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Interpolation and extrapolation on the path of apparent motion

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Abstract

An object moving in discrete steps can appear to move continuously even along sections of the path in which no stimulus is presented. We investigated whether the internal representation of such an object is constructed by extrapolation, along the expected trajectory of the object, or by interpolation, after the subsequent reappearance of the object. Observers viewed two discs moving in an unambiguous apparent motion display, which either occasionally reversed direction or continued moving along the predicted path. Observers carried out a speeded 2AFC task on probes presented between the possible disc locations. In the continuous condition, observers' reaction times to detect and identify a probe were longer when it occurred ahead of the disc than when it occurred elsewhere on the motion path. Conversely, when the disc reversed direction, significantly *less* interference was observed *ahead* of the disc (along the predicted motion path), and significantly *more* interference was observed *behind* the disc (along the updated motion path). We conclude that the representation of a moving object in an apparent motion display is constructed by interpolation as well as extrapolation. We demonstrate that this representation is maintained and updated even outside the locus of focused attention, and that it is possible to dissociate the contributions of interpolation and extrapolation mechanisms to an object's representation.

Keywords: Interpolation; Extrapolation; Apparent motion

1. Introduction

Almost a century ago, Wertheimer (1912) reported that under appropriate spatiotemporal conditions, sequentially presented stationary visual stimuli can induce the experience of motion—a phenomenon known as apparent motion. The strength of the impression of motion depends on the spatial and temporal separation of consecutive presentations (Korte, 1915; Gepshtein & Kubovy, 2007). Importantly, the impression of motion is experienced even in positions in the visual field where no physical stimulus is presented, and during the inter-stimulus interval (ISI) when no stimulus is on the screen. Studies using stimuli controlled for low-level motion content suggest that a relatively high-level representation of a moving object is maintained in the brain.

For example, Yantis and Nakama (1998) had observers monitor a bistable quartet—an ambiguous stimulus which can be seen as either two vertically or two horizontally moving discs—for the appearance of a probe which could appear between any neighboring discs in the quartet. They found that observers were slower to detect and identify a probe when it appeared on the perceived motion path than when it appeared off the motion path. Since the stimulus was physically identical in on-path and off-path trials, the authors proposed that feedback from higher to lower visual cortical areas activates a neural representation of a moving object, which then disrupts the processing of visual stimuli in the path of movement.

Using functional magnetic resonance imaging (fMRI), Sterzer, Haynes, and Rees (2006) provided the first neurophysiological evidence that such feedback between cortical areas might underlie apparent motion. Areas of retinotopic

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visual cortex corresponding to the sections of the apparent motion path in which no stimulus is presented have previously been found to be activated by apparent motion (Muckli, Kohler, Kriegeskorte, & Singer, 2005). Sterzer and colleagues (2006) demonstrated that this activation is mediated by feedback connections to motion-sensitive area hMT+/V5—an area that had already been implicated in the perception of apparent motion (Liu, Slotnick, & Yantis, 2004).

Further evidence that a high-level representation of a moving object is maintained during apparent motion was provided by Shioiri, Cavanagh, Miyamoto, and Yaguchi (2000). They had observers covertly tracking a disc in an ambiguous apparent motion display, which contains equal motion energy in clockwise and counterclockwise directions such that there is no net direction present in the stimulus. The percept of movement during the ISI therefore must rely on feedback from a high-level, continuing representation. Observers reported the perceived position of the tracked disc during the ISI, and the authors found that it varied smoothly along the motion path as a function of time. The position of the disc's representation was therefore continuously updated even while no stimulus was physically present.

There are at least two mechanisms by which feedback could update the position of the representation of an apparently moving object during the ISI. An extrapolation mechanism, such as the mechanism guiding smooth pursuit eye movements and suggested to underlie the flash-lag effect (Nijhawan, 1994; but see Brenner & Smeets, 2000), would adjust the position of the object representation according to an expected trajectory—predicting the future position on the basis of known past positions. Conversely, an interpolation mechanism would retroactively 'fill in' the object's trajectory once it is known where the object is headed—interpolating the object's past position with knowledge of its current position. The fact that just two successively presented targets are sufficient to generate illusory motion (Wertheimer, 1912), a situation in which there is insufficient information to predictively form a representation of a moving object, suggests that such a mechanism might be involved in the construction or maintenance of a representation of a moving object.

Here, we investigated how the representation of an object in apparent motion is updated, by separating the contributions of interpolation and extrapolation mechanisms to the determination of its position. In a simple continuous apparent motion stimulus, consisting of successively presented spatially separated discs, the two mechanisms are indistinguishable: both mechanisms would place the representation of the object during an ISI just ahead of its most recent physical position. However, by unexpectedly reversing the direction of motion of the object, we created situations in which extrapolation would place the representation *ahead* of its last position, whereas interpolation would place the representation *behind* its last position.

2. Experiment 1

We adapted the interference paradigm used by Yantis and Nakama (1998), in which the representation of a moving object results in longer RTs on a detection and identification task at the position of the object's representation. We expanded their bistable quartet stimulus into an unambiguous apparent motion display with eight possible disc locations, with placeholders (gray digital eights) presented on the motion path (Fig. 1). Observers monitored the array of placeholders, and reported which of two possible probes appeared by pressing an appropriate button. By measuring RTs at eight positions on the array, we were able to calculate the degree to which each position experienced interference, allowing us to map out the representation of the moving disc. For clarity, we refer to the two discs physically present in the frame immediately preceding the appearance of the probe as the disc *tokens*, to distinguish them from the internal representation of the disc. Consequently, we express the positions at which the probe could appear relative to the nearest disc token, such that a probe can appear 2 steps behind, 1 step behind, 1 step ahead, or 2 steps ahead of a disc token (Fig. 1).

We tested two experimental conditions. In the *continuous* condition, the discs continued on their original trajectory after the probe was presented. Since both extrapolation and interpolation processes would place the representation of the disc during the ISI ahead of the disc token, we expected to find maximum interference on the task when the probe appeared just ahead of the disc token (as in the example trial in Fig. 1).

In contrast, in the *reversal* condition, the discs reversed direction at the moment the probe was presented. In this situation, interference ahead of the disc token would be evidence for the presence of a representation at the extrapolated position, whereas interference behind the disc token would support the representation being at the interpolated position.

Critically, the two conditions only diverged *after* the presentation of the probe, such that any effect of condition on the distribution of interference must be due to an interpolation mechanism.

2.1. Method

2.1.1. Observers

Eight observers (including one of the authors) with normal or corrected-to-normal vision participated in the experiment.

2.1.2. Stimuli

Observers were tested in a dark room with a chin rest 30 cm away from an AppleColor monitor (1024 × 768 pixels, 75 Hz refresh rate) controlled by a Macintosh G4 computer running Matlab with PsychToolbox extensions (Brainard, 1997; Pelli, 1997). All stimuli were presented on a gray background (17.9 cd/m^2). A black fixation point

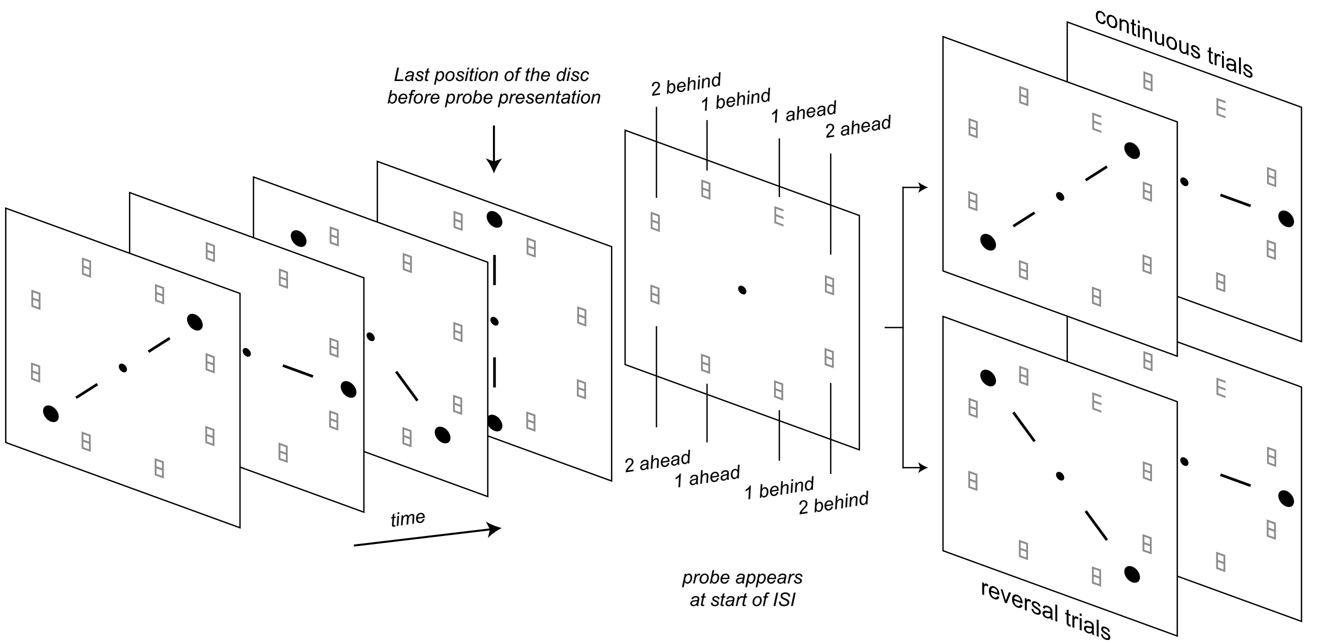

Fig. 1. Observers monitored an array of placeholders for the appearance of a probe (one of the digital eights changing into a 3 or E), and made a speeded 2AFC decision on the probe's identity. The eight placeholders were presented midway between the possible locations of two task-irrelevant black discs which moved around the array in apparent motion. At the end of the ISI following the appearance of the probe, in one experimental condition (continuous), the two discs were presented in the next position along their expected trajectory and continued in the same direction until the observer responded. In the other condition (reversal), the two discs were instead presented behind the last presented disc (the disc token), and accordingly continued in the opposite direction. Reversal and continuous trials were therefore indistinguishable until after the appearance of the probe. Reaction times were analyzed as a function of the position of the probe relative to the nearest disc token (in the trial illustrated here, the probe was presented just ahead of the disc token).

(0.1 cd/m^2, radius 0.3° of visual arc) was presented at the center of the screen. Eight placeholders, dark gray (13.4 cd/m^2) digital eights made up of seven line segments (total size 0.6° by 1.1° of visual arc), were presented at the vertices of an imaginary octagon around the fixation point. Black discs (radius 0.5° of visual arc, 0.1 cd/m^2) could appear in between the placeholders, at the eight compass directions. The discs and digital eights were presented 6.8° away from the fixation point. The distance between the centers of a placeholder and a neighboring disc was 2.6°. A black line (0.1 cd/m^2, width 0.1°) was presented between fixation and each of the black discs, starting at 2.6° from the center of the screen and extending 2.1° radially outwards, in order to enhance the impression of circular motion.

2.1.3. Procedure

At the start of each trial, all placeholders appeared and remained visible for the entire duration of the trial. A pair of discs was presented at randomly chosen opposite positions around fixation, along with the corresponding radial black lines. The discs and lines were present for 106.7 ms, after which they were removed from the screen for 66.7 ms. This sequence was repeated at sequential positions around the array such that the disc pair appeared to rotate around fixation. Clockwise and counterclockwise trials were randomly interleaved.

At a randomly chosen point between 10 and 25 such steps, two elements were removed from a randomly chosen placeholder, changing it from a digital eight into either a digital 3 or a digital E. This change always occurred at the start of an ISI, coinciding with the disappearance of the two discs. After the appearance of the probe, in *continuous* trials the disc pair continued moving around the array in the same fashion as it did before the appearance of the probe, whereas in *reversal* trials, the disc pair changed direction (from counterclockwise to clockwise or vice versa). In this way, continuous and reversal trials were identical from trial start until 66.7 ms after the appearance of the probe. The probe was equally likely to appear in any of the eight possible positions.

Observers were instructed to monitor the array of placeholders for a change, and to indicate which of the two target characters appeared using appropriate buttons. They were instructed to respond as quickly as possible while minimizing errors and made aware of the fact that the black discs were task-irrelevant. Error trials were discarded and rerun at the end of the experiment. All observers completed 320 trials, spread over two blocks.

Results were analyzed according to the position of the probe with respect to the last position of the nearest disc, taking into account its direction of motion. Since the display was symmetric, this resulted in four positions: 2 steps behind, 1 step behind, 1 step in front, and 2 steps in front,

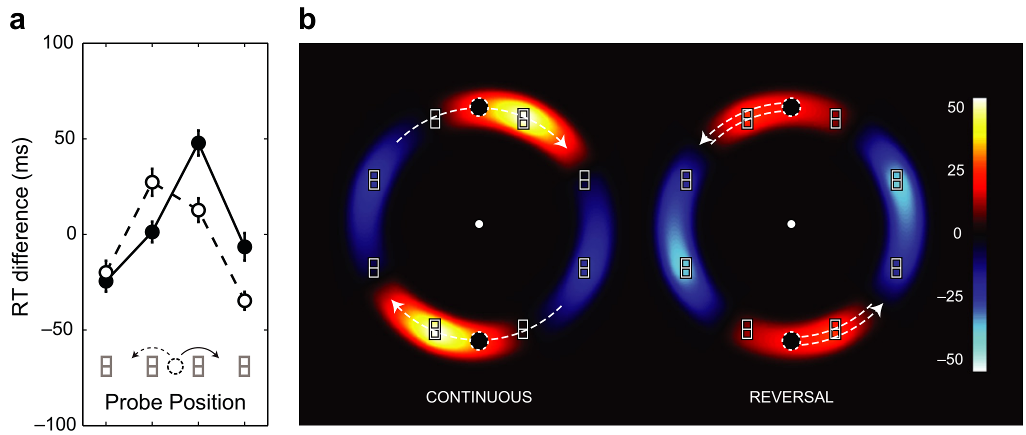

Fig. 2. Results from Experiment 1. (a) RT as a function of probe location for trials in which the discs continued on their original trajectory (filled circles, solid line) and reversed (open circles, dashed line). RT is expressed as a difference from overall mean RT. Probe location is plotted on the horizontal axis, expressed relative to the nearest disc token. Left and right halves the chart correspond to probe locations behind and ahead of the disc token, respectively. Error bars indicate standard errors of the mean. (b) The same RT data overlaid on a sample trial to form a map indicating areas of high (yellow and red) and low (blue) interference. All trials are aligned such that the disc tokens are always at the top and bottom points on the circular array, moving clockwise.

for each of two experimental conditions (continuous and reversal). Reaction time (RT) distributions for each observer were trimmed, discarding RTs below 300 ms and above 1000 ms in order to reduce the impact of outliers. Trials (7.5%) of trials were discarded in this way, and overall mean RT after trimming was 620 ms. The difference between each observer's overall mean RT and the mean RT for each combination of conditions was entered in a 4×2 repeated measures ANOVA.

2.2. Results

A 4×2 repeated measures ANOVA revealed a significant main effect of probe position ($F = 22.25$, df = 3, $p < 0.001$). Post-hoc tests showed that observers were significantly slower to report a probe when it occurred in a placeholder just ahead of or just behind the disc token than when it occurred elsewhere ($p < 0.01$). Additionally, observers were slower to report a probe just ahead of the disc token than just behind it ($p < 0.05$). Fig. 2a shows mean-corrected RTs for each experimental condition as a function of position.

Fig. 2b shows the pattern of interference superimposed on the example trial from Fig. 1, in which the discs (initially) moved clockwise and in which the last positions of the two discs before the probe were the top and bottom positions. Hot and cool areas indicate positions which experienced relatively high and low interference, respectively. The left diagram (the continuous condition) shows that maximum interference was observed just ahead (i.e. just clockwise) of the disc tokens. This supports our main hypothesis and the findings of Yantis and Nakama (1998), but does not yet allow us to distinguish between interpolation and extrapolation. However, the right diagram (reversal condition) shows that when the discs instead reversed direction after the appearance of the probe, interference ahead of the disc token was reduced, whereas interference behind it increased.

Since the two conditions were identical until *after* probe presentation, the extrapolation mechanisms contributing to the position of the disc representation had identical input available to them in both conditions. The effect of experimental condition, which was evident as an interaction between position and experimental condition ($F = 14.41$, df = 3, $p < 0.001$) therefore demonstrated the involvement of interpolation mechanisms in determining the position of the representation of the moving disc during the ISI.

Conversely, the contribution of extrapolation processes cannot be concluded from the results of this experiment without making assumptions about the manner in which a discrepancy between interpolation and extrapolation processes is resolved. The fact that maximum interference was found when interpolation and extrapolation processes were in agreement (ahead of the disc token on continuous trials) does suggest that output from the two processes is somehow additive. Furthermore, when the two processes were dissociated in reversal trials, we found intermediate levels of interference in the extrapolated and interpolated positions (ahead of and behind the disc token, respectively), suggesting that the relative contributions of interpolation and extrapolation processes are comparable. Experiment 3 below addresses the role of extrapolation more directly.

3. Experiment 2

Wertheimer (1912) proposed that attention might be the mechanism mediating the illusion of motion in apparent motion. The fact that it is possible to see unidirectional motion in ambiguous apparent motion displays by attending to one of the two possible motion directions indicates that attention is sufficient to create an impression of motion (Cavanagh, 1992; Verstraten, Cavanagh, & Labianca, 2000), but whether attention is necessary for a high-level representation to be maintained remains an open question.

In Experiment 2, we investigated the role of attention in the maintenance of the representation of a moving disc in an apparent motion display by explicitly manipulating the locus of focused attention. To do this, we introduced an additional attentive tracking task requiring observers to covertly attend one of the two discs as it progressed around the array, while still monitoring the array of placeholders for a probe. If attention were necessary to maintain or update a representation of a moving object, then we would expect to find an interference effect similar to the one found in the previous experiment around the attended disc token, but not around the unattended disc token. Conversely, if the representation were updated outside of the focus of attention, we would expect to find a similar pattern of results around both disc tokens.

3.1. Methods

3.1.1. Observers

Eight observers (including one of the authors) with normal or corrected-to-normal vision participated in the experiment.

3.1.2. Stimuli

Observers were tested in a dark room with a chin rest 57 cm away from a LaCie ElectronBlue monitor (1280×1024 pixels, 75 Hz refresh) controlled by a Macintosh G4 computer. The stimulus layout was identical to the stimulus layout in Experiment 1, with the exception that before each trial, one of the two discs was presented in bright red (17.5 cd/m^2) to indicate which disc was to be tracked, and that in catch trials, small black arrows 1° in length were briefly presented centered on the locations of the discs.

3.1.3. Procedure

The procedure was similar to the one used in Experiment 1, with the following exceptions. Observers were instructed to carry out a dual task: in addition to monitoring the array of placeholders for the appearance of a probe character, they were asked to track one of the two discs with covert attention. Which of the two discs was to be tracked was indicated at the start of the trial: for the first 8 steps, the to-be-attended disc was presented in red, after which it reverted to black.

Additionally, in order to increase the attentional demand of the task, we slightly increased the rate at which discs moved around the array while maintaining the same duty cycle. The discs and lines were present for 80 ms, after which they were removed from the screen for 53 ms. In 80% of trials, a probe was presented at one of the placeholders at a randomly chosen point between 5 and 25 steps after the cued disc reverted to black.

The remaining 20% of trials were catch trials, included to ensure that observers were attentively tracking the cued disc as instructed. In catch trials, at the point in time when the probe would normally appear, instead randomly oriented backward masked arrows were presented for 250 ms centered on the last positions of both discs, and observers performed an 8AFC discrimination task on the direction of the arrow presented at the position of the tracked disc. All observers achieved at least 60% and no more than 90% accuracy on catch trials, confirming that they were tracking as instructed and that the task was sufficiently difficult. Observers carried out a total of 640 trials, including 128 randomly inserted catch trials, in two blocks. Error trials were discarded from the analysis. We did not record eye movements, but Verstraten, Hooge, Culham, and van Wezel (2001) have previously demonstrated that it is possible to covertly track an apparent motion stimulus without making systematic eye movements. Given that observers were monitoring an array of placeholders in addition to tracking, we believe that they were maintaining fixation as instructed.

RTs on the main task were analyzed according to the position of the probe with respect to the last position of the nearest disc, taking into account its direction of motion. This resulted in four positions: 2 steps behind, 1 step behind, 1 step in front, and 2 steps in front, around either the attended or unattended disc, for each of two experimental conditions (continuous and reversal). Reaction time (RT) distributions for each observer were trimmed, discarding RTs below 300 ms and above 1000 ms—14% of trials were discarded in this way, and overall mean RT after trimming was 703 ms. The difference between each observer's overall mean RT and the mean RT for each combination of conditions was entered in a $4 \times 2 \times 2$ repeated measures ANOVA.

3.2. Results

Fig. 3a displays RT differences as a function of position and experimental condition, separately around the attended and unattended disc tokens. A $4 \times 2 \times 2$ repeated measures ANOVA revealed a significant main effect of attention ($F = 5.67$, $\mathrm{df} = 1$, $p < 0.05$): observers were slower to report a probe presented near the unattended disc than a probe presented near the attended disc. Furthermore, in line with the findings from Experiment 1, the interaction between probe position and experimental condition was significant ($F = 5.22$, $\mathrm{df} = 3$, $p < 0.01$). Post-hoc tests showed that when the discs reversed direction, observers were slower to report a probe when it was presented either directly behind or 2 steps behind either of the disc tokens than when it was presented 2 steps ahead ($p < 0.05$).

A visualization of interference as a function of relative position is shown in Fig. 3b. The diagrams are aligned such that the upper of the two disc tokens is the attended disc. Note that the interaction pattern of interference around

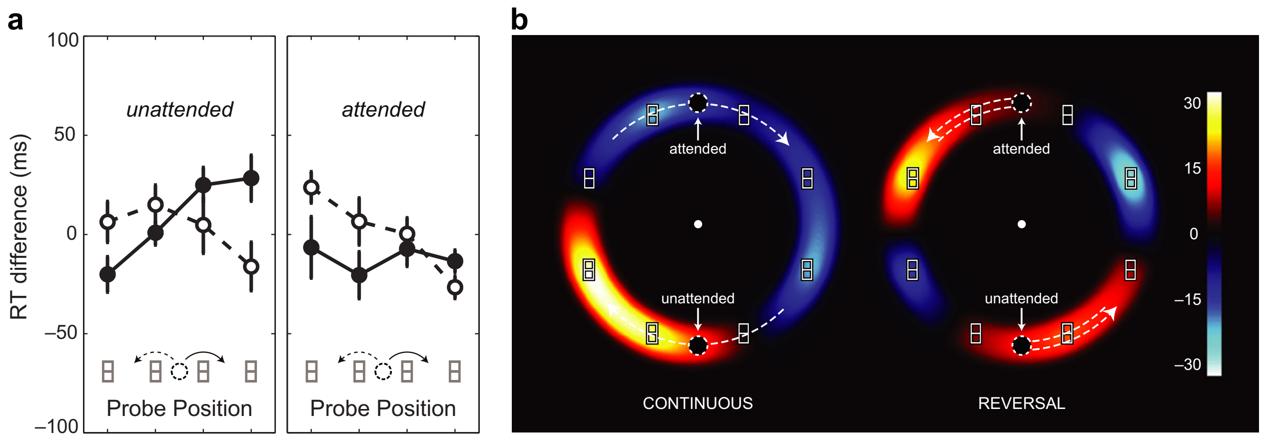

Fig. 3. Results from Experiment 2. (a) RT as a function of probe location for trials in which the discs continued on their original trajectory (filled circles, solid line) and reversed (open circles, dashed line). The two panels plot RTs near the unattended (left) and attended (right) discs separately. Probe location is plotted on the horizontal axis, expressed relative to the nearest disc token. Left and right halves of each chart corresponds to probe locations behind and ahead of the disc token, respectively. Error bars indicate standard errors of the mean. (b) The same RT data overlaid on a sample trial to form a map indicating areas of high (yellow and red) and low (blue) interference. All trials are aligned such that the attended disc token is always at the top of the circular array, moving clockwise.

the unattended disc (i.e. the bottom half of each diagram) replicates the findings of Experiment 1 (Figs. 2b and 3b), although the point at which maximum interference is experienced lies slightly further away from the disc token than in Experiment 1 (see Section 5). However, around the attended disc token we see a slightly different pattern. Although there is a similar effect of reversal (the dashed lines in the two panels of Fig. 3a are comparable), there is no interference ahead of the attended disc token in the continuous condition (the solid line in the right panel of Fig. 3a is flat, and there is no area of high interference clockwise of the top disc token in the left diagram in Fig. 3b).

In Experiment 1 the discs were task-irrelevant, so observers did not need to attend them. However, because we did not explicitly manipulate attention, we could not eliminate the possibility that attention is involved in the maintenance or updating of the object's representation. Since the pattern of interference around the unattended disc token in Experiment 2 replicates the results from Experiment 1, we can conclude that focused attention is not necessary for the maintenance and updating (at least by interpolation) of the representation of an object in apparent motion.

We believe that the presence of focused attention (which was bound to the representation of the moving disc by the demands of the task) somehow offset the interference caused by the representation of the disc. Either attentional facilitation compensated for the interference caused by the representation of the moving disc, or the availability of attention prevented the representation from disrupting visual processes critical to the task. At any rate, our results demonstrate that focused attention is not necessary for the integration of an apparent motion display into a single representation of a moving object. In fact, we found that within the locus of focused attention (i.e. ahead of the attended disc token), interference on the detection and identification task is reduced.

Using a detection sensitivity paradigm, Shioiri, Yamamoto, Kageyama, and Yaguchi (2002), similarly reported performance enhancement on the path of an attentively tracked apparent motion display. They interpreted their results as evidence for a smoothly moving attentional spotlight which predicted (i.e. extrapolated) the future position of the tracking target. Although the authors did not consider the contribution of a possible interpolation mechanism to the position of the attentional spotlight, our results nonetheless support their interpretation. If the position of the attentional spotlight were updated by interpolation mechanisms, we would expect to find facilitation behind the tracked disc token on reversal trials. Instead, we find facilitation ahead of the tracking target on both continuous and reversal trials—the predicted position of the tracking target. Our findings therefore support the notion that attention moves according to a predictive mechanism during attentive tracking (Hogendoorn, Carlson, & Verstraten, 2007; Shioiri et al., 2002).

4. Experiment 3

By their very nature, interpolation and extrapolation processes differ in the temporal interval over which they integrate information. When determining the apparent position of a (physically absent) object during an ISI, an extrapolation process accumulates input from *before* the ISI, whereas an interpolation process also integrates input from *after* the ISI. As such, for sufficiently long ISIs, output from extrapolation mechanisms about the position of the representation of an object in apparent motion might become available before output from interpolation mechanisms. We hypothesized that it might therefore be possible to dissociate the two mechanisms using a task with appropriate temporal parameters.

In Experiments 1 and 2, observers carried out a detection and identification task, which presumably required multiple visual processing stages as well as a decision stage, resulting in relatively long reaction times of around 700 ms. Although we cannot yet say exactly which processing stages were disrupted by the representation of the apparent motion disc, it is apparent from our results that these critical stages had not yet reached completion by the time output from the interpolation mechanism became available.

In Experiment 3, we had observers carry out a simple detection task. Observers simply pressed a button as quickly as possible after the appearance of a Gaussian luminance blob. This probe was well above detection threshold, and no identification or discrimination was required. RTs on this task were much lower (around 350 ms), and we hypothesized that the critical stages that might experience interference from the representation of the moving disc (if any) might have reached completion before information from interpolation processes became available.

As such, we conceived of three a priori possibilities:

(1) The pattern of results might replicate those from the previous experiments, which would indicate that despite the simpler task, interpolation processes had sufficient time to affect the position of the representation and disrupt a critical processing stage.
(2) Conversely, we might find no effect of position whatsoever, which would indicate that observers experienced no interference from the disc representation. This could be either because critical stages were completed before input from either extrapolation or interpolation processes became available, or because the new task called on different processing stages which were insensitive to disruption.
(3) Finally, critical processing stages might be completed before information from interpolation becomes available, but after output from extrapolation has had time to affect the position of the representation. In this case, we would expect to find an effect of position similar to the continuous condition in Experiment 1 (i.e. maximal interference ahead of the disc token). However, we would expect no effect of experimental condition, since the disc reversal would occur too late to influence critical stages of the task.

4.1. Methods

4.1.1. Observers

Eight observers (including one of the authors) with normal or corrected-to-normal vision participated in the experiment.

4.1.2. Stimuli

Observers were tested in a dark room with a chin rest 57 cm away from a LaCie ElectronBlue monitor (1280 × 1024 pixels, 60 Hz refresh) controlled by a Macintosh G4 computer. The stimulus layout was identical to the stimulus layout in Experiment 1, except that no placeholders were presented. Instead, a Gaussian luminance blob was used as a probe (central luminance 45 cd/m^2, 0.5° of visual arc wide at half maximum luminance), which could be presented centered on any of the eight positions occupied by the placeholders in Experiment 1. Discs and lines were presented for 100 ms followed by 66 ms blank ISIs.

4.1.3. Procedure

Instead of a speeded discrimination task, observers carried out a speeded detection task: they were simply instructed to monitor the display and press a key as quickly as possible after detecting the probe, which was presented for 33 ms and was well above detection threshold for all observers. The procedure was otherwise identical to the one used in Experiment 1. All observers completed 1024 trials, spread over 8 blocks.

RTs were analyzed in four positions: 2 steps behind, 1 step behind, 1 step in front, and 2 steps in front, for each of two experimental conditions (continuous and reversal). Reaction time (RT) distributions for each observer were trimmed, discarding RTs below 200 ms and above 500 ms—2.8% of trials were discarded in this way, and overall mean RT after trimming was 349 ms. The difference between each observer's overall mean RT and the mean RT for each combination of conditions was entered in a 4 × 2 repeated measures ANOVA.

4.2. Results

A 4 × 2 repeated measures ANOVA revealed a significant main effect of probe position ($F = 9.00$, df = 3, $p < 0.001$). Post-hoc tests showed that observers were significantly slower to report a probe presented just ahead of ($p < 0.01$) or just behind ($p < 0.05$) the disc token than when it occurred elsewhere. Additionally, there was a trend that observers were slower to report a probe just ahead of the disc token than just behind it, although it was not significant ($p = 0.08$). There was no main effect of experimental condition ($F = 0.02$, df = 3, $p = 0.89$) and no interaction between probe position and experimental condition ($F = 0.19$, df = 3, $p = 0.90$).

Mean-corrected RTs at all probe positions for both experimental conditions are plotted in Fig. 4a. A graphical representation of the spatial distribution of interference (Fig. 4b) shows that observers experienced maximal interference when the probe was presented ahead of the disc token (i.e. coinciding with its extrapolated position), irrespective of whether the discs subsequently reversed direction or not (yellow and red areas in Fig. 4b are clockwise of the disc token in both the upper and lower diagrams). The fact that the reversal of the discs' trajectory did not affect performance on the task suggests that critical processing stages in the detection task were completed after

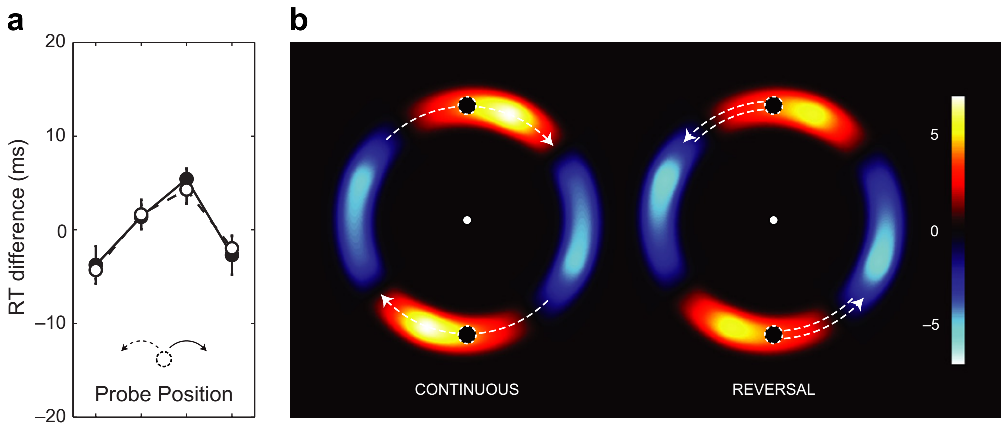

Fig. 4. Results from Experiment 3. (a) RT as a function of probe location for trials in which the discs continued on their original trajectory (filled circles, solid line) and reversed (open circles, dashed line). Probe location is plotted on the horizontal axis, expressed relative to the nearest disc token. Left and right halves the chart correspond to probe locations behind and ahead of the disc token, respectively. Error bars indicate standard errors of the mean. (b) The same RT data overlaid on a sample trial to form a map indicating areas of high (yellow and red) and low (blue) interference. All trials are aligned such that the disc tokens are always at the top and bottom points on the circular array, moving clockwise.

extrapolation, but before interpolation processes had time to influence the position of the representation.

These results show that it is possible to dissociate the contributions of interpolation and extrapolation processes to the position of the representation of an object in apparent motion: information from extrapolation influenced representation before information from interpolation became available. Furthermore, by eliminating the contribution of interpolation, this experiment verifies what the results from Experiment 1 suggested: an extrapolation mechanism exists that is involved in updating the position of this representation.

5. Discussion

An apparent motion display with appropriate spatiotemporal parameters can induce a strong impression of a moving object, even on sections of the motion path where no stimulus is presented. In three experiments, we investigated how the representation of this object is updated during the ISI between successive presentations. In Experiment 1, we demonstrated the role of an interpolation mechanism in updating the position component of the representation. In Experiment 2 we demonstrated that the position of this representation is updated even outside of the locus of focused attention. Finally, the results from Experiment 3 confirm the involvement of an extrapolation mechanism, and demonstrate that interpolation and extrapolation processes can be separated in time.

Whereas in Experiments 1 and 3 maximal interference was observed just behind and just in front of the disc token (in reversal and continuous conditions, respectively), in Experiment 2 we observed maximal interference further away from the disc token. We believe that this is related to the slightly higher rate at which discs moved around the array. In a very simple model in which there is a fixed delay between probe onset and a given visual process (form processing, for example), then if the discs are moving faster, the representation of the moving disc will have moved further by the time that process starts. If that particular process suffers from the presence of the representation, the point at which interference is maximal will depend on the speed of the discs. We speculate that it may be possible to use this method to probe the temporal properties of specific visual processes. By manipulating the requirements of the task and the spatiotemporal parameters of the apparent motion display, this paradigm would allow an experimenter to determine a time frame during which a particular visual process is susceptible to interference.

The results of Experiment 2 additionally provide supporting evidence that attention moves according to a predictive mechanism during attentive tracking. Within the time frame we investigated, we found no evidence for interpolated updates to the position of the attentional spotlight. However, a moving target deviating from its predicted path is not lost forever, so a reorienting mechanism must exist, which presumably operates on a longer timescale. Interestingly, we found no effect of inhibition of return (Posner & Cohen, 1984) on the main task: RTs to a probe appearing just behind the disc token, in the recent position of the attentional spotlight, were no higher than elsewhere on the array. However, to the best of our knowledge inhibition of return has not been studied during attentive tracking (Klein, 2000), and we did not acquire sufficient performance data on catch trials to be able to describe how the attentional spotlight reorients after the unexpected change in trajectory of the tracking target. Further research will therefore be necessary to conclude whether inhibition of return generalizes to the smooth shifts of attention involved in attentive tracking or whether it is limited to paradigms involving discrete, saccade-like attentional shifts.

In our experiments, we probed the representation of a moving disc during stable apparent motion. It would be interesting to see how interpolation and extrapolation processes develop and decay over time after changes in the stimulus. In particular, extrapolation of the disc's position is only possible once at least 2 disc tokens have been presented. In our experiments, between 10 and 25 disc tokens were presented before the target was presented. We found no difference between trials in which the target appeared relatively early and trials in which the target appeared later. We therefore hypothesize that the contribution of extrapolation to the position of the disc representation builds up rapidly as successive disc tokens are presented, reaching an asymptote before 10 tokens. Similarly, deviations from the expected motion path, such as reversals, require adjustments to the extrapolation mechanism. Characterizing how extrapolation processes develop and adjust over time might shed light on a possible common substrate between mechanisms subserving the maintenance of object representations and mechanisms involved in smooth pursuit eye movements.

Yantis and Nakama (1998) proposed that the representation of a moving object might interfere with form processing on the motion path. However, the results from Experiment 3 demonstrate that the interference is more general, since it adversely affects even the detection of a Gaussian luminance blob, which presumably does not rely on form processing. Another explanation is that the interference we observe at the position of the representation of the moving disc is an instance of object substitution masking (Enns & DiLollo, 1997). Two hallmarks of object substitution masking (OSM) are (1) it is particularly strong when attention is diverted or spread across multiple positions, whilst being much weaker when focused attention is available and (2) that it occurs even when stimulus and mask are separated by a relatively large distance. In our experiments, we similarly found interference when observers distributed attention over 8 placeholders, whilst interference was reduced within the attentional spotlight when one of the discs was tracked. Furthermore, discs were presented about 2° of visual angle away from probes—much too distant for conventional metacontrast masking to explain our effects. Both of these observations are in line with an OSM account.

It has been suggested that object substitution masking occurs at a relatively high-level in the visual hierarchy, at a point where information has been integrated into objects (Enns & DiLollo, 1997). The standard OSM mask consists of four small dots surrounding (but not touching) the stimulus which is to be masked. According to DiLollo, Enns, and Rensink (2000), this mask is effective because it is initially processed as an empty square surface bounded by the four dots—in this way, a representation is created of an object in a location where no physical stimulus is presented, which interferes with what is *actually* presented at that location (i.e. within the four dots). We believe that this is exactly what happens in the apparent motion display: the representation of the moving object moves over the position at which the probe is presented and causes interference, whereas the masking object is not physically presented at that location. Lleras and Moore (2003) came to a similar conclusion after finding that presenting a four dot mask a second time after a short ISI (such that the two presentations were perceived as a single, moving object) caused significant masking even when the first presentation of the mask offset simultaneously with the target—a situation in which OSM usually does not occur (Enns & DiLollo, 1997). Interestingly, in their experiments they use just two sequential presentations to induce apparent motion—indicating the involvement of interpolation processes in constructing the representation of a single, moving object.

Functional neuroimaging work has identified a crucial role for hMT+/V5, the human homologue of the macaque motion-sensitive area MT, in mediating early visual activation in response to apparent motion. Using an object substitution paradigm Carlson, Rauschenberger, and Verstraten (2007) recently demonstrated the role of an adjacent area, the lateral occipital complex (LOC), in the formation of a persistent object representation. These two areas together are therefore ideally situated to integrate sequentially presented stationary objects into a single representation of a moving object, and subsequently cause interference on the path of that object by object substitution masking.

Although the limited temporal resolution of fMRI makes it difficult to discriminate between predictive and postdictive motion mechanisms, we believe this might be possible using techniques with higher temporal sensitivity, such as electro-encephalography (EEG). We hypothesize that it may be possible, on the basis of event-related potentials, to identify when feedback from these two mechanisms arrives in early visual areas.

In summary, we have shown in three experiments that both extrapolation and interpolation mechanisms contribute to updating the representation of a moving object during viewing of apparent motion, and that output from extrapolation processes is separable in time from output from interpolation processes. The representation of the moving object continues to be updated even outside the locus of focused attention, probably involving areas hMT+/V5 and LOC. We propose that this representation causes interference on the motion path through feedback connections to lower visual areas via an object substitution masking mechanism.

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