As the number of steps is increased at a fixed rotational rate, the number of steps per second is also increased, and the step size in degrees of visual angle decreased. If either of these factors affects the tracking rate, performance should change as a function of the number of steps.

### 3.1. Methods

### 3.1.1. Observers

The three observers from Experiment 1 participated.

### 3.1.2. Stimuli

The stimuli and apparatus were identical to those of Experiment 1 with the following exceptions. There were always four discs visible around the circular array. A complete series of intermediate positions required 3, 4, 5, 6, 7, or 8 frames. Between each frame, the four discs moved 1/3, 1/4, 1/5, 1/6, 1/7, or 1/8, respectively, of the interval between adjacent visible discs (given that there were always four evenly spaced discs, this interval spanned one quarter of the circumference). There was no ISI with this display. Each array was followed immediately by the next where the discs were shifted to their next set of locations. Because of the 67 Hz rate of the display, the discs can make no more than 67 steps  $s^{-1}$ . For this four-disc, apparent motion display, the number of steps per second is given by  $4 \times \text{number}_of_\text{steps} \times \text{rotation}_\text{rate}$ . The upper limit of rates that can be presented therefore drops as the number of steps increases from about 5 rps with three steps (60 steps  $s^{-1}$ ) to about 2 rps with eight steps (64 steps/ $s^{-1}$ ). This upper limit is shown on Fig. 6 as a dotted line.

#### 3.1.3. Procedure

The method of adjustment as described before was used. Observers were instructed to locate one disc and track it for two full revolutions. The observer used the mouse to control the flicker rate of the discs. The upper temporal limit at which the observer was able to track the target disc for two full revolutions was recorded. At least three settings were taken for each condition. The direction of rotation of the array reversed following each setting.

# 3.2. Results and discussion

The results are shown in Fig. 6 in terms of the maximum rate (both in terms of revolutions per second and Hz). There is very little change from the ambiguous case (the 2-step data for four discs are taken from Experiment 1) to the 3-step, unambiguous case. Observers report clear motion in the expected direction at slower rates for the 3-step stimulus but, interestingly, at the limiting rate which supports tracking, observers report that the motion becomes ambiguous.

As the number of steps increases from 3 to 8, all the observers improve their maximum tracking rate. Most of the improvement occurs between 3 and 5 or 6 steps with little additional improvement at 7 or 8 steps. Overall, the effect of increasing the number of steps (and decreasing step size) is modest, an improvement of about 20 or 30%. How important is the number of steps (or step size) in determining tracking performance? The number of steps around the display also varied in Experiment 1 — it was always twice the number of visible discs. The total number of steps around the array varied from 8 to 32 in Experiment 1 and from 12 to 32 in this experiment. However, the effect on maximum tracking speed (in terms of rps, revolutions per second) was very different in the two cases: the maximum speed dropped strongly in Experiment 1 as number of steps increased (Fig. 3) but it increased slightly in this experiment (Fig. 6). Clearly, neither the number of steps nor the step size alone sets the limiting speed of tracking.

The flicker rate at individual locations does seem to be the critical factor. The upper tracking rate again stayed in the 5-8 Hz range. Note that the data of Fig. 6 rules out any role of the flicker rate of the target itself. For a given rotation rate, the rate at which the target disc flickers as it moves increases directly with the number of steps. For example, if the target is rotating at 1 revolution  $s^{-1}$  in the 3-step condition, it turns on and off 12 times in the one second it takes to make a full circuit, whereas it flickers 32 times  $s^{-1}$  in the 8-step case. Conversely, a given location only flickers 4 times (it is crossed by four discs) in the 1 s it takes for a moving disc to make a full revolution and this is true no matter how many steps (intervening positions) are used. Thus, the data suggest that it is the flicker rate of each location which counts, not the flicker rate of the moving disc.

What might explain the slight improvement in maximum tracking rate seen in Fig. 6 as the number of steps increases? One possibility is that the multi-step stimuli are activating low-level motion detectors and this additional signal contributes to the accuracy of tracking. If there is a motion signal that is independent of tracking, observers might be able to judge motion direction at speeds to fast to track. It was already mentioned that the 3-step case did not provide any clear sense of motion to our observers at speed above the tracking limit (nor did, or could, the 2-step case). What of the stimuli with more steps?

Direction discrimination were tested on a 120 Hz monitor to extend the range of rates to well above the tracking limits. For the 4- through 8-step cases, direction could be judged accurately (above 80% correct in 2AFC) up to the highest rates available: 7.5 rps for 4-steps down to 3.75 rps for the 8-step stimulus, equivalent to flicker rates of individual discs of 30 and 15 Hz, respectively. This motion appeared as a faint streaming coursing around the ring of flicker discs. Moreover, when alternate disc locations were opposite polarity (white, then black), the perceived motion followed the true motion direction at low rates where tracking was possible but reversed direction at speeds above tracking rates for all arrays with closer spacing than the 3-step array. This reverse apparent motion effect (Anstis and Rogers, 1975) is a clear indicator of low-level motion response as was the motion aftereffect which could be produced by adapting to the motion displays at their highest rate (tested with a brief, low-contrast, counterphasing grating replacing the ring of dots).

The suggestion that low-level motion was present for the smaller step sizes in apparent motion led one to examine tracking for smoothly moving sinewaves, a stimulus with strong responses from low-level detectors.

# 4. Experiment 3: tracking continuous sinewave motion

The previous experiments all involved stimuli moving in discrete steps around the display. In this experiment, a radial sinewave grating moving smoothly (within the limits of the monitor's 67 Hz resolution) around an annulus was used. Observers now tracked one of the bars of the grating as it moved around the display and the number of bars in the grating (its spatial frequency) and the rate at which it moved were varied. Both the method of constant stimuli where one can verify the accuracy of the tracking and the method of adjustment where the observers evaluated their own tracking were again used.

The sinewave stimulus provides robust signals for low-level motion as was shown by the large motion aftereffect that could be observed whenever the grating was stopped after prolonged viewing.

One was interested in whether these advantages smoothly changing, unambiguous motion and strong low-level motion signals — would improve the upper rates possible for tracking. In addition, the sinewave grating generated clear motion when there were only two cycles of the grating around the annulus. The ambiguous motion stimulus could not be tracked with only two discs so this gives one a greater range of stimulus density to explore than in Experiment 1.

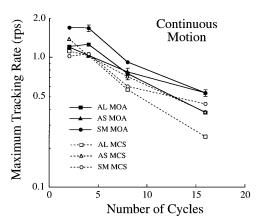


Fig. 7. Maximum rate for tracking in revolutions per second. Data for each of three observers is shown for both method of adjustment (MOA, solid lines, filled symbols) and method of constant stimuli (MCS, dashed lines, outline symbols). Standard errors ( $\pm 1$  S.E.) are shown where the value is larger than the data symbols.

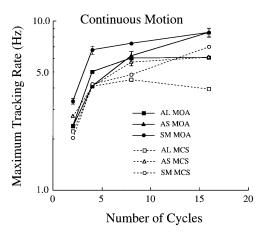


Fig. 8. The data of Fig. 7 are replotted in terms of the temporal rate of the grating, the flicker rate at each fixed location. Data for each of three observers is shown for both method of adjustment (MOA, solid lines, filled symbols) and method of constant stimuli (MCS, dashed lines, outline symbols). Standard errors ( $\pm 1$  S.E.) are shown where the value is larger than the data symbols.

### 4.1. Methods

#### 4.1.1. Observers

Three observers were used one of whom had participated in the previous two experiments. All observers had normal or corrected to normal vision and were experienced observers.

#### 4.1.2. Stimuli

The stimuli were presented on the same apparatus previously described. However, the observers now tracked one light bar of a radial grating. The grating filled an annulus with inner and outer radii of 3.5 and 8 deg of visual angle, respectively and had a mean luminance of 45 cd m<sup>-2</sup> and a contrast of 50%. Four different gratings were used having 2, 4, 8, and 16

cycles around the annulus. For a given rate of rotation, the grating moved by a small amount between frames to match the overall rate, giving the appearance of smooth motion. The output of the monitor was calibrated for linearity so that the sinewave modulation of luminance was accurate to within about 1%. The central fixation point was a high contrast bull's-eye 0.5 deg in diameter. The background of the display was dark  $(0.25 \text{ cd } \text{m}^{-2})$ . In the method of constant stimuli, a guide bar was provided to mark the target bar. The guide was red and started 0.5 deg inside the inner radius of the annulus and continued 0.5 deg beyond it. Its width was 1/4 of a cycle of the grating and it was aligned with the center of the light target bar of the grating (which, itself was 1/2 cycle). The guide bar was not superimposed on the grating itself but stuck out on the either side.

### 4.1.3. Procedure

The method of constant stimuli and method of adjustment were used as described before. The procedure for the method of constant stimuli was the same as in Experiment 1 with the guide bar taking the place of the central red mark to indicate the target bar and then the test bar. The guide bar remained on for 1 s to indicate the bar to be tracked and then it went off for a 2 s tracking period. The guide bar then returned as the test for 800 ms either on the tracked bar or either of the adjacent light bars of the grating. Observers reported whether or not the guide bar was adjacent to the bar they had tracked. Maximum tracking rate was taken from the 75% correct criterion.

In the method of adjustment, observers attempted to follow a bar of their choice for two full revolutions. If they were successful, they increased the rate of rotation, if not they decreased it. At least three settings were taken for each condition.

### 4.2. Results and discussion

In Fig. 7 the results are displayed for three observers in the same manner as for Experiment 1 (see Fig. 3). The solid symbols plot the upper limit at which observers could track a bar for two revolutions. The outline symbols show the maximum rates supporting 75% accuracy from the method of constant stimuli. In Fig. 8, these same data are shown in terms of the temporal rate of the grating as it passed any given point. For a rate of rotation of 1 rps, for example, the 2 cycle grating would have a temporal rate of 2 Hz, the 8 cycle grating, 8 Hz, and so on.

Two features are clear in these results. The maximum rate is again best characterized as a fairly constant temporal rate of 4-8 Hz, depending on observer and method. Observer AS, for example, participated in both Experiment 1 and Experiment 3. She shows a limit of

about 5.8 Hz for the method of constant stimuli here and a limit of about 5.5 Hz (again MOA) in Experiment 1. The temporal limit to the tracking appears to be a general limit for all the displays. On the other hand, for displays with the smallest number of cycles, 2-4, the maximum rate may be limited by the rotation rate in rps, not the temporal rate in Hz. The curves in terms of revolutions per second plateau between 2 and 4 before dropping in Fig. 7 and, over the same range, the curves in terms of temporal frequency rise steeply before flattening out in Fig. 8.

Why would one find a suggestion of a limited rotation rate here and not in the preceding experiments? The likely answer is that this is the first experiment using only two elements. In the 2-element display, rotation rates can reach 3-4 rps before the temporal rate exceeds the critical 4-8 Hz limit. In other words, this is the first display which has used where the temporal rate can be low enough to reveal a limit on the rotation rate. This limit on the rotation rate, in this display at least, appears to be about 1-2 rps, depending on the observer and method.

It may be that attentive tracking is limited by two factors: (1) an absolute speed of rotation around fixation of 1-2 revolutions s<sup>-1</sup>; and (2) a maximum rate of flicker in the stimulus, about 7 Hz, beyond which the features of the rotating stimulus are no longer sufficiently well defined to pick out and track.

Finally, following prolonged viewing of the sinewave stimulus, strong motion aftereffects were visible when the sinewave motion was stopped. Moreover, it was noted that the direction of motion was easy to determine at speeds well beyond those that supported tracking. In an informal test, directions could be judged for temporal rates of 25 Hz or higher for all the sinewave stimuli, equivalent to about 1.5 rps for the 16-cycle display and 12 rps for the 2-cycle display. These values are consistent with published data from Burr and Ross (1982). Clearly, there is a very strong low-level signal available to support direction judgements and create motion aftereffects. The presence of this additional motion signal did not appear to contribute to the highest rate at which tracking could be performed. This result suggests that tracking is based on signals other than low-level motion.

# 5. General discussion

The maximum speed was measured for attentive tracking of a specified target in both ambiguous and unambiguous motion displays. In all the experiments, the upper limit appeared to be set by the temporal rate which, at 4-8 Hz, was surprisingly slow, about one order of magnitude less than the maximum rate at which motion can be perceived in the unambiguous stimuli.

In Experiment 1, the maximum possible tracking speed depended strongly on the number of discs around the array, implying that tracking speed itself was not the limiting factor. The maximum flicker rate which supported tracking appeared to be more stable in face of varying disc spacing. A similar limit was found, 4-8 Hz, in Experiment 2 when the maximum speed was estimated for a target in unambiguous apparent motion in a display otherwise similar to that of Experiment 1. When the maximum speed possible for tracking a continuously moving target was examined (Experiment 3), again a limit of 4-8 Hz was found.

In Experiment 3, for the display with the smallest number of bars, there was also an indication of a maximum speed for tracking. An informal test showed that, with two cycles in the grating, the maximum tracking rate was unaffected by eccentricity suggesting that the tracking speed is limited in terms of rotations per second (about the fovea) as opposed to being limited in terms of degrees of visual angle per second. With this one exception, all of the results appeared to indicate that the limit on attentive tracking was in terms of a maximum flicker rate of 4-8 Hz.

This limiting rate of 4–8 Hz is, in fact, quite close to the well-documented limits on apparent motion (more specifically, at this rate and spacing, phi motion, Neuhaus, 1930; Caelli & Finlay, 1979, 1981; Tyler, 1973), on phase discrimination of flickering lights (He & MacLeod, 1993; He et al., 1998; Rogers-Ramachandran & Ramachandran, 1998), on motion of drifting stereodefined and motion-defined gratings (Patterson et al., 1992; Lu & Sperling, 1995a), on Gestalt fusion (see Grüsser & Landis, 1991; van de Grind et al., 1973) and on smoooth pursuit for sampled motion (Morgan & Turnbull, 1978). In this discussion it will be suggested that these phenomena might be limited by a common factor: the temporal resolution of attention.

Fig. 9 depicts the different factors that may limit the ability to track the targets with attention. The horizontal arrows show the spatial separation of the targets and the adjacent discs or bars. It has been previously demonstrated (Intriligator & Cavanagh, in preparation) that items can be selected by attention with 95% accuracy or better as long as they are spaced no more densely than about 25 around the circumference of a circular array. The maximum density used was 16 discs or bars around the display so it was felt that spatial crowding was not a limiting factor in the tracking performance of the experiments.

The diagonal arrows in Fig. 9 show the trajectory of the tracked target. The arrow has a characteristic angle on the space-time plot that corresponds to its speed. Speed was possibly a limiting factor in the final experiment when there were only two bars in the display but did not appear to limit performance otherwise. In addition, along the trajectory in Fig. 9 one can see the factor of step size or target flicker rate. As the step size decreases, the rate at which the target flickers increases. In the middle panel, the flicker rate is 50% higher than in the left panel whereas the spatial and temporal (the vertical arrow) separations are the same. This difference did not seem to play much of a role in limiting performance. The maximum tracking rate with apparent motion (3 steps as shown here, or more) was similar to that for ambiguous motion (2 steps). If anything, one might expect higher flicker rate of the target to be helpful. The task requires that the events along the trajectory be integrated into a single path and that should be easier when there are more samples along the path. Moreover, high target flicker rates are equivalent to small target step sizes and again, a small step should make path integration easier. The final, right hand panel takes this factor to the extreme where the samples are continuous (within the refresh rate limits of the monitor). This did not seem to help or hinder tracking. Temporal separation, the vertical arrows in Fig. 9, appeared to account for almost all the results in the three experiments. Why would temporal separation be so important?

# 5.1. Temporal resolution of attention

It will be argued that the limiting factor is the access to the individual events in a rapid stream of events. In the case of ambiguous or apparent motion, each disc in the display is turning on and off and the task is to pair the offset of one disc with the onset of the next, adjacent disc. If each disc is turning on and off very rapidly, it is possible that the timing of the offsets and onsets is no longer available. The loss of individuation of the on and off intervals would then prevent linking the offset of one disc with the subsequent onset of its neighbor. At low rates of flicker, say, 1 or 2 Hz, an individual disc appears to turn on and turn present but flickering — there is no access to the separate on and off intervals, and no way to link the offset of one disc to the onset of the neighboring disc. Tracking fails at these rates, 4-8 Hz and higher. At even higher rates of flicker, beyond the flicker fusion frequency, the sensation of flicker goes away and each disc appears to be on steadily. This rate can be as high as 50 Hz.

Between the highest rate which allows individuation (of the sequential on and off intervals) and the flicker fusion limit, the disc is seen as flickering. Clearly some part of the visual system is registering the temporal change of the disc but the actual timing of onsets and offsets is no longer available. The temporal variation becomes a texture rather than a series of individually addressable events. As mentioned above several other reports support this description of the loss of individuation of events in a rapid sequence.

However, for the apparent motion conditions with closely spaced steps and for the continuous motion stimulus, the impression of motion remained at rates much beyond those that support tracking. Just as some mechanism exists that responds to flicker even when separate on and off intervals are no longer experienced, some mechanism exists that responds to motion at rates beyond those which support tracking individual targets. The motion system which processes these higher rates is undoubtedly the low-level system based on directionally selective cells of the early visual cortices.

How does the temporal individuation argument apply to the continuous motion of the sinewave grating (Experiment 3)? The moving grating does not consist of discrete elements flickering on and off. Nevertheless, the data show clearly that it is the flicker rate that limits tracking (for stimuli with more than 2 cycles). Observers report that above about 7 Hz, the stimulus motion is clear but the bars are ill defined. Some spatial structure is apparent in the display but it is not sufficient to allow selection of a specific bar. At even higher rates, while motion is still evident, the spatial structure becomes more blurred and the motion appears as a streaming effect not linked to any spatial features.

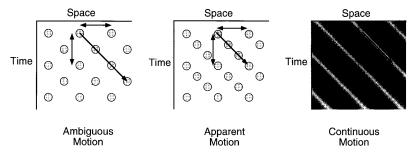


Fig. 9. The motions used in each of the three experiments are depicted in space-time plots with space along the horizontal axis and time going down the vertical axis. For ambiguous motion in the first experiment, the chosen trajectory could have followed a line of discs in either direction. The diagonal arrow shows the selected trajectory. The horizontal arrow indicates the spatial separation between the target and the adjacent distracters. The vertical arrow shows the temporal separation between the target at a given location and preceding and following appearances of distracters at that same location. The equivalent target trajectory and separations are shown in the middle panel for the apparent motion stimulus with three steps (Experiment 2) and in the right hand panel for continuous motion (Experiment 3).

One has called the limit on temporal individuation the temporal resolution of attention, or at least of its selection mechanism. This would clearly be the case if attention were the only process that showed this limit. An alternative is that the representation which has this 4-8 Hz temporal limit is one that is accessed by attention and by other processes. One cannot as yet rule this out.

# 5.2. Speed limit

In one case, the sinewave with two cycles, the limit to tracking appeared to be set by speed not flicker rate. With so few elements moving around the display, the maximum rate of rotation could become much higher with this stimulus without exceeding the 4-8 Hz flicker limit. Although the evidence of this one condition needs further verification, it suggests that observers could not make their attention track at speeds higher than 1-2revolutions  $s^{-1}$ . The observers reported that, subjectively, the bars were clearly visible but they were just moving too fast. An informal test of the limiting tracking speed at different eccentricities suggested that the limit was in terms of revolutions per second, not degrees of visual angle per second. Interestingly, this rate is in the range reported for mental rotation tasks (Shepard & Metzler, 1971; Cooper, 1976) where an internal model of an object is assumed to be rotated mentally.

# 5.3. Low-level motion

What is the role of low-level motion in tracking objects? Low-level and high-level motion systems should respond in tandem for the majority of stimuli. A moving object may first trigger a low-level response and that will often draw attention to the object. Its progress is then tracked with attention while, at the same time, its motion continues to drive low-level detectors. This paired response ought to create opportunities for lowlevel motion to develop an input to tracking, one which might improve accuracy or extend the range of conditions over which tracking is possible. However, no evidence was found for this contribution. Low-level motion was present to some extent for the apparent motion display with four or more steps between neighboring discs and strongly present for the continuously moving sinewave. However, the upper limits for tracking were little or no better in these cases. Earlier studies have shown that attentive tracking is possible in the absence of low-level motion and even when low-level motion opposes the direction of tracking (Cavanagh, 1992; Ashida & Verstraten, 1998). The data now suggest that tracking gets little or no low-level input even when that input could be beneficial.

Recall that Julesz (1971) suggested that when cues for both motion streams are present, the low-level stream usually dominates and the operation of the higher-order mechanism is concealed. It has been shown that, actually, the reverse appears to be the case when tracking is required: the high-level stream dominates and the low-level stream is concealed.

# 5.4. Attentive tracking: is it feature-salience motion?

Lu and Sperling (1995b) and Sperling and Lu (1998) suggest that the feature-salience motion mechanism could underlie both their feature-salience motion phenomenon and attentive tracking. It has already been argued that the extraordinary practice requirements seen for feature-salience motion (up to an hour practice to reverse the direction in the stimulus) are simply not found for attentive tracking. Observers can reverse the perceived direction in the ambiguous motion display basically at will with little or no practice. Nevertheless, Lu and Sperling (1996) have claimed that the featuresalience mechanism has a temporal frequency for halfmaximum sensitivity of about 4 Hz. This corresponds very well to a maximum rate of about 7 or 8 Hz, the same maximum rate that was find for attentive tracking. Could this indicate that their feature-salience mechanism is after all mediating tracking? Their papers provide no evidence in support of this possibility. In particular, the temporal frequency limits that Lu and Sperling report are not for their feature-salience phenomenon itself but simply for motion direction judgments of drifting stereo-defined and motion-defined gratings (among others). In all of the cases they report, attentive tracking may mediate the performance they measure. This explains the common temporal frequency limit. Moreover, the temporal limit found holds as well for phenomena not related to motion such as Gestalt flicker and phase discrimination. The limits on these phenomena and on attentive tracking all appear to be well described by a common temporal limit to attentional resolution. There is little to group these phenomena with feature-salience motion.

# 5.5. Apparent motion: is it attentive tracking?

In 1912, Wertheimer suggested that apparent motion between two successive flashes was simply the result of attention being dragged from the first flash to the second. He then rejected his idea because he could see two apparent motions at once and he believed that attention could select only one item at a time. However, given that recent demonstrations by Pylyshyn and Storm (1988) and others (Intriligator, Cavanagh, & Nakayama, 1991; Yantis, 1992) show that attention can track multiple targets, it is perhaps time to reconsider Wertheimer's suggestion.

First, what are the alternatives? Apparent motion, especially with closely spaced steps, could be just the low-level motion response to the motion energy of the stimulus. A target making small steps at rapid rates can be indistinguishable from a continuously moving target (Morgan, 1979, 1980; Burr, Ross, & Morrone, 1986; see also Watson & Ahumada, 1985), one that would clearly drive low-level detectors. Of course, the question is not whether the discrete nature of the apparent motion stimuli was detectable but whether the discrete steps fell within the spatial range that drives low-level detectors (referred to as D<sub>max</sub> in studies of random dot kinematograms, Braddick, 1974). Recent evidence suggests that the spatial range of the filters for low-level motion depends on the scale of the stimulus (Morgan, 1992, see also Bex, Brady, Fredericksen, & Hess, 1995). In short, apparent motion stimuli that take small steps relative to their size ought to engage low-level detectors and apparent motion stimuli that take large steps probably forego any assistance from low-level detectors. In these experiments, the apparent motion stimuli with the largest steps gave no impression of motion beyond the rates that supported attentive tracking. In that range, and that range only, it was concluded that apparent motion is based solely on attentive tracking.

Wertheimer (1912) pointed out that with passive viewing of his alternating cross-and-plus display, observers reported a rocking motion. The ambiguous motion display of Experiment 1 also produced this back-and-forth motion when viewed passively. This passive apparent motion appears to be a complete contradiction of the suggestion that apparent motion is based on attentive tracking. Clearly, apparent motion is being seen in the absence of voluntary guidance. This leads one to an important distinction that has been common in the attention literature: the difference between voluntary (endogenous) attention and involuntary (exogenous) attention. It has been shown that voluntary selection of a trajectory can turn ambiguous motion into an organized, directional motion. This is unmistakably motion supported by voluntary attentive tracking. In the absence of a selected target and trajectory, it was assumed that attention is simply drawn involuntarily from one target to the next, as Wertheimer originally proposed. Why is this involuntary attentive tracking almost always a rocking motion? The answer is not obvious but it might be that this is the least effortful path along which attention may be drawn. If attention just rocks more or less in place, it avoids being drawn out into new areas.

Overall, it has been shown that tracking an object with attention requires that it can be individuated at each step. With one exception, tracking broke down when the flicker rate of each location in the trajectory exceeded the limit of 4-8 Hz. It was suggested that this limit is the temporal resolution of attention. Beyond

this rate, features can no longer be individuated and selected for further analysis. Individuation is not necessary for the perception of motion. When gratings moved at speeds above 8 Hz, the individual bars of the grating were no longer easily picked out. Nevertheless, the grating's motion remained visible up to much higher rates.

# Acknowledgements

We are grateful to Hiroshi Ashida, Jody Culham, Sheng He, James Intriligator, Sara Mednick, Satoshi Shioiri and Adriane Seiffert for helpful discussion and/ or participation in the experiments. This research was supported by grant EY09258, the Niels Stensen Foundation, the Royal Netherlands Academy of Arts and Sciences (KNAW) and the Netherlands Organisation for Scientific Research (NWO).

### References

- Adelson, E. H., & Bergen, J. R. (1985). Spatio-temporal energy models for the perception of motion. *Journal of the Optical Society of America A*, 2, 284–299.
- Anstis, S. M. (1980). The perception of apparent movement. *Philosophical Transactions of the Royal Society of London B*, 290, 153–168.
- Anstis, S. M., & Rogers, B. J. (1975). Illusory reversal of visual depth and movement during changes of contrast. *Vision Research*, 15, 957–961.
- Ashida, H., & Verstraten, F. A. J. (1998). Attentive tracking of motion: interaction between low-level and high-level motion systems. In S. Saida, & P. Cavanagh, *Selection and integration of visual information* (pp. 229–233). Tsukuba, Japan: STA & NIBH-T.
- Bex, P. J., Brady, N., Fredericksen, R. E., & Hess, R. F. (1995). Energetic motion detection. *Nature*, 378, 670–672.
- Borst, A., & Egelhaaf, M. (1989). Principles of visual motion detection. *Trends in Neurosciences*, 12, 297–306.
- Braddick, O. (1974). A short-range process in apparent motion. Vision Research, 14, 519–527.
- Braddick, O. J. (1980). Low-level and high-level processes in apparent motion. *Philosophical Transactions of the Royal Society of London B*, 290, 137–151.
- Burr, D. C., & Ross, J. (1982). Contrast sensitivity at high velocities. Vision Research, 22, 479–484.
- Burr, D. C., Ross, J., & Morrone, M. C. (1986). Smooth and sampled motion. Vision Research, 26, 643–652.
- Caelli, T., & Finlay, D. (1979). Frequency, phase, and colour coding in apparent motion. *Perception*, 8, 59–68.
- Caelli, T., & Finlay, D. (1981). Intensity, spatial frequency, and temporal frequency determinants of apparent motion. *Perception*, 10, 183–189.
- Cavanagh, P. (1991). Short-range vs. long-range motion: not a valid distinction. Spatial Vision, 5, 303–309.
- Cavanagh, P. (1992). Attention based motion perception. *Science*, 257, 1563–1565.
- Cooper, L. A. (1976). Mental transformations and visual comparison processes: effects of complexity and similarity. *Journal of Experimental Psychology: Human Perception and Performance*, 2, 503– 514.

Giaschi, D., & Anstis, S. (1989). The less you see it, the faster it moves: shortening the 'on-time' speeds up apparent motion. *Vision Research*, 29, 335–347.

- van de Grind, W. A., Grüsser, O.-J., & Lunkenheimer, H. U. (1973). Temporal transfer properties of the afferent visual system. Psychophysical, neurophysiological and theoretical investigations. In: Jung, R. (Ed.), *Handbook of sensory physiology*, vol. VII/3, Chapter 7, Berlin: Springer, pp. 431–573.
- Grüsser, O.-J., & Landis, T. (1991). Visual agnosias and other disturbances of visual perception and cognition. London: The Macmillan Press.
- He, S., & MacLeod, D. I. A. (1993). The perception of fluctuating contrast. *Investigative Ophthalmology and Visual Sciences*, 34(Suppl.), 18.
- He, S., Intriligator, J., Verstraten, F. A. J., & Cavanagh, P. (1998). Slow mechanism for phase discrimination of both luminance and color flicker. *Investigative Ophthalmology & Visual Science*, 39(Suppl.), 1110.
- Hubel, D. H., & Wiesel, T. N. (1968). Receptive fields and functional architecture of monkey striate cortex. *Journal of Physiology*, 195, 215–243.
- Intriligator, J., & Cavanagh, P. (in preparation). Individuation and the resolution of attention.
- Intriligator, J., Cavanagh, P., & Nakayama, K. (1991). Attentive tracking of multiple moving objects at different scales. *Investigative Ophthalmology and Visual Science*, 32(Suppl.), 1040.
- Julesz, B. (1971). Foundations of cyclopean perception. Chicago: University of Chicago Press.
- Kolers, P. A. (1972). *Aspects of motion perception*. Oxford: Pergamon Press.
- Lu, Z.-L., & Sperling, G. (1995a). The functional architecture of human visual motion perception. *Vision Research*, 35, 2697–2722.
- Lu, Z.-L., & Sperling, G. (1995b). Attention-generated motion perception. *Nature*, 377, 237–239.
- Lu, Z.-L., & Sperling, G. (1996). Three systems for visual motion perception. Current Directions in Psychological Science, 5, 44–53.
- Mather, G. (1994). Motion detector models: psychophysical evidence. In A. T. Smith, & R. J. Snowden, *Visual detection of motion* (pp. 117–143). London: Academic Press.
- Morgan, M. J. (1979). Perception of continuity in stroboscopic motion: a temporal frequency analysis. *Vision Research*, 19, 491–500.
- Morgan, M. J. (1980). Analogue models of motion perception. *Philosophical transactions for the Royal Society B*, 290, 117–135.
- Morgan, M. J. (1992). Spatial filtering precedes motion detection. *Nature*, 355, 344–346.
- Morgan, M. J., & Turnbull, D. F. (1978). Smooth eye tracking and the perception of motion in the absence of real movement. *Vision Research*, 18, 1053–1059.
- Nakayama, K. (1985). Biological image motion processing: a review. Vision Research, 25, 625–660.
- Neuhaus, W. (1930). Experimentelle Studien über das Schein von Bewegung. Pflügers Archiv für die Gesamte Psychologie des Menschen und der Tiere, 75, 315–458.

Patterson, R., Ricker, C., McGary, J., & Rose, D. (1992). Properties of cyclopean motion perception. *Vision Research*, 32, 149–156.

- Patterson, R., Bowd, C., Phinney, R., Pohndorf, R., Barton-Howard, W. J., & Angilletta, M. (1994). Properties of the stereoscopic (cyclopean) motion aftereffect. *Vision Research*, 34, 1139–1147.
- Petersik, J. T. (1989). The two-process distinction in apparent motion. *Psychological Bulletin*, 106, 107–127.
- Pylyshyn, Z. W., & Storm, R. W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spatial Vision*, *3*, 179–197.
- Ramachandran, V. S., & Anstis, S. M. (1983). Perceptual organization in moving patterns. *Nature*, 304, 529–531.
- Reichardt, W. (1961). Auto-correlation, a principle for the evaluation of sensory information by the central nervous system. In A. Rosenblith, *Sensory communication*. New York: Wiley.
- Rogers-Ramachandran, D. C., & Ramachandran, V. S. (1998). Psychophysical evidence for boundary and surface systems in human vision. *Vision Research*, 38, 71–77.
- van Santen, J. P. H., & Sperling, G. (1985). Elaborated Reichardt detectors. Journal of the optical Society of America A, 2, 300-321.
- Schouten, J. F. (1967). Subjective stroboscopy and a model of visual movement detectors. In W. Wathen-Dunn, *Models for the perception of speech and visual form* (pp. 44–45). Cambridge Mass: MIT Press.
- Sekuler, R. (1996). Motion perception: a modern view of Wertheimer's 1912 monograph. *Perception*, 25, 1243–1258.
- Shepard, R. N., & Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science*, 171, 701–703.
- Shipley, T., Ed. (1961). Classics in psychology. New York: Philosophical Library.
- Sperling, G., van Santen, J. P. H., & Burt, P. J. (1985). Three theories of stroboscopic motion detection. *Spatial Vision*, 1, 47–56.
- Sperling, G., & Lu, Z.-L. (1998). In T. Watanabe, *High-level motion processing* (pp. 153–183). Cambridge: MIT Press.
- Tyler, C. W. (1973). Temporal characteristics in apparent movement: omega movement vs. phi movement. *Quarterly Journal of Experimental Psychology*, 25, 182–192.
- Watson, A. B., & Ahumada, A. J., Jr (1985). Model of human visual-motion sensing. *Journal of the optical Society of America A*, 2, 322–342.
- Watson, A. B., Ahumada Jr. A. J., & Farell, J. E. (1982). The window of visibility: a psychophysical theory of fidelity in time-sampled motion displays. NASA Technical Paper 2211.
- Wertheimer, M. (1912). Experimentelle Studien über das Sehen von Bewegung. Zeitschrift für Psychologie, 61, 161–165.
- Yantis, S. (1992). Multi-element visual tracking: attention and perceptual organization. *Cognitive Psychology*, 3, 295–340.
- Zanker, J. (1994). Modeling human motion perception. I Classical stimuli. Naturwissenschaften, 81, 156–163.
- Zanker, J. (1996). On the elementary mechanism underlying secondary motion perception. *Philisophical Transactions of the Royal Society of London B*, 351, 1725–1736.