Tracking the Changing Feature of a Moving Object

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by

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The thesis is dedicated to Kia Nobre. Obrigado por todo.

Contents

I. Abstract

Tracking the Changing Feature of a Moving Object

The mind can track not only the changing locations of moving objects, but also changing features, which are often meaningful for guiding action. In the real dynamic world, features are often changing even as the objects they belong to move. How does the mind track such features? I found that this ability is enabled by a highly feature-specific process that *continuously* tracks the feature — even during occlusion, when the feature is completely invisible. This suggests that the mental representation of a changing feature and its moving object are continuously transformed. I also found a systematic error in performance, whereby the feature was reliably perceived to be further ahead than it truly was. This effect appears to occur because during occlusion the mental representation of the feature is transformed at a quicker rate than the veridical rate, perhaps in order to conservatively anticipate future feature states. Finally, I found an age-related decline in this feature tracking ability, and discuss ongoing work with lesion patients into the neural substrates of this process.

0. Introduction

Object Tracking

Moving objects are ubiquitous in the world, and so it is perhaps not surprising that much research has focused on how the mind keeps track of object locations, even through visual interruptions such as occlusion, e.g. a cyclist riding behind a car, or a person walking behind a crowd. Although a moving object is invisible during this period, it is perceived as having a continuous, persisting identity, rather than as jumping from one location to the next (for a review, see Scholl & Flombaum, 2010). Two paradigms which are commonly used to study how the mind tracks occluded objects are *production tasks,* in which observers have to press a button when they think an occluded object reaches the other end of the occluder (e.g., Rosenbaum, 1975) and *discrimination tasks,* in which the object disappears and then reappears further along its trajectory at either the correct or incorrect time, and observers have to discriminate between these possibilities in a two-alternative forced-choice task (DeLucia & Liddell, 1998). Such studies find that observers are fairly accurate at judging when an object will reemerge (Battaglini, Campana, & Casco, 2013; Benguigui & Bennett, 2010; Benguigui, Broderick, & Ripoll, 2004; DeLucia & Liddell, 1998; Makin & Poliakoff, 2011; Peterken, Brown, & Bowman, 1991; Rosenbaum, 1975). This is because even during occlusion the mind continues to ‘track’ the object as if it were still there (the *tracking hypothesis,* DeLucia & Liddell, 1998), using the smooth pursuit oculomotor system to continuously allocate visuospatial attention to the invisible object’s location (DeLucia, Tresilian, & Meyer, 2000; de’Sperati & Deubel, 2006; de’Sperati & Santandrea, 2005; Gilden, Blake, & Hurst, 1995; Lyon & Waag, 1995; Makin &

Poliakoff, 2011). Observers do not, however, appear to employ the equally viable strategy of discretely estimating the point of reemergence based on the visual information that came before occlusion (Hecht & Savelsburgh, 2004; Lee, 1976; Tresilian, 1995).

Feature Tracking

The mind can also track changing features, since features often carry useful information that guides action, e.g. a revolving speedometer gauge, or a changing facial expression. Several studies have investigated the perception of motion through feature space (Blaser, Pylyshyn, & Holcombe, 2000; Blaser & Sperling, 2008; Sheth, Nijhawan, & Shimojo, 2000), and two recent studies have begun looking into how this is accomplished during occlusion, studying changes in number, color, spatial accumulation (dots increasingly filling a grid), and orientation (Makin & Bertamini, 2014; Makin & Chauhan, 2014). Since similar performance levels were found across these feature dimensions and also for tracking of spatial locations, the authors concluded that 'tracking' of these various features may rely on a common rate control mechanism (Makin & Bertamini, 2014; Makin & Chauhan, 2014). This common rate controller may then be responsible for guiding the rate of attentional allocation to the tracked item.

Tracking the Changing Feature of a Moving Object

The existing studies on feature tracking have all investigated feature changes at a static location, e.g. a static circle with a rotating clock hand. But in our dynamic world the mind must often deal with the more complex task of tracking changing features of objects that *themselves are moving*, e.g. tracking the changing luminance or size of an approaching vehicle, or the changing orientation of a gymnast or diver travelling through the air. How does the mind accomplish this feat? This question, to my knowledge, remains unanswered.[1]

Object-Specific or Feature-Specific Tracking?

To get a grip on the problem, one would like to know how the feature is processed in relation to its object over time. Tracking the changing feature of a moving object is an especially interesting case of tracking, since the mind must somehow reconcile changing feature information with changing object locations. It is well known that cognitive processes often operate over entire, feature-bound object representations (e.g. Kahneman & Henik, 1981; O'Craven, Downing, & Kanwisher, 1999), such as in memory (Alvarez & Cavanagh, 2004; Luck & Vogel, 1997), spatial attention (Egly, Driver & Rafal, 1994; Scholl, 2001), and temporal attention (De Freitas, Liverence, & Scholl, 2014). On the other hand, there are also cases in which cognitive processes can operate over features alone (Blaser, Pylyshyn, & Holcombe, 2000; Blaser & Sperling, 2008; Howard & Holcombe, 2008; Nobre, Rao, & Chelazzi, 2006; Sheth, Nijhawan, & Shimojo, 2000). Does tracking the changing feature of a moving object rely on object-specific or feature-specific processing?

Discrete or Continuous Feature Transformations?

Relatedly, one would like to know what happens to the mental representation of both the changing feature and the changing location of the surrounding object boundaries during tracking. Since the recent work by Makin and colleagues shows that

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[1] One study did look at 'rolling motion', although it studied observer's conscious impressions of the motion, for example, by asking them to draw out the trajectory they thought the end of a wheel traced. They found that observers believed the wheel traced a curtate cycloid (Isaak & Just, 1995; Proffitt, Kaiser, & Whelan, 1990).

tracking ability for a changing feature at a static location closely resembles that for tracking changing object locations (Makin & Bertamini, 2014; Makin & Chauhan, 2014), this suggests that feature tracking, too, may rely on a continuous tracking mechanism. But aside from this correlational evidence, no existing experiments have been able to speak to this possibility directly. Does the mind truly simulate continuous featural change during occlusion, dynamically transforming and updating a representation of the feature? And even if so, can it manage this while the object itself is changing location?

The Current Studies

I see the current studies as a step toward understanding more complex, dynamic tracking in the real world, where both feature and object information can be changing simultaneously. To this end, I created a new paradigm using orientation as a case study, in which observers were required to keep track of the changing orientation of a rolling wheel as it went behind an occluder. The wheel then reemerged, but only partially, so that observers could still not see its feature (see Fig. 1). At this point, observers provided an exact estimate of the feature's orientation. The increased sensitivity of the continuous recall measure allowed me to detect whether there were any systematic biases in observer's responses. Furthermore, a modeling approach in my analyses enabled me to measure both the temporal and spatial precision of tracking across various experimental manipulations. Eye-tracking measures offered a window into observer's mental representations during occlusion, when the stimulus was invisible. Finally, by studying lesion patients, I am determining the neural underpinnings of the process.

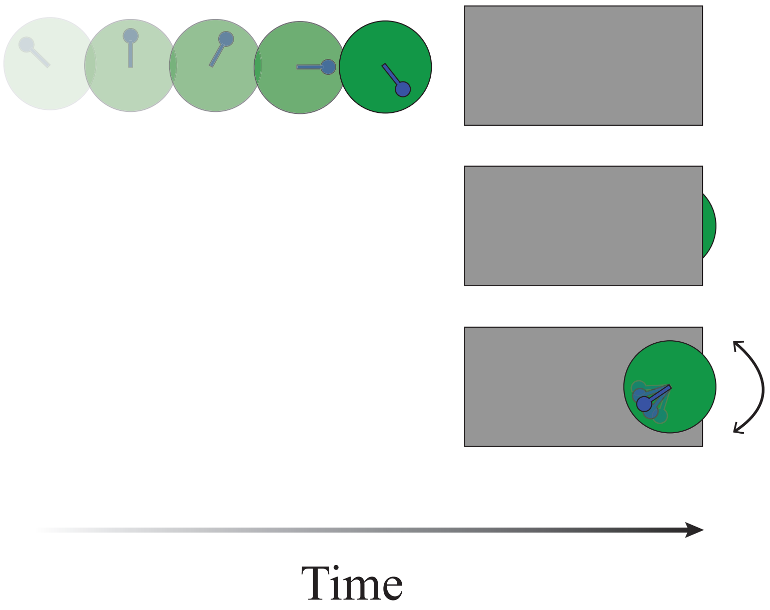


Fig. 1. Depiction (not to scale) of the feature tracking task.

Seven experiments address the extent to which tracking the changing feature of a moving object is feature- or object-specific, whether it is continuous or discrete, and what its neural underpinnings are. I found that observers were indeed able to track the changing features of a moving object (Experiment 1), and at various speeds of motion (Experiment 2). Further, they demonstrated a significant feature displacement effect — perceiving the feature to be further along its trajectory than it truly was. I found similar feature tracking performance for stationary objects (Experiment 3), and when the feature rotated in the opposite direction than it was supposed to, given the direction in which the object was moving (Experiment 4), suggesting that the tracking process employed in these experiments was highly feature-specific (not influenced by the object's spatial behavior). Then, by manipulating expectations (Experiment 5) and using eye movements as a window into observer's mental representations (Experiment 3B), I discovered that both the changing orientation of the wheel and its changing location were continuously transformed mentally during occlusion, even though they were invisible. I also replicated the feature tracking effects in older adults, though a much greater relative proportion of older adults needed to be excluded for responding uniformly (Experiment 7), suggesting an age-related decline in the ability to track changing features of moving objects. Finally, I discuss ongoing work into the neural underpinnings of dynamic feature tracking.

1. Tracking the Changing Feature of a Moving Object

The aim of the first Experiment was to establish whether observers are able to track the changing feature of a moving object, both when the stimulus is visible and occluded. Further, I investigated whether there were any biases in observers' responses, and determined the spatial and temporal precision of their tracking ability.

Method

Ethics. All experimental protocols were approved by the University of Oxford Central University Research Ethics Committee, and were carried out in accordance with the provisions of the World Medical Association Declaration of Helsinki.

Paradigm. The paradigm consisted of a wheel-like object with a 'spoke' in its wheel that 'rolled' across a computer monitor display, changing orientation as it did so, then went behind an occluder. The wheel then emerged from the opposite end of the occluder, but only partially, so that observers could still not see the orientation of the spoke at that location (Fig. 1). Observers had to predict its true orientation when the wheel stopped, by manually adjusting the orientation of a randomly oriented spoke that appeared soon after the wheel stopped.

Observers. 13 observers ($M_{\text{age}} = 24$, 8 female) with normal or corrected visual acuity completed a 60-min session in exchange for £10 payment. In the absence of any previous studies that had used the paradigm created for the present experiments, I began with the heuristic assumption that the required sample size would be comparable to that of previous studies on object-persistence, which had used similar sample sizes (e.g. Liverence & Scholl, in press; Scholl & Pylyshyn, 1999). In all studies, observers gave written informed consent before testing.

Apparatus and stimuli. Stimuli were created in MATLAB using the Psychophysics Toolbox libraries (Brainard, 1997; Pelli, 1997) and presented on a Dell personal computer. Observers sat in a dimly lit booth at 74 cm from the monitor (22-inch Samsung SyncMaster 2233; screen size: 35.24º * 22.17º (resolution: 1680 * 1050 pixels); refresh rate: 60Hz; screen width: 47cm). A chin rest was used to stabilize observers' heads. Gaze locations were continuously recorded with a video-based eye tracker at 500 Hz (EyeLink 1000, SR Research, Ontario, Canada). On each trial, a 2.69º green disk with a randomly oriented blue 'spoke' centered on it, moved rightwards from the mid left edge of the screen (with the disc initially centered at 1.08º in the x-axis) at 3.90º/s for 6.82s. The spoke consisted of a 1.53º by 0.15º bar with a 0.34º by 0.76º ellipse attached to its end. As the disc moved, the spoke rotated at 120º/s around the centre of the circle, giving the impression of a rolling wheel. The spoke always rotated clockwise as the wheel moved rightwards. The wheel moved behind a gray rectangle (7.08º by 9.69º; RGB=150/150/150), the left border of which was located at 21.47º in the x-axis.

After 1.14s of complete occlusion, the wheel then emerged, stopping so that only 7.06% of its diameter was visible, and thus observers could see where the wheel stopped but not the spoke's current orientation. Since the spoke did not span the full radius of the circle, it was not visible when the disc stopped. After 0.5s, the entire wheel then popped up in front of the occluder, but without its spoke. Observers then pressed the spacebar key to make a randomly oriented spoke appear inside the wheel, which they could then adjust using the mouse until the orientation matched that which they thought was the true orientation of the wheel when it stopped. They clicked the left mouse button to submit their response. Each observer completed 300 experimental trials, preceded by three practice trials that provided participants with feedback on their degree of error for each trial (no feedback was provided during the experimental trials). Observers were instructed to "just say what you see", and not to think of the task as a math problem nor to use any special strategies.

Data processing and analysis. I planned to calculate the displacement angle between the response orientation and the true orientation (i.e. the bias), then exclude any participants whose overall distribution of errors failed Rayleigh's test, which tests whether a distribution is significantly different from a circular uniform distribution. To measure mean displacement, I planned to fit the biases with a mixture model, which applies a Gaussian to the response distribution. In recent years, this method of analyzing continuous responses has gained popularity within the psychological study of visual working memory (e.g. Brady, Konkle, & Alvarez, 2011; Zhang & Luck, 2008). It is preferable to simply using a traditional measure of central tendency such as the mean or mode, which can be skewed by extreme responses. The mixture model, in contrast, provides an overall fit to the distribution of responses. Furthermore, it provides estimates of variability (which I term 'precision') and guess rate for each trial.

Since I wanted the model to be able to handle fits that were not fixed at the origin, I specifically chose a mixture model with a bias term, using the Memtoolbox libraries (Suchow et al., 2013). This model ended up outperforming other models I tried to fit to pilot data, such as the standard mixture model, or the resource + swops model (Bays et al., 2009). I also planned to exclude any single participant whose mean displacement (as estimated by the model) lay outside 3 standard deviations of the mean displacement of all the other subjects.

Results

I excluded one observer who responded uniformly (Rayleigh's test, $p = .420$) and one observer whose mean response angle was three standard deviations beyond the group mean. This left 11 observers. For all trials, I calculated the displacement angle between the response orientation and the true orientation at the end of occlusion, which I term the *bias*. I then used the Memtoolbox (Suchow et al., 2013) to fit each observer's responses with a mixture model, which also included a bias term. The model treats responses as drawn from a mixture of two distributions: the probability of correctly recalling the orientation (with Gaussian error), and the probability of randomly guessing the orientation. The bias term ensures that the central tendency of the data is not fixed at zero. For each observer, I extracted their mean bias, and also their proportion of guesses and precision, in line with recent efforts to understand the spatial and temporal precision of the visual system (Holcombe, 2009; Linares, Holcombe, & White, 2009). The resulting parameter estimates were then compared using traditional statistical tests.

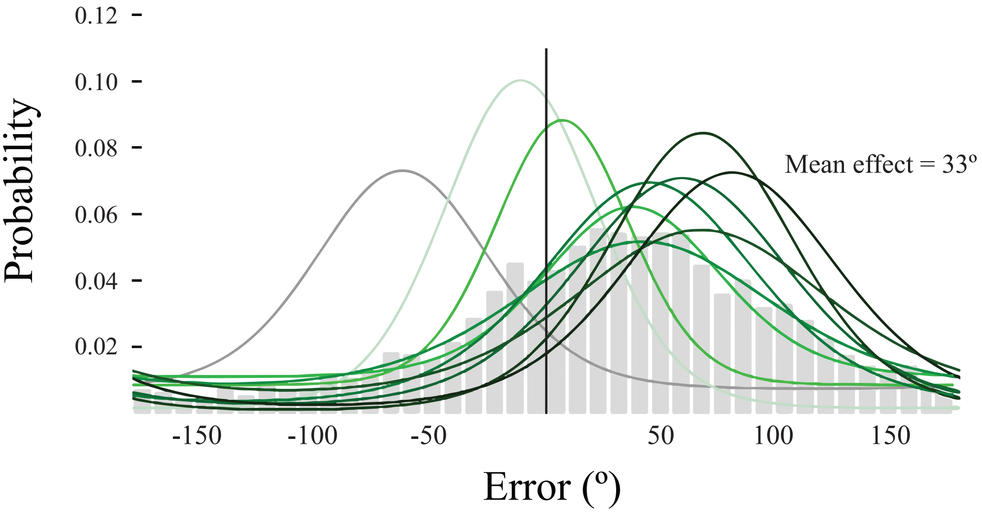


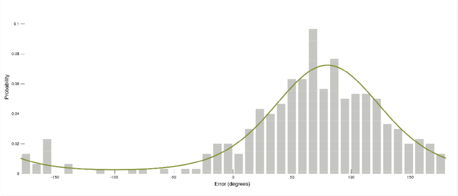
Fig. 2. Mixture model fits of performance for each observer, showing the mean probability of their prediction errors, which tended toward forward displacement. The histogram shows the distribution of responses across all observers.

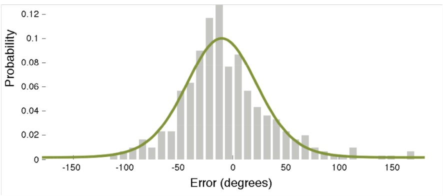
Only one out of 12 observers showed a uniform distribution, with the others showing a clear clustering of responses, indicating that they could do the task. At the same time, I found that observers systematically over-rotated the spoke relative to its true orientation, displacing it forwards in time by 33.08 degrees (or 275.67 ms) on average ($t_{(10)} = 2.64$, $p = .025$, $d = 1.12$; Fig. 2); nine out of eleven observers showed this positive bias. The mean precision and guess rates were .124 and 50.62º (421.83 ms) respectively. The means for both guess rate (0.124) and variability (50.62º) were reasonably low.

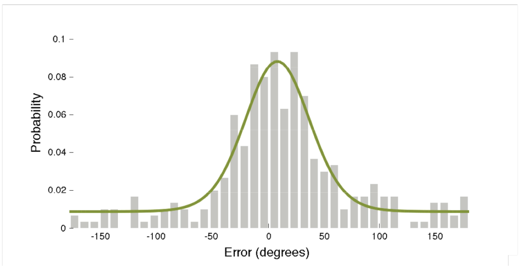
In order to ensure the validity of the model, I also inspected all of the individual fits, including fits to the excluded participants (Fig 3); the model performed consistently well. Finally, note that using just the mean or mode of errors (i.e. without mixture modeling) showed the same qualitative and statistical outcomes: means (27.31º; $t_{(10)} = 2.94$, $p = .025$, $d = 1.26$) and modes (32.38º; $t_{(10)} = 2.49$, $p = .032$, $d = 1.06$).

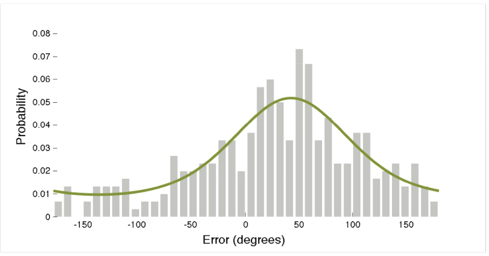
Discussion

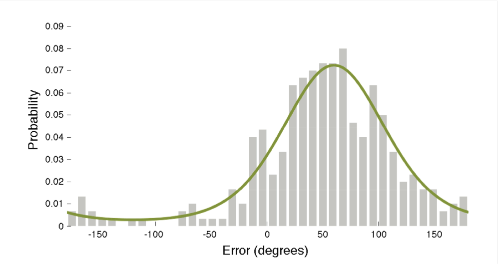
This experiment found that people are indeed capable of tracking the changing feature of a moving object, and through occlusion, since only one observer out of 13 responded randomly. To my knowledge, this is the first time that this has been confirmed experimentally. I also found a surprising, systematic bias in observer's responses, whereby they perceived the feature to be further ahead in its trajectory than it truly was.

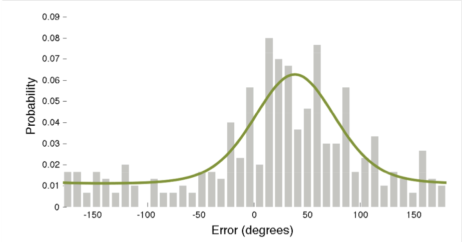


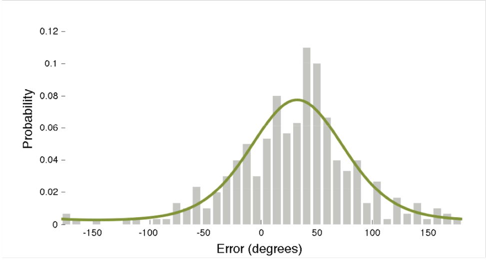


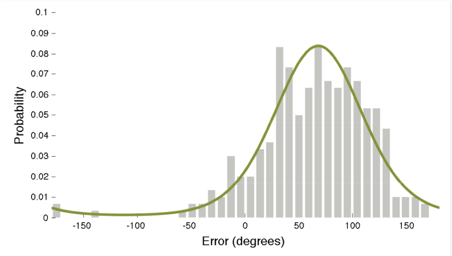


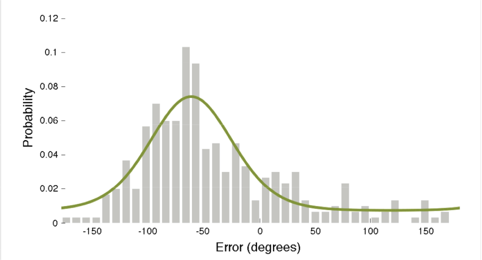


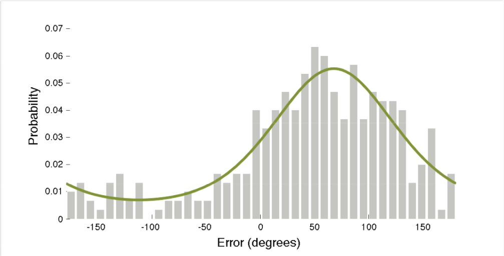


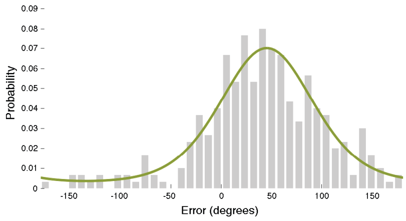


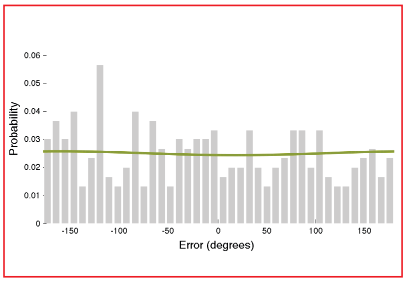




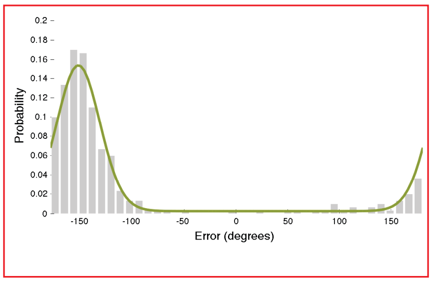








Excluded based on rayleigh's test



Excluded for being < 3 SDs from the mean

Fig. 3. Mixture model fits to each of the individual observers (including exclusions).

Since there are various variables that could be driving the current ability and accompanying displacement effect, in the following experiments I try to get a handle on how dynamic feature tracking is accomplished, as well as why the bias occurs. But first, I investigate whether the current effects generalize across various speeds, in order to confirm that they are robust across and flexibly scale with such variations.

2. Various Motion Speeds

Experiment 2 tested whether the feature displacement effect scales with speed, growing larger as speed increases. Alternatively, it is possible that the effect is always the same size, regardless of speed, or that it is idiosyncratic to the particular speed that I happened to choose in Experiment 1.

Method

Observers. 29 new observers (M_{age} =29, 16 female) with normal or corrected visual acuity completed a 60-min session in exchange for £10 payment. Since the effect size for Experiment 1 was very large, but the current experiment tripled the number of conditions in Experiment 1, in the current experiment I conservatively used double the sample size of Experiment 1.

Apparatus and stimuli. This experiment was identical to Experiment 1, except as noted here. Randomized for each trial, the speed of both the disc's motion and the spoke's rotation were either the same as in Experiment 1 (translation: 3.90º/s, rotation: 120º/s around the center of the circle), half as fast (translation: 1.95º/s, rotation: 60º/s around the center of the circle), or 5/3 times as fast (translation: 6.50º/s, rotation: 200º/s around the center of the circle). Since I always kept the length of the occluder constant, occlusion duration was not constant across conditions, i.e., occlusion duration decreased in proportion to the increase in speed across conditions. Each observer saw 80 trials of each speed, preceded by two practice trials at the medium speed. Relative to Experiment 1, all stimuli were shifted down vertically by 5.02º, in order to make space for a central fixation cross, which was not task relevant (utilized in a later experiment).

Results

I excluded four observers for responding uniformly in any of the individual conditions (Rayleigh's test, *p*s = .786, .588, .228, and .138), and one observer whose mean was three standard deviations beyond the group mean. This left 24 observers. I fit the same mixture model from Experiment 1 to each of the speed conditions for each observer.

First, I wanted to determine the speed of mental rotation across the different conditions. To do this, I calculated: (1) the actual amount of rotation during occlusion (true speeds * occlusion durations), (2) amount mentally rotated (errors + actual amount of rotation), (3) mental rotation speed (amount mentally rotated/occlusion durations), and (4) speed difference between the mental speed and actual speed (mental rotation rate – actual speed). A repeated measures ANOVA revealed a linear increase in this speed difference across conditions (*slow:* 18.51°/s, *medium:* 44.48°/s, *fast:* 91.43°/s, $F_{(1,23)} = 35.91$, $p = 4*10^{-6}$, $\eta_p^2 = .610$). There was also a linear increase in proportional speed (mental rotation speed/actual rotation speed), (*slow:* 1.31, *medium:* 1.37, *fast:* 1.46, $F_{(1,23)} = 14.03$, $p = .001$, $\eta_p^2 = .379$).

One-sample t-tests (two-tailed) revealed that the displacement effect replicated in every speed condition (*slow:* 41.83° (or 697.09 ms), $t_{(23)} = 4.18$, $p = 3.59*10^{-4}$, $d = 1.21$; *medium:* 50.26° (418.83 ms), $t_{(23)} = 4.94$, $p = 5.48*10^{-5}$, $d = 1.42$; *fast:* 62.17° (310.86 ms), $t_{(23)} = 5.78$, $p = 6.82*10^{-6}$, $d = 1.67$), and a repeated measures ANOVA found that the effect scaled linearly with speed ($F_{(1,23)} = 14.22$, $p = .001$, $\eta_p^2 = .382$; Fig. 4). However, performing the same analysis on the corresponding time values for each degree error (thereby controlling for the rotational speed) actually reveals a linear decrease in error as speed condition increases ($F_{(1,23)} = 9.85$, $p = .005$, $\eta_p^2 = .300$; Fig. 5), which could also be due to the shorter occlusion durations for higher speed conditions.

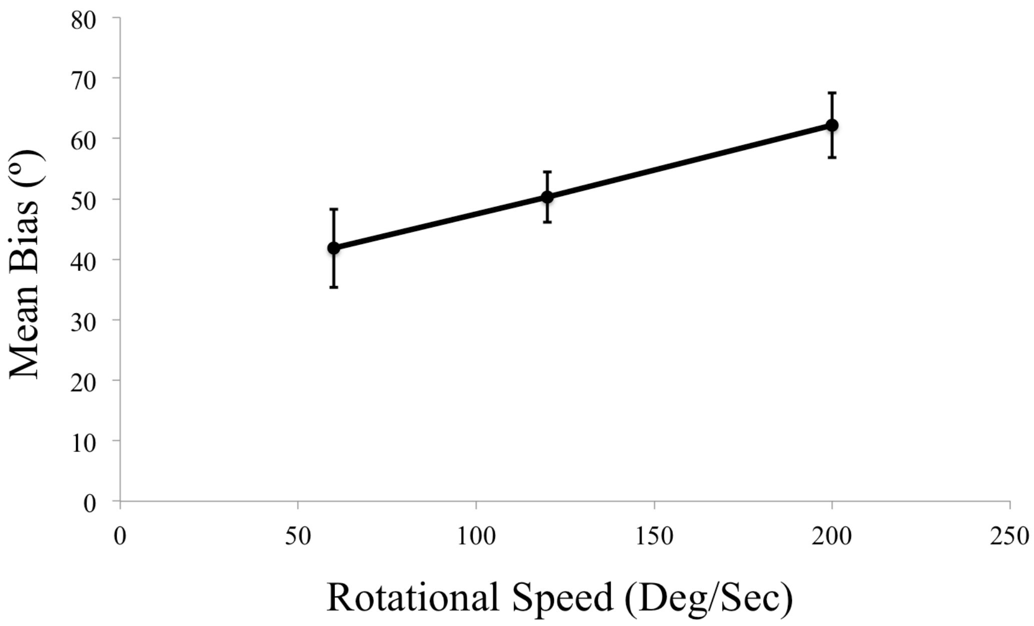


Fig. 4. Displacement errors scaled linearly with the speed of the stimulus. Error bars depict 95% confidence intervals within subjects.

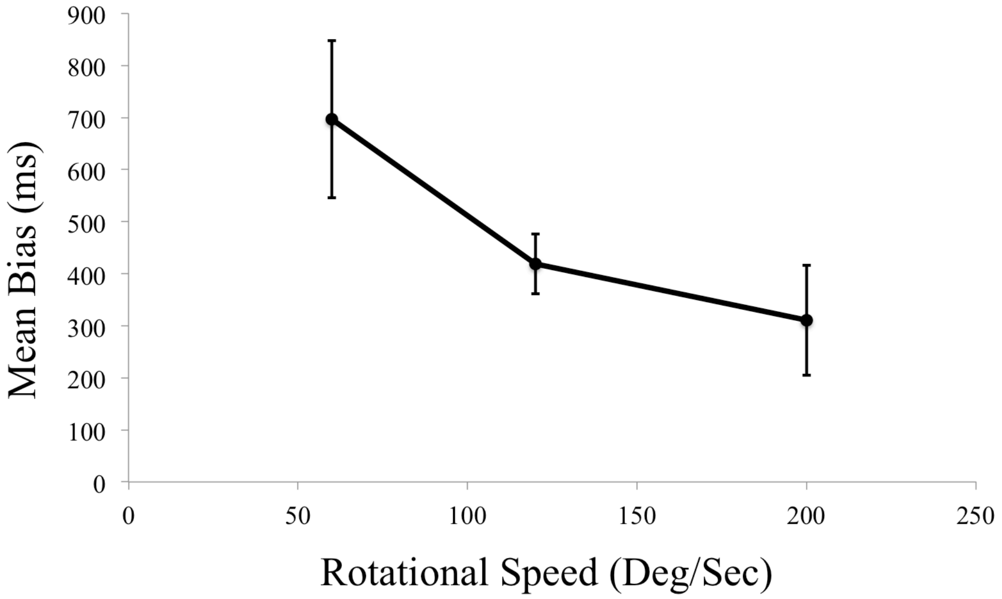


Fig. 5. Displacement errors, after being corrected for the speed of rotation, decreased as rotational speed increased. Note that quicker rotational speeds also corresponded to shorter occlusion intervals. Error bars depict 95% confidence intervals within subjects.

A repeated measures ANOVA found no difference in precision across the different speed conditions (*slow:* 44.86º (747.73 ms)*, medium:* 51.61º (430.07 ms)*, fast:* 47.93º (239.64 ms), $F_{(1,23)} = .80$, $p = 0.379$, $\eta_p^2 = .034$). However, comparing the corresponding time values for each degree error (thereby controlling for the rotational speed) actually revealed an increase in precision as speed condition increased, ($F_{(1,23)} = 78.44$, $p = 7.17*10^{-9}$, $\eta_p^2 = .773$; Fig. 6), which again could also be due to the decreasing occlusion durations as speed condition increased. A repeated measures ANOVA revealed no significant differences across speeds in guess rate (*slow:* .119*, medium:* .101*, fast:* .150, $F_{(1,23)} = .79$, $p = .384$, $\eta_p^2 = .033$), and once again the guess rates were reasonable given the typical values found in memory research.

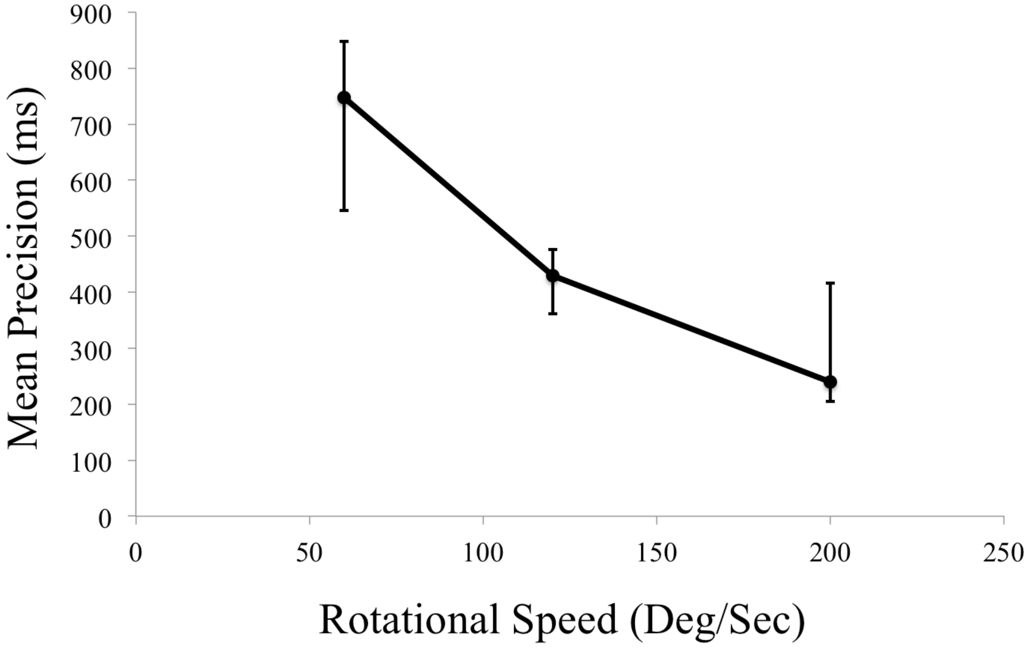


Fig. 6. Precision of errors, after being corrected for the speed of rotation, decreased as rotational speed increased. Note that quicker rotational speeds also corresponded to shorter occlusion intervals. Error bars depict 95% confidence intervals within subjects.

Discussion

In short, longer occlusion intervals (or slower speeds) corresponded to larger errors and decreased precision (controlling for rotational speed), although it is hard to definitively know whether this pattern was driven by the slower mental rotation rates or the longer occlusion intervals that were intrinsic to the slower speed conditions. Future work should directly tease these factors apart by parametrically varying occlusion duration over a wide range while keeping speed constant, then measuring final spoke orientation estimates as a function of occlusion duration. Most importantly for the current purposes, however, these results suggest that the bias is not uniform, since it flexibly scaled with speed.

3. Moving vs. Stationary Objects

Having found that observers are able to track the changing feature of a moving object (though with a systematic forward displacement error), I next wanted to understand how the different aspects of the stimulus — location and orientation — are prioritized during tracking. Specifically, I investigated the extent to which feature tracking behavior resulted from processing the stimulus as a feature-bound object versus in a more feature-specific manner (whereby orientation and location tracking are separable).

To do this, I started by comparing tracking performance for moving versus stationary objects, reasoning that if processing is to some extent separable, then I should not see a tracking impairment in the moving object condition relative to the stationary object condition. For instance, I should not expect the moving object condition to yield lower precision, or an increase in the size of the forward displacement. On the other hand, if feature tracking *is* accomplished in an integral matter, then I might expect to see exactly these sorts of differences between conditions.

Aside from assessing the extent to which tracking a changing feature relies on a separable vs. integral process, this experiment also provided an opportunity to investigate whether the effects generalize to different kinds of object motion, further speaking to the ubiquity of the results from Experiments 1 and 2.

Method

Observers. 27 new observers (M_{age} =28, 12 female) with normal or corrected visual acuity completed a 60-min session in exchange for £10 payment. This sample size was chosen to match that of Experiment 2 and can be justified post hoc based on the results of that experiment.

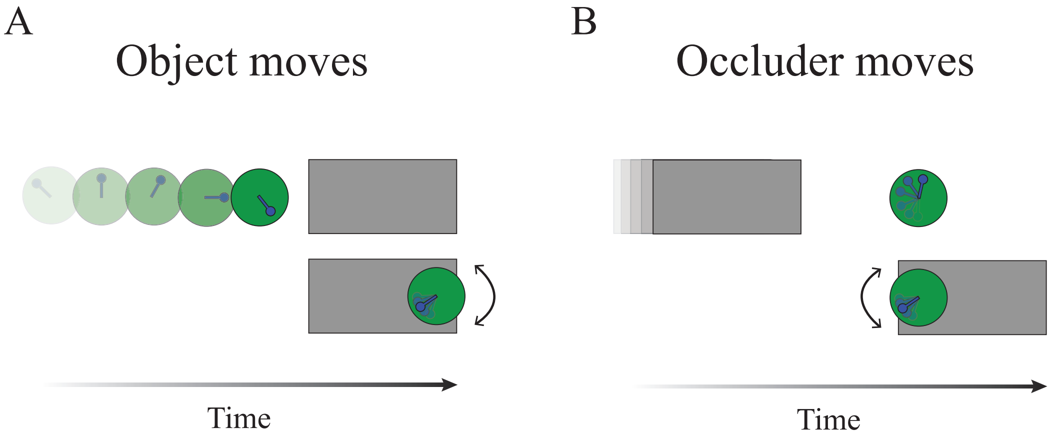


Fig. 7. Depiction (not to scale) of the two conditions of the feature tracking task in Experiment 3: The object rolls behind the occluder **(7A)**, and the occluder moves over the object, which rotates at a fixed location **(7B)**.

Apparatus and stimuli. This experiment was identical to Experiments 1 and 2, except as noted here. All objects travelled at the same speed (3.90º/s). Each observer completed 2 practice trials, followed by two blocks of 150 trials each, in counterbalanced order between observers. In the standard block, the wheel moved behind the occluder (as in the previous experiments). In the stationary wheel block, the occluder moved over the wheel, which rotated at a fixed coordinate location 27.14º pixels from the left hand edge of the screen (i.e. the stopping location of the wheel in the moving wheel condition). The moving occluder had the same starting position, speed, and travel duration as did the travelling wheel in the standard block: The occluder moved from the mid left edge of the screen, then occluded the rotating wheel for the same occlusion duration as in the standard condition, continuing to move until the wheel then reappeared partially (and by the same amount as in the standard block) from the left border of the overlain occluder, which then stopped (see Fig. 7).

Results

I excluded two observers for responding uniformly in any of the individual conditions (Rayleigh's test, *ps* = .116, .179), and one observer whose mean was three standard deviations beyond the group mean. This left 24 observers. The same standard mixture model with bias from the previous experiments was fit to each of the movement conditions for each observer. Observer debriefing reports led me to expect carryover effects between blocks. Confirming this, a 2 (condition) by 2 (block order) ANOVA revealed a potential trend toward a condition by block order interaction ($F_{(1,22)} = 3.38$, $p = .079$, $\eta_p^2 = .133$). When the traveling wheel block was presented first, the displacement effect was reduced in the subsequent stationary wheel block (28.46º (or 237.17 ms) vs. 2.99º (24.92 ms), $t_{(11)} = 2.89$, $p = .015$, $d = .74$), whereas when the stationary wheel block was presented first, its displacement effect remained unaffected (38.87º (323.92 ms) vs. 34.55º (287.92ms), $t_{(11)} = 0.58$, $p = .572$, $d = .09$).

Thus, in order to factor out this unanticipated order effect, the main comparison focused on only the first block presented to an observer, comparing condition between observers. The effect replicated in both the travelling wheel condition (28.46º (237.17 ms), $t_{(11)} = 2.89$, $p = .015$, $d = 1.18$), and stationary wheel condition (34.55º (287.92 ms), $t_{(11)} = 2.21$, $p < .05$, $d = 0.90$). Observers were able to track the feature in both conditions, and displaced the feature to a similar extent in both conditions (Fig. 8; 28.46º (237.12 ms) vs. 34.55º (287.92 ms), $t_{(22)} = -0.33$, $p = .745$, $d = -0.13$). There were also no significant differences between conditions in guess rate (.194 vs. .094, $t_{(22)} = 0.97$, $p = .343$, $d = .40$) or precision (45.43º (378.58 ms) vs. 48.52º (404.33 ms), $t_{(22)} = -0.41$, $p = .685$, $d = -.17$).

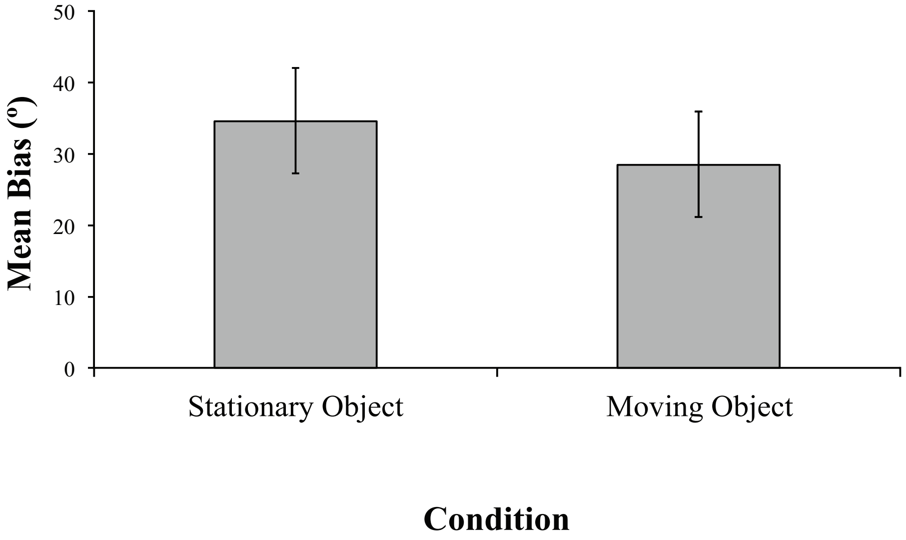


Fig. 8. Feature displacement did not differ significantly between the moving and stationary object condition. Error bars indicate 95% CIs within subjects.

Discussion

The fact that I did not find any differences between conditions on any of the performance measures shows that dynamic feature tracking can extend to different kinds of occlusion events — the perceptual system was always able to hone in on the relevant feature information, forming predictions based on this information regardless of whether the object moved or not. Further, the fact that a forward displacement effect also occurred in the stationary object condition suggests that the forward bias is one of feature tracking per se, rather than resulting from a carryover affect of object momentum on feature tracking. Finally, the current results also suggest that feature tracking was accomplished in a separable (rather than integral) fashion, since there were no differences in any of the parameters for the moving vs. stationary object conditions. Were the tracking process integral, one would expect the object' motion to have had at least some relative effect on feature tracking performance.

Though at this point one may begin to wonder just how feature-specific the feature displacement effect really is. Experiment 4 investigated this question further.

4. Object-Congruent vs. -Incongruent Feature Changes

Experiment 4 directly pitted object and feature behavior against each other, by sometimes having the direction of the wheel's rotation (now anti-clockwise) conflict with the direction of object motion (left to right, which would normally entail clockwise rotation). If dynamic feature tracking is dependent on the behavior of the surrounding boundaries of the object (entailing an integral, object-selective process), then we should expect some reduction or impairment in the feature displacement effect for this incongruent condition. By contrast, if dynamic feature tracking is strongly feature-specific (entailing a more separable process), then we should expect feature tracking and the associated feature displacement effect to be robust even across such an incongruity. That is, in the incongruent condition observers should still be able to track the feature, and should show equal precision and forward displacement in the opposite (anti-clockwise) direction.

Method

Observers. Twenty-six new observers (M_{age} = 23, 19 female) with normal or corrected visual acuity completed a 90-min session in exchange for £15 payment. This sample size was chosen to match that of Experiments 2 and 3 and can be justified post hoc based on the results of those experiments.

Apparatus and stimuli. The experiment was identical to Experiment 3, except as noted here. The wheel moved behind the occluder (rather than vice versa) on all trials. Each observer completed two practice trials, followed by two blocks of 150 trials each, in counterbalanced order between observers. In the congruent block, the wheel moved from left to right and went behind the occluder, with the feature rotating clockwise as the object moved (as in the previous experiments). In the incongruent block, the object moved from left to right in the same way, but the feature rotated anti-clockwise (rather than clockwise) as the object moved. Aside from the reversed direction of feature rotation, all other aspects of the trial were matched between conditions. For both blocks, observers had the same task as in the previous experiments: to predict the wheel's final orientation when it stopped.

Results

I excluded one observer for responding uniformly in any of the individual conditions (Rayleigh's test, p = .188), and one observer whose mean was three standard deviations beyond the group mean. This left 24 observers. The mixture model with bias was fit to each of the movement conditions for each observer. Observers were able to track the changing feature in both conditions, and the positive displacement bias in the direction of rotation was replicated in both the congruent condition (i.e. clockwise displacement; 41.31º (or 344.25 ms), $t_{(23)} = 3.04$, $p = .006$, $d = .88$) and incongruent condition (i.e. anti-clockwise displacement; -34.34º (286.17 ms), $t_{(23)} = 2.63$, $p = .015$, $d = .76$), with no significant difference between conditions in the extent of absolute displacement (Fig. 9; 41.31º (344.25 ms) vs. 34.34º (286.17 ms), $t_{(23)} = 0.38$, $p = .708$, $d = .11$). Therefore, the orientation and location information were tracked in a highly separable fashion, since feature-tracking performance remained unaffected by the incongruent spatial behavior of the surrounding object boundaries.

A 2 (condition) by 2 (block order) ANOVA revealed no significant condition by block order interaction ($F_{(1,22)} = 1.96$, $p = .175$, $\eta_p^2 = .082$), and there were also no significant differences between conditions in guess rate (*congruent:* .083 vs. *incongruent:* .067, $t_{(23)} = 0.83$, $p = .417$, $d = .10$) or absolute precision (*congruent:*

51.54° (429.50 ms) vs. *incongruent:* 53.51° (445.92 ms), $t_{(23)} = -0.60$, $p = .557$, $d = -0.09$).

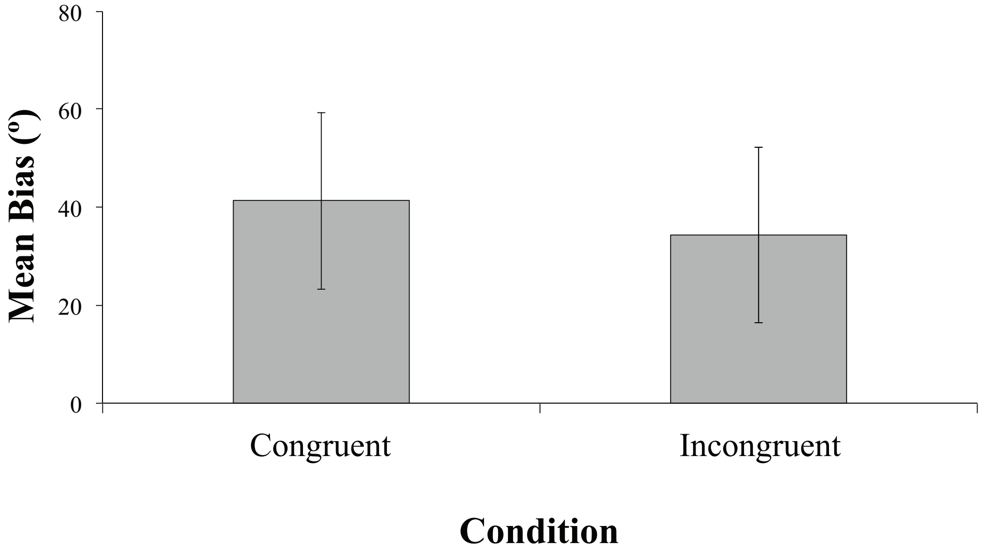


Fig. 9. Feature displacement did not differ significantly between the congruent and incongruent motion conditions. Error bars indicate 95% CIs within subjects.

Discussion

This experiment found that regardless of whether the direction of feature change was congruent or incongruent with the bounded object's direction of motion, the feature displacement occurred. This suggests that the effect is both highly robust and strongly feature-specific, arising from tracking of the changing feature per se. Thus, there appears to be some flexibility in how the system processes the feature in relation to its bounded object. These results suggest that dynamic features may provide an interesting case in which the features of objects are not fully bound in the strictest sense. This may be because — unlike in the case of static features — dynamic features can sometimes be task relevant in a way that may not always cohere with the behavior of the bounded object itself, in which case it may be useful to process the feature and object boundaries in a separable fashion.

These findings can be contrasted with other work on the irresistible nature of feature binding (Kahneman & Henik, 1981; O'Craven, Downing, & Kanwisher, 1999), or studies on the object-based structure of working memory (Cowan, 2001; Luck & Vogel, 1997; Rensink, 2000; Xu, 2002) and attention (e.g. De Freitas, Liverence, & Scholl, 2014; Egly, Driver & Rafal, 1994). In contrast, the current findings are consistent with work showing that in some cases attention can hone in on specific features (Blaser, Pylyshyn, & Holcombe, 2000; Blaser & Sperling, 2008; Howard & Holcombe, 2008; Nobre, Rao, & Chelazzi, 2006; Sheth, Nijhawan, & Shimojo, 2000).

It would be interesting to investigate the conditions under which a changing feature is processed in a separable rather than integral manner, and whether this balance can be shifted (see also Garner, 1974). As an example, the system might switch between separable and integral processing depending on the extent to which object positions are reliable (see Kwon, Tadin, & Knill, 2015). Also, if such a shift occurs, does it occur gradually or as a discrete shift (suggestive of an encapsulated process)? Another open question is whether all dynamic features are separable in this way, or whether there are dynamic features that are more integral, as might be the case given previous work showing differences in memory encoding ability for various feature dimensions (Fougnie & Alvarez, 2011).

I have been assuming in my interpretation of these results that what makes them especially interesting is the possibility that the system is tracking the feature separably, despite also (somehow) taking into account the changing location of the object (even if object behavior conflicts with feature behavior). Yet based on these results it is still not clear *how* the system is tracking the feature, and whether it truly is tracking the object location simultaneously (rather than ignoring location changes and simply providing a response when the object emerges). The next experiments tackled these questions.

5. Manipulating Expectations

This experiment investigated the manner in which the changing feature was processed during tracking. In particular, I sought to tease apart two possibilities: 1) that observers performed some kind of discrete mental operation based on the visible stimulus information before occlusion, in order to determine the final emerging state of the feature, or 2) that observers *continually* tracked the feature, even during occlusion.

Temporal expectations can often be manipulated in order reveal something about how an underlying process works (for a review, see Nobre, 2010). To tease apart the two tracking possibilities, Experiment 5 manipulated whether the object reemerged from occlusion at the correct time or prematurely. Notice that if observers simply base their estimates on the visible information available before occlusion, then we should find no difference between conditions, since the visible information before and after occlusion is held constant between these conditions. But if observers continually track the feature even during occlusion (which of course would no longer strictly be ‘tracking’, but a mental transformation that in some sense simulates tracking), then their tracking estimates should be relatively reduced in the premature condition. This is because a premature arrival of the object would induce observers to interrupt their continuous mental rotation of the feature, leading them to under-report the extent of rotation (i.e. relative to what they would otherwise report, if the object arrived at the later, correct time.)

Method

Observers. 25 new observers (M_{age} =22, 17 female) with normal or corrected visual acuity completed a 75-min session in exchange for £15 payment. This sample size was chosen to match those of Experiments 2, 3, and 4 and can be justified post hoc based on the results of those experiments.

Apparatus and stimuli. The experiment was identical to Experiment 4, except as noted here. The wheel rotated in a manner consistent with its direction of motion (i.e. clockwise) on all trials. In one block, the object reappeared at the correct time, as in the previous experiments. In the other block, the object reappeared 350 ms prematurely. Block order was counterbalanced between observers.

A series of increasingly specific debriefing questions confirmed that not a single observer noticed this difference between blocks. Specifically, each participant was first asked whether they had any ideas about what the study was testing, and then whether they noticed any difference between the two blocks. Finally, they were asked whether they noticed the specific experimental manipulation that was employed. For all questions, not a single participant noticed that in the premature block the object reemerged earlier than it was supposed to.

Results

I excluded one observer whose mean was three standard deviations beyond the group mean, leaving 24 observers. I then fit the mixture model with bias to each of the conditions for each observer. The displacement effect replicated when the object arrived at the correct time (31.76° (264.67 ms), $t_{(23)} = 3.82$, $p = 8.69*10^{-4}$, $d = 1.10$), but was reduced in the premature condition relative to what its orientation would have been had it arrived on time (2.13° (17.75 ms), $t_{(23)} = 0.21$, $p = .835$, $d = .06$), with the magnitude of the effect (or lack thereof) differing significantly between conditions (31.76° (264.67 ms) vs. 2.13° (17.75 ms), $t_{(23)} = 3.39$, $p = .003$, $d = .65$; Fig. 10).

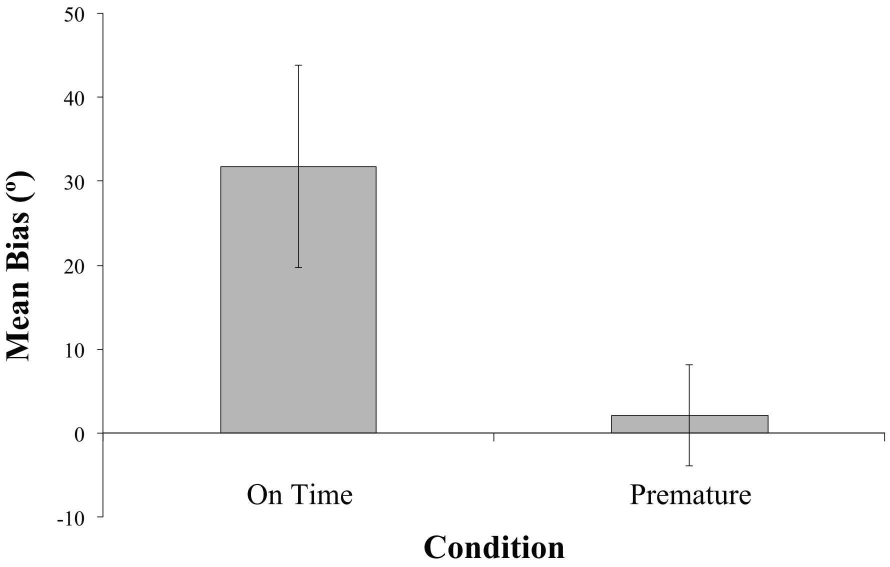


Fig. 10. Displacement errors extracted from the mixture model differed significantly between conditions. Error bars indicate 95% confidence intervals within subjects.

These results provide evidence that the dynamic feature was tracked and updated to its object *throughout occlusion*, since observer's estimates were sensitive to how long the feature was occluded, rather than being indistinguishable across conditions. In other words, given the different magnitudes of the feature displacements observed in the correct arrival time and premature conditions, it is clear that the amount of time that the object was invisible was taken into account during tracking. This suggests that a representation of the feature was *continuously transformed* during occlusion, with the premature condition interrupting this process and thus resulting in a relatively lagged orientation response.[1]

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[1] It should also be noted that if I instead calculate the errors for the premature condition relative to the true orientation of a fictional wheel whose occlusion period truly is 350 ms shorter (corresponding to a shorter occluder), then the displacement effect replicates as usual relative to this (fictional) final orientation (44.13º (367.75 ms), $t_{(23)} = 4.37$, $p = 2.25*10^{-4}$, $d = 1.26$). Further, this displacement does not differ significantly from the displacement in the on time condition (44.13º (367.75 ms) vs. 31.76º (264.67 ms), $t_{(23)} = 1.42$, $p = 0.170$, $d = 0.27$), suggesting that the basic mental transformation mechanism was applied in both conditions — the only difference was that in one case this same mental transformation process was interrupted prematurely.

Aside from the difference in bias, I did not expect any differences in guess rates or precision, which I expected to remain consistent between conditions. And indeed I found no differences: guesses (*on time:* .087 vs. *premature:* .130, $t_{(23)} = -1.23$, $p = .233$, $d = -.24$), precision of responses (*on time:* 48.13º (401.08 ms) vs. *premature:* 46.75º (389.58 ms), $t_{(23)} = 0.33$, $p = .742$, $d = .08$).

Conclusion

This experiment manipulated when an occluded object re-emerged in order to investigate whether observers were making discrete estimates, or tracking the changing feature continuously (even when it was invisible). When the object appeared earlier than it was supposed to, people's estimates were lagged relative to their estimates when the object appeared on time. These results rule against a discrete operation account of tracking, which would have yielded statistically indistinguishable behavior between the conditions. Rather, the current results are consistent with the interpretation that observers were continuously rotating a mental representation of the feature, and that the premature condition merely interrupted this process before it reached its natural conclusion. Another way of framing this finding is that during occlusion the perceptual system appears to continuously 'track' the feature *as if it were still visible.*

Yet although the above results suggest the existence of a continuous feature tracking mechanism, they do not actually settle whether observers' feature representations tracked changes in *both* rotation and location, or whether observers simply rotated a static mental representation of the feature until they saw the object reemerge. The latter possibility would be less interesting, suggesting a kind of shortcut approach rather than a continuous tracking of both changing orientation and changing location. Ideally, then, one would like to have a continuous window into how the mental representation of the stimulus evolves *throughout the entire occlusion period*, in order to inspect whether it is tracking all aspects of the stimulus' behavior.

6. Eye Movements

Experiment 6 employed eye tracking as a window into observers' mental representations during the entire tracking period. I was curious whether I would find converging evidence for a continuous tracking mechanism, whereby eye positions track both the location and orientation of the rotating, moving stimulus even during occlusion.

Although such a result would agree with those from Experiment 5, it is not immediately obvious why the eyes should give insight into this process in the first place. Previous work has found that eye movements during visual imagery resemble those during actual viewing of the same scene (Laeng & Teodorescu, 2002), suggesting that eye positions serve as a kind of spatial index for an internal visual image (Kosslyn et al., 1995; Mast & Kosslyn, 2002; Pinker, 1999). It is also well-known that visual imagery is employed during rotation tasks, since the amount of time it takes to discriminate the orientation of two objects increases as the orientation disparity between the objects increases (as if observers are mentally rotating the images until they match; Shepard & Cooper, 1986; Shepard & Metzler, 1971), and this sort of 'mental chronometry' is also found in other sorts of visual imagery tasks (see Kosslyn 1973; 1994; Kosslyn, Ganis, & Thompson, 2001; Finke, 1989; Finke & Shepard, 1986). Finally, a recent study found that eye movements during mental rotation followed the trajectory of mental rotation (Xu & Franconeri, in press).

Therefore, if visual imagery is employed when tracking the changing feature of a moving object, and if the orientation and location are in fact tracked continuously (as suggested by Experiment 5), then I should find that eye movements follow the changing feature and location of the moving object even during occlusion.

Finally, I was also curious 1) whether observers were able to track the stimulus using peripheral vision, and if so, whether the mind employs the same tracking process as during focal vision, and 2) whether eye movements would reveal why I had been finding a forward feature displacement in the previous five experiments.

Method

Observers. 27 new observers (M_{age} =25, 12 female) with normal or corrected visual acuity completed a 75-min session in exchange for £15 payment. This sample size was chosen to match those of Experiments 2-5 and can be justified post hoc based on the results of those experiments.

Apparatus and stimuli. This experiment was identical to Experiment 5, except as noted here. The wheel arrived at the correct time for all trials. In one block, observers were free to move their eyes (as in the previous experiments). In the other block, they were required to fixate on a central fixation cross while performing the task in their peripheries. The bottom of the fixation cross was aligned in the y-axis to the top of the occluder, and located 3.47º above the top of the disc. Block order was counterbalanced between observers. Eye movements were recorded with a desktop mount eye tracker at 500 Hz (EyeLink 1000, SR Research, Ontario, Canada), using the Eyelink Toolbox extensions for Matlab (Cornelissen et al., 2002). Drift correction was performed before every trial. Eyetracking data were preprocessed offline for eyeblink correction. For each trial, vertical eye position was median-corrected. Eye blinks and other artifacts were then identified as time periods with missing samples, high velocity (larger than 500°/s), or high acceleration (larger than $375°/s^2$). Samples during artifacts (and 50 ms before and after the artifact) were removed and linearly interpolated (based on the last sample before and first sample after the removed period). Interpolation had no effect on the results, as repeating the analyses with data omitting these periods showed the same qualitative and statistical outcomes, i.e., all tests reported here remained significant.

Results

Behavior. I excluded two observers for responding uniformly in any of the individual conditions (Rayleigh's test, *ps* = .986, .197). Individual trials in the fixation condition were excluded if fixations fell beyond two degrees of the screen fixation point for more than 10% of fixation samples in a trial. I excluded one additional observer because all their trials failed this criterion. This left 24 observers. I fit the mixture model with bias to each of the conditions for each observer. Observers were able to provide non-random predictions in both conditions. Furthermore, the forward displacement effect replicated in the free eye movement condition (37.74º (314.50 ms), $t_{(23)} = 2.83$, $p = .009$, $d = .82$). The effect did not, however, replicate in the fixation condition (6.40º (53.33 ms), $t_{(23)} = .48$, $p = .634$, $d = .14$; Fig. 11A), with the magnitude of the displacement effect (or lack thereof) differing significantly between free eyes and fixation conditions (37.74º (314.50 ms) vs. 6.40º (53.33 ms), $t_{(23)} = 3.65$, $p = .001$, $d = .48$). There were no significant differences between conditions in the proportion of guesses (*free eyes:* .095 vs. *fixation:* .072, $t_{(23)} = .78$, $p = .443$, $d = .18$), although responses were marginally more precise in the free eye movement condition, (*free eyes:* 46.58º (388.17 ms) vs. *fixation:* 52.28º (435.67 ms), $t_{(23)} = -2.05$, $p = .052$, $d = -.31$).

Eye Tracking. First, I found that an observer's gaze followed the changing object location (see Fig. 11B). I was particularly interested in whether observers tracked the revolving *feature*, during both presentation and occlusion. To this end, I tested whether the feature's starting angle on each trial affected vertical eye position, i.e., the component of eye motion that was orthogonal to the horizontal movement of the object, and therefore could only be influenced by feature motion within the object. At each time point, I used linear-circular regression (Jupp & Mardia, 1980) to measure the sensitivity of vertical eye position to the starting angle. If observers continuously fixated the rotating feature, I would expect vertical eye position to be highest when the feature was oriented vertically (pointing up). In this case, the preferred feature angle (i.e. the angle at which the y-position of the eye was, on average, the highest) would be 0º (i.e., vertical feature position and vertical eye position are in perfect alignment). However, eye gaze could also consistently lead or lag the rotating feature. In such cases, the preferred angle is unknown, because it depends on the degree of leading/lagging (i.e., if eye gaze consistently leads the feature orientation by 10º, then the preferred angle would be phase-shifted to +10º). Because the preferred angle at each time point was not known a priori, my measure of sensitivity was derived from regressing both the sine and cosine of the starting angle onto the (z-scored) eye position using a general linear model (in analogy to the use of sine and cosine in linear-circular correlations, for example). In other words, at each timepoint in the trial, I solved the following general linear model:

$$\mathbf{y_t} = \sin(\boldsymbol{\theta})*b_1 + \cos(\boldsymbol{\theta})*b_2;$$

where $\mathbf{y_t}$ is the vector of vertical eye positions (across all trials) at timepoint t, $\boldsymbol{\theta}$ is the vector of feature starting angles (across all trials), and b_1 and b_2 are the two regression coefficients of the sine and the cosine regressor, respectively.

Sensitivity S was then calculated as the square root of the sum of squared regression coefficients:

$$S_t = \surd(b_1^2 + b_2^2).$$

Therefore, the sensitivity at each timepoint t measured the degree to which vertical eye movements were predicted by the vertical position of the spoke at t. I next generated a shuffling distribution (2,000 permutations) of regression amplitudes by randomly permuting starting angles of the spoke across trials, and calculating sensitivity to starting angle for each permutation. The (within-observer) p-value of the real effect was then calculated as the rank within the shuffling distribution. I transformed p-values into z-scores (using the inverse of the normal cumulative distribution function, with 0 mean and standard deviation of 1), and tested z-scores against 0 using t-tests to measure the strength of the effect at the group level. I expected sensitivity to be significantly higher when the relationship between starting angle and eye position on each trial was preserved, compared to removing that relationship through random permutation. The regression also allowed me to estimate the preferred angle at each time point (using the inverse tangent of the regression weights for the sine and cosine of the starting angle; see Gould et al., 2012). By estimating the change in preferred angle over time (throughout the trial, and during the occlusion period alone) I was able to track the angular velocity of the sinusoidal component of vertical eye position (by calculating the mean change per time). My aim was to test whether angular velocity (thus defined) predicted feature displacement. As an alternative to this regression approach, I also used circular-linear correlations between feature angle (the circular variable) and vertical eye position (the linear variable). Again, I used permutation tests to assess significance (by permuting the feature angles with respect to the eye position 2,000 times).

In the baseline period (the 1,000 ms of visible feature rotation prior to the object first touching the border of the occluder), vertical eye position strongly depended on starting angle (one-sample t-test (two-tailed) on z-scored sensitivity, $t_{(23)}$

= 34.36, $p = 2.86*10^{-21}$, $d = 14.33$; circular-linear correlation coefficient rho = 0.60 ± 0.04, permutation test $p = 3.1*10^{-21}$, Fig. 11C), indicating that observers followed the rotating feature ($p < 10^{-5}$ at every time point in the 5s leading up to occlusion onset). This effect persisted during the occlusion period (i.e., the period during which the entire stimulus was invisible, one-sample t-test (two-tailed) on z-scored sensitivity, $t_{(23)} =13.75$, $p = 1.40*10^{-12}$, $d = 5.73$, rho = 0.37 ± 0.03, $p = 9.8*10^{-12}$), although it was reduced compared to the baseline period (18.4 ± 5.1% reduction, $t_{(23)} = 3.49$, $p = 0.002$, $d = 0.73$). Additionally, within 20 out of 24 individual observers I saw a significant effect of starting orientation on vertical eye position during the occlusion interval (as measured against the shuffling distribution, $p < 0.05$ one-sided), indicating that this was a pervasive phenomenon. In these 20 observers, I found that my estimate of the angular velocity during the baseline interval (116.1 ± 3.6°/s) roughly matched that of the feature (120°/s), even during occlusion (114.0 ± 9.5°/s, compared to baseline: $t_{(19)} = -0.199$, $p = 0.845$, $d = -0.09$). Furthermore, the magnitude of the displacement effect significantly correlated with angular velocity of the eye during occlusion (Spearman's $r = 0.699$, $p = 0.0008$), but not during the baseline period (Spearman's $r = 0.039$, $p = 0.871$).

Next I tested whether eye position led the feature during tracking. Instead of using the feature angle at the beginning of the trial, I recalculated the linear-circular regression using the current feature angle at each timepoint. If observers' eyes tracked the feature exactly, then the average preferred angle should be 0°. Systematic deviations from zero would indicate that the eyes are leading the feature (values > 0°) or are lagging the feature (values < 0°). I found that eye position began leading the feature during the baseline period (mean ± s.e.m. leading: 15.4 ± 4.3°, $t_{(23)} = 3.23$, $p = 0.004$, $d = 1.35$) and persisted during occlusion (21.4 ± 8.2, $t_{(23)} = 2.74$, $p = 0.012$, $d =$

1.14). As with the angular velocity analysis, the amount of eye leading during occlusion correlated significantly with mean displacement (Spearman r = 0.534, *p* = 0.008), but there was no correlation with the amount of eye leading during the baseline period (r = 0.11, *p* = 0.60). Restricting the correlation to the 20 observers who showed a significant effect of feature starting angle on eye position led to the same result (Fig. 11D, occlusion: r = 0.522, *p* = 0.020, baseline: r = 0.152, *p* = 0.521).

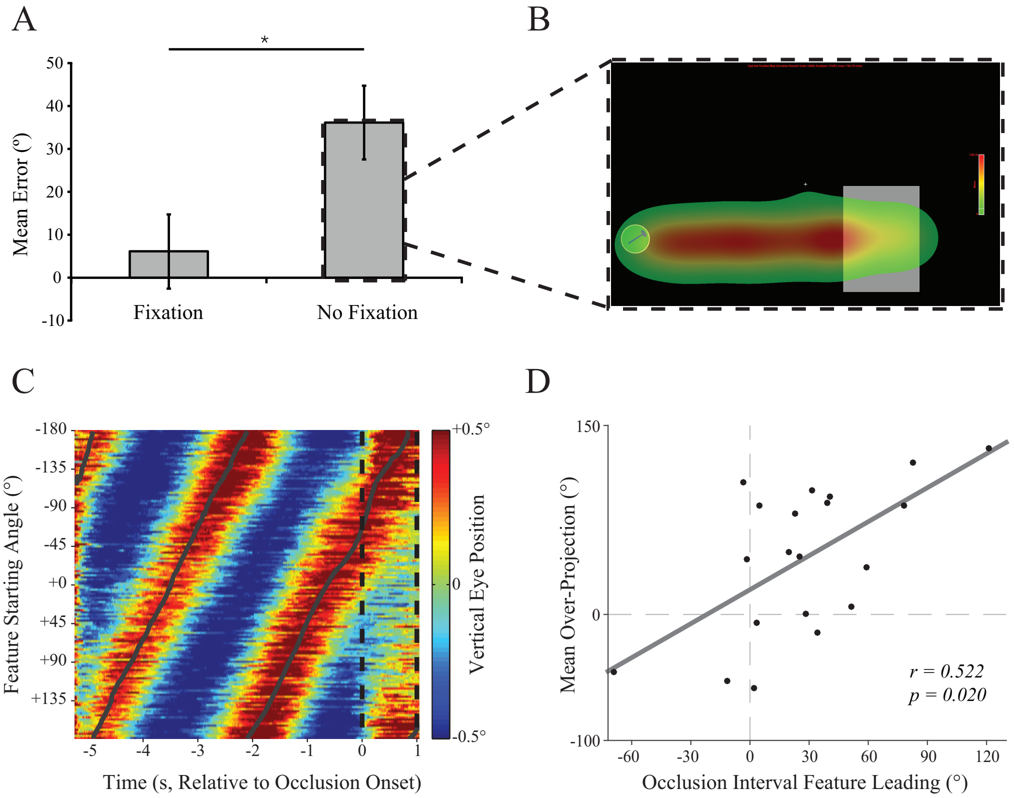


Fig. 11A. Feature displacement was only observed during free eye movements, not fixation. Heat maps of eye positions across observers show that during occlusion observers continued to track both the object's location **11B)** and the feature's orientation (**11C)**, since the vertical position of the eyes at each timepoint depended on the starting orientation of the spoke at the beginning of the trial. The black diagonal lines depict the preferred angle at each timepoint, i.e. the angle at which the y-position of the eye was, on average, the highest. **11D.** Leading of the feature by the eyes during occlusion (i.e., the circular distance between the location of the eyes and that of the feature) correlated positively with the mean displacement effect for the 20/24 observers who showed a significant effect of starting feature position on eye position.

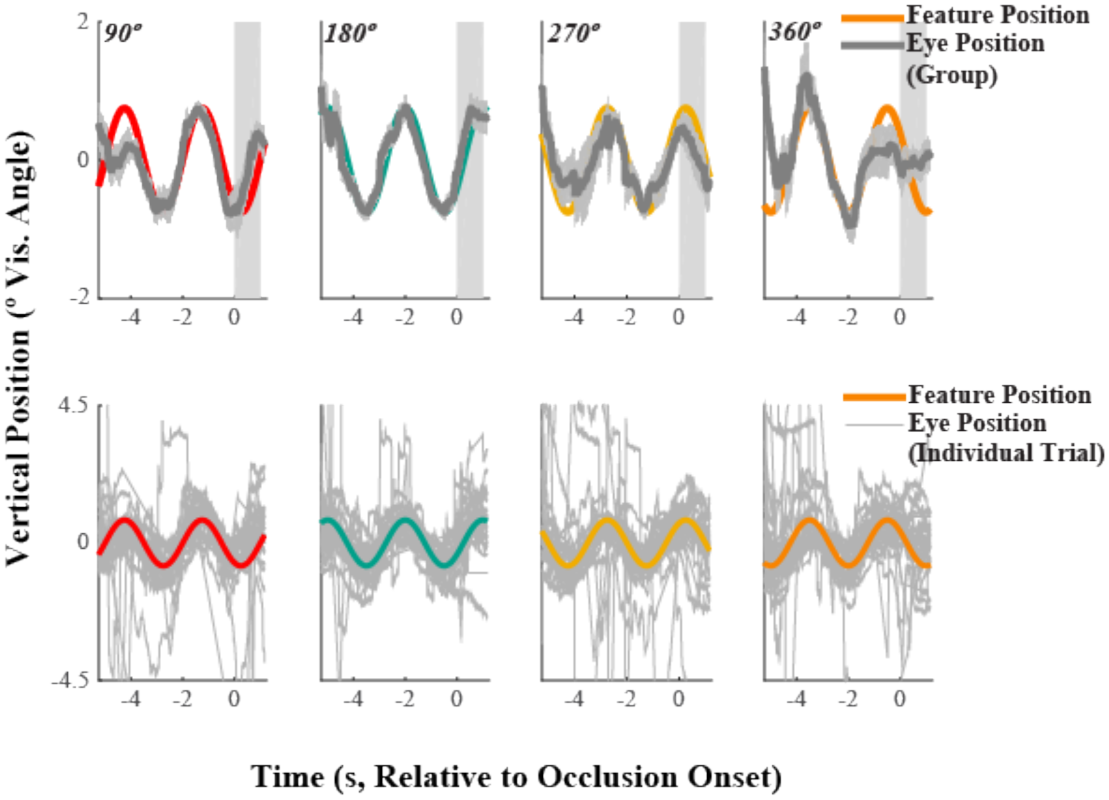


Fig. 12. Vertical eye position tracks vertical feature position on single trials. Each panel in the top row shows the average vertical eye position (grey line, with shading showing s.e.m. across 24 participants) for a different starting feature angle (90, 180, 270, or 360º, with colored lines indicating vertical feature position on the screen over the course of the trial). The eye position follows the feature position closely over the course of the trial, even when the stimulus is occluded (0-1 s, grey box). The bottom row shows individual participants' vertical eye positions for the same trials (thin grey lines). The individual traces indicate that participants generally used smooth pursuit to track the feature, interrupted by occasional saccades.

Discussion

This experiment sought evidence that the changing feature and location of a moving object are continuously tracked both before and during occlusion. The eye tracking results revealed that, in an analogous manner to how the smooth pursuit system allocates attention to entire object locations both before and during occlusion (Barborica & Ferrera, 2003, 2004; Makin & Poliakoff, 2011; Makin, Poliakoff, & El-Deredy, 2009; Orban de Xivry, Missal, & Lefèvre, 2008; Xiao, Barborica, & Ferrera, 2007), both the changing feature and location of a moving object are continuously tracked. It appears that during occlusion a mental representation of the stimulus is continually transformed, as if the stimulus were still visible. Furthermore, I found evidence that forward displacement occurs because the feature representation is accelerated relative to the veridical rate of change. This result is consistent with a rate controlling mechanism (Makin & Bertamini, 2014; Makin & Chauhan, 2014) that speeds up the rate of mental transformation during occlusion.

Observers were also able to provide non-random predictions when using peripheral vision, although they were surprisingly accurate (no forward displacement effect). This increased accuracy (i.e., lower bias) suggests that the typical forward displacement relies on dynamic eye movements, which by design were not possible in the fixation condition. Alternatively, it may be that in the fixation condition participants tended to track the stimulus using peripheral vision (e.g. Posner, Snyder, & Davidson, 1980), which might be more accurate.

Although it might seem perplexing that performance during fixation would be more accurate than that during free eye movements (which are more common during natural vision), I suspect that the forward displacement I typically find during free eye movements serves an adaptive function in conservatively anticipating the future emergence of feature states (see General Discussion).

7. Neural Underpinnings

Experiment 7 investigates the neural underpinnings of the ability to track a changing feature of a moving object, by comparing brain lesion patients to older controls. This sort of approach has been leveraged many times before in order to understand aspects of spatial attention, e.g. by using patients with hemispatial neglect (Driver & Mattingley, 1998; Vallar & Perani, 1986) and visual extinction (Chechlacz, Rotshtein, Hansen, Deb, Riddoch & Humphreys, 2013; Karnath, Himmelbach & Küker, 2003), and many of these studies have ended up focusing on patients with lesions to the inferior parietal cortex. Newer work has also implicated the inferior parietal cortex in temporal aspects of perception, including duration perception (e.g. Alexander, Cowey, & Walsh, 2005; Danckert et al., 2007; Rao, Mayer, & Harrington, 2001), temporal attention to specific moments in time (Coull & Nobre, 1998), spatio-temporal segmentation tasks (in which one keeps track of which objects are near each other in space and time; Olivers & Humphreys, 2004), and temporal order judgment tasks (Baylis, Simon, Baylis, & Rorden, 2002; Roberts et al., 2012; Rorden, Mattingley, Karnath, & Driver, 1997).

Most relevant to the current work, the inferior parietal cortex has also been implicated in the refresh rate of temporal attention (Howard, Bashir, Chechlacz, & Humphreys, 2015). In this study, observers monitored a continuously changing stimulus until it disappeared unexpectedly. Observers were then required to report the final featural state of the stimulus (e.g. its spatial thickness). Patients with parietal lesions performed poorly in this experiment relative to healthy adult controls and neurological controls, suggesting that they suffered an impairment in the ability to update the featural state of the stimulus over time, and hence were too slow to register the final state.

Since tracking the changing feature of a moving object similarly requires refreshing/updating of a feature representation over time, I predict that lesions to the posterior parietal cortex should impair dynamic feature tracking ability (Howard, Bashir, Chechlacz, & Humphreys, in press). Behaviourally, this could manifest as a reduction in the forward displacement effect I would otherwise expect to replicate in older controls. That is, to the extent that forward displacement of the feature requires constant updating of a temporal representation of the feature, slower updating in patients with posterior parietal damage could lead to a lagged transformation relative to controls. Further, there is also evidence that the posterior parietal cortex is implicated in visual binding over time (Gillebert & Humphreys, 2010), and the current experiments require binding of changing feature states to changing locations over time.

Finally, since Experiment 6 found that the forward displacement effect is only predicted by leading of the feature by the eyes during occlusion, and since the eye movements during occlusion suggested that visual imagery was employed, we may also expect any reduction in forward displacement to correlate with lesions in areas involved in mental rotation imagery. Work on mental imagery has found that brain areas implicated during imagery are much the same as those involved in perception in the same modality (Kosslyn et al., 2001). For instance, patients with lesions to the ventral and dorsal streams show impairments in a variety of visual tasks (e.g. Levine, D. N., Warach, J. & Farah, M. J., 1985). At the same time, it is worth remembering that mental imagery is not a single ability, but consists of many different sub-processes (Kosslyn et al, 2001; O'Craven & Kanwisher, 2000). For instance, studies involving brain-damaged patients have found that some patients have no problem mentally imagining color and yet struggle to imagine rotation (see Kosslyn et al., 2001). Therefore, since behavior in mental rotation is typically accompanied by activation in the parietal (bilaterally) and right frontal lobes (e.g. Cohen et al., 1996; Jordan et al., 2001; Kosslyn et al., 1998; Ng et al., 2001; Richter et al., 2000), damage to these areas may also affect performance in the current experiments.

Method

Patients. Thirteen patients participated (M_{age} = 63, 2 female, 1 left-handed). All of the patients were at least 6 months postlesion and showed a stable cognitive deficit.

Older Controls. Thirty-four older adults (M_{age} = 69, 19 female, 3 left-handed) served as age-matched controls.

Exclusions. I excluded five patients (Rayleigh's test, p = .170, .589, .130, .749, .332) for responding uniformly, leaving 8 patients: R. R.; M. G.; N. B.; J. B.; P. H.; P. F.; T. J.; D. R. Further details on these patients can be found in Table 1 and Figure 13. I excluded eleven older controls (Rayleigh's test, p = .437, .317, .541, .097, .065, .205, .208, .097, .110, .219, .565) for responding uniformly, leaving 23 older controls. The proportions excluded for responding randomly (38% and 32% respectively) are about five times that found in the younger populations (mean of 6.70% across the six previous experiments), suggesting an age-related impairment in the ability to track the changing feature of a moving object.

Apparatus and stimuli. The experiment was identical to Experiment 1, except as noted here. Observers completed only 100 trials total, and in a given trial the wheel could also move from right to left, not only left to right. The direction of motion was randomized on a trial-by-trial basis, with an equal number of trials presented per direction condition. All other aspects of the two conditions were matched. For both blocks, observers had the same task as in the previous experiments: to predict the wheel's final orientation when it stopped.

Table 1

Patient Details

Patient	Sex	Age (yrs)	Clinical Symptoms	Lesion	Etiology
R. R.	Male	22	Nonfluent aphasia	L Temporal/ L Parietal	Stroke
M. G.	Fem	70	Minimal clinical impairment	R (some L) Cerebellum & R Thalamus	Stroke
N. B.	Male	55	Word finding difficulties	B Cerebellum, L/R Parietal, R Occipital, some L Temporal	Stroke
J. B.	Male	68	Aspects of dysexecutive syndrome	R frontal into Basal Ganglia (Lentiform Nucleus), R Insula, slight R sup. temp. gyrus	Stroke
P. H.	Male	42	Nonfluent aphasia	Large L hemi lesion (inc. frontal/temporal/parietal/occipital/subcortical	Stroke
P. F.	Male	73	Aspects of left neglect	R(close to midline) Occipital	Stroke
T. J.	Male	66	Minimal clinical impairment	L Thalamus	Stroke
D. R.	Male	80	Aspects of dysexecutive syndrome	R Cerebellum	Stroke

Results

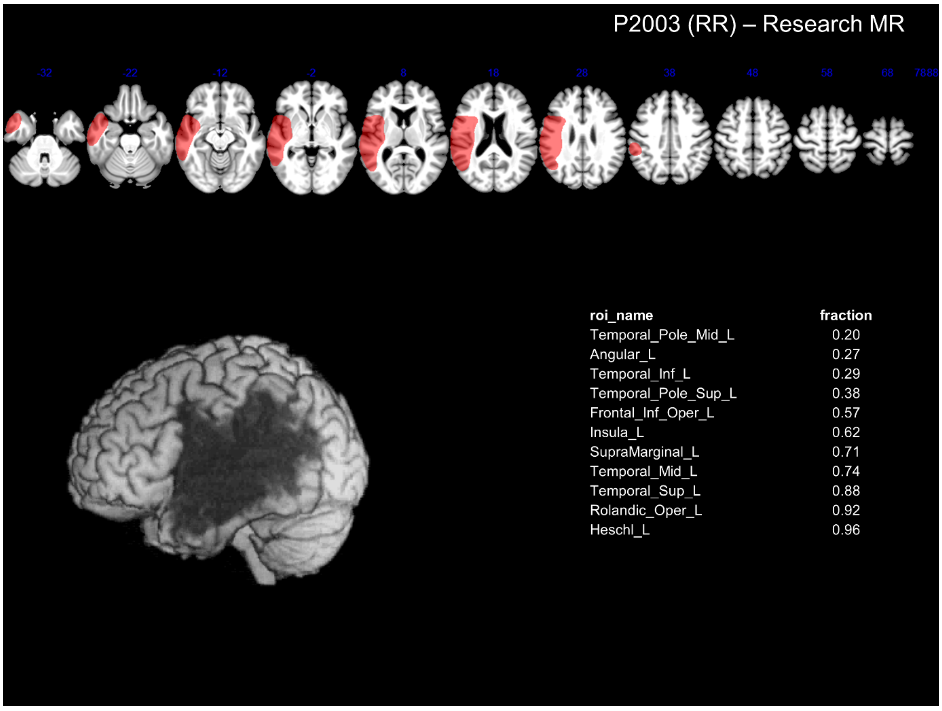
The mixture model with bias was fit to each of the observer groups. The older controls were able to track the changing feature, and showed the same positive displacement bias as found in the younger observers in previous experiments (47.39º (or 394.92 ms), $t_{(22)} = 2.86$, $p = .009$, $d = .84$), with 18 out of 23 controls showing this forward bias. However, so far there is no evidence for a significant forward bias in the 8 patients (-8.70º (or -72.50 ms), $t_{(7)} = 0.23$, $p = .83$, $d = .11$; see Fig. 13 for individual fits to each patient), with only 3 out of 8 patients showing a forward bias, and the majority of the others showing negative biases of considerable magnitude (-31.74º, -102.12º, -51.34º, -171.18º, -1.46º).

Finally, after only 8 patients, there is already a potential trend toward a difference between groups in the bias (*older controls:* 47.39º (394.92 ms) vs. *patients:* -8.70º (-72.50 ms), $t_{(29)} = 1.57$, $p = .127$, $d = .58$), as well as toward less precise responses in the patients (*older controls:* 46.26º (385.50 ms) vs. *patients:* 64.58º (538.17 ms), $t_{(29)} = 1.85$, $p = .075$, $d = .69$). I am less confident about whether a significant difference might emerge for guess rate (*older controls:* 0.257 vs. *patients:* 0.106, $t_{(29)} = 1.43$, $p = .162$, $d = .53$).

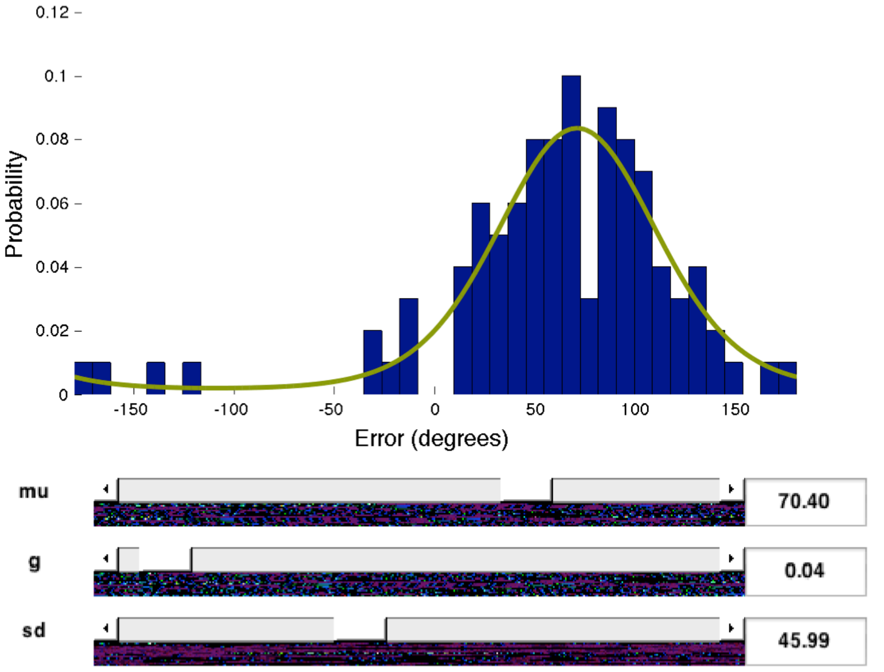
Planned analyses will focus on those patients who showed a negative displacement bias, in order to determine whether they share main lesion sites in common. I will also compare performance in these patients between the two direction conditions, in order to determine whether impairment is greatest in a particular hemifield versus across the entire visual field.

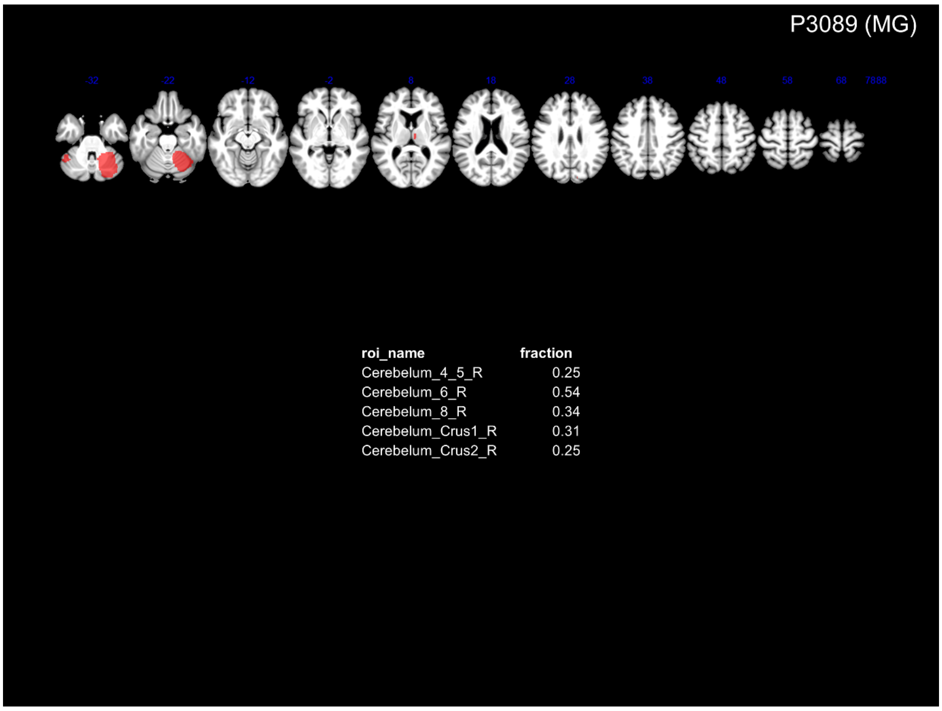
Finally, although I have already noted the increase in the proportion of exclusions for the older observers compared to the younger observers tested in the previous six experiments, I was also interested in whether there would be any other differences between these groups along the other performance parameters. For this purpose, I compared the current results for the older adult controls with those from Experiment 1 (though note that experiment 1 had only 11 younger adult participants instead of the 23 older adult controls from this experiment). I found no differences in bias, (*young:* 33.08º (275.67 ms) vs. *older:* 47.39º (394.92 ms), $t_{(32)} = 0.56$, $p = .581$, $d = .20$), precision, (*young:* 50.62º (421.83 ms) vs. *older:* 46.26º (385.50 ms), $t_{(32)} = 0.61$, $p = .545$, $d = .22$), or guess rate, (*young:* 0.124 vs. *older:* 0.257º, $t_{(32)} = 1.43$, $p = .161$, $d = .51$).

Figure 13. Lesion reconstructions from MRI scans and mixture model fits for each of the patients in Table 1.


P2003 (RR) – Research MR

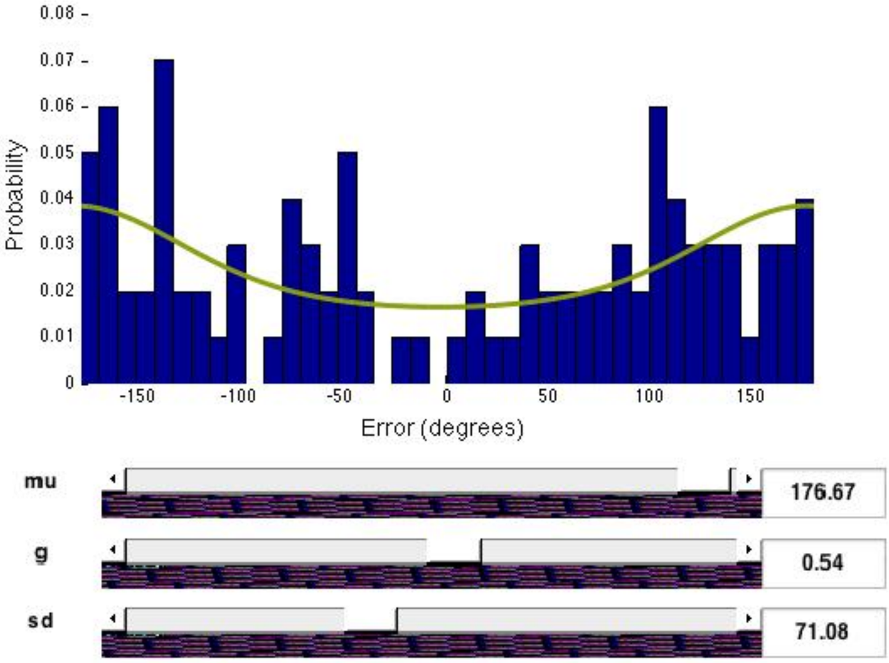
roi_name	fraction
Temporal_Pole_Mid_L	0.20
Angular_L	0.27
Temporal_Inf_L	0.29
Temporal_Pole_Sup_L	0.38
Frontal_Inf_Oper_L	0.57
Insula_L	0.62
SupraMarginal_L	0.71
Temporal_Mid_L	0.74
Temporal_Sup_L	0.88
Rolandic_Oper_L	0.92
Heschl_L	0.96





P3089 (MG)

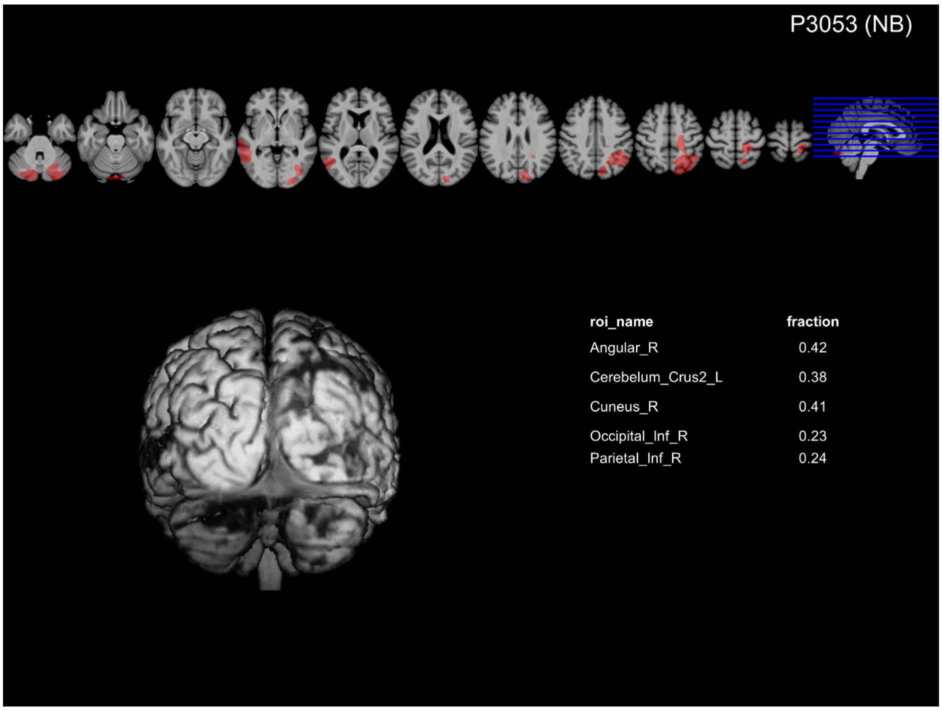
roi_name	fraction
Cerebelum_4_5_R	0.25
Cerebelum_6_R	0.54
Cerebelum_8_R	0.34
Cerebelum_Crus1_R	0.31
Cerebelum_Crus2_R	0.25



mu 176.67

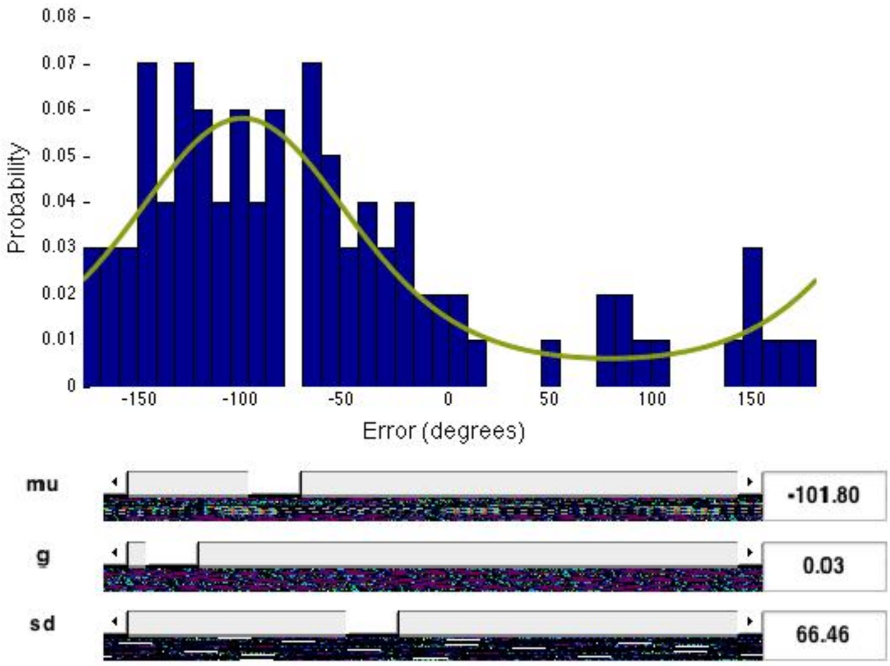
g 0.54

sd 71.08



P3053 (NB)

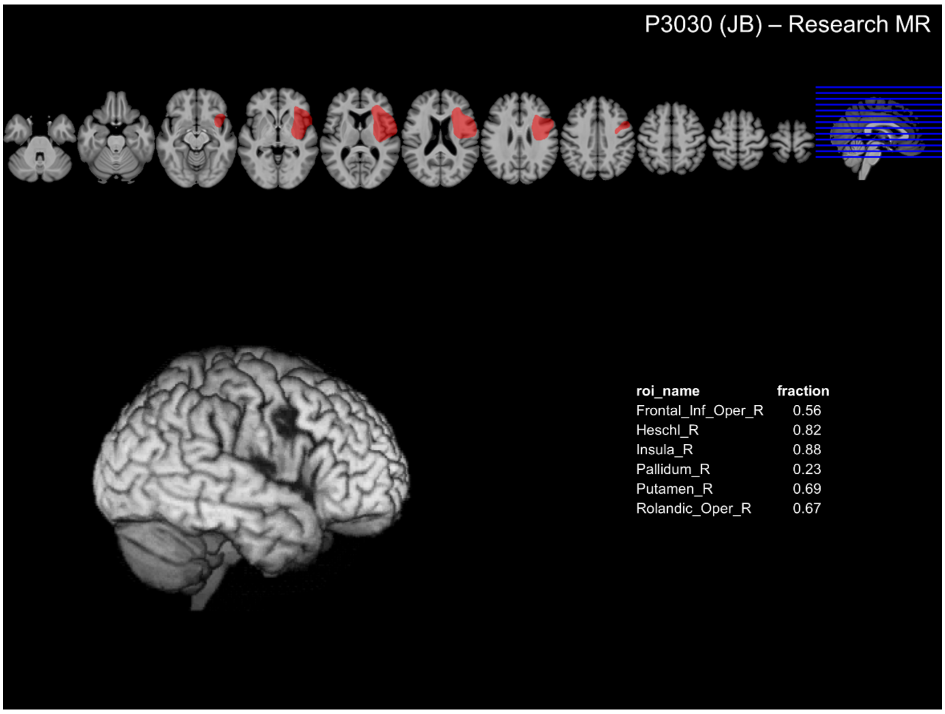
roi_name	fraction
Angular_R	0.42
Cerebelum_Crus2_L	0.38
Cuneus_R	0.41
Occipital_Inf_R	0.23
Parietal_Inf_R	0.24



mu -101.80

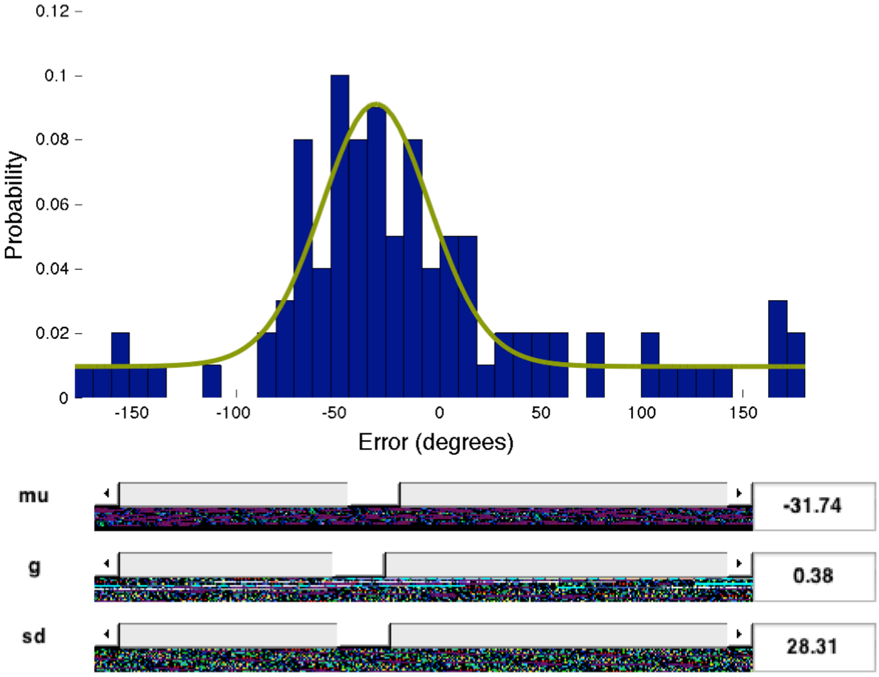
g 0.03

sd 66.46



P3030 (JB) – Research MR

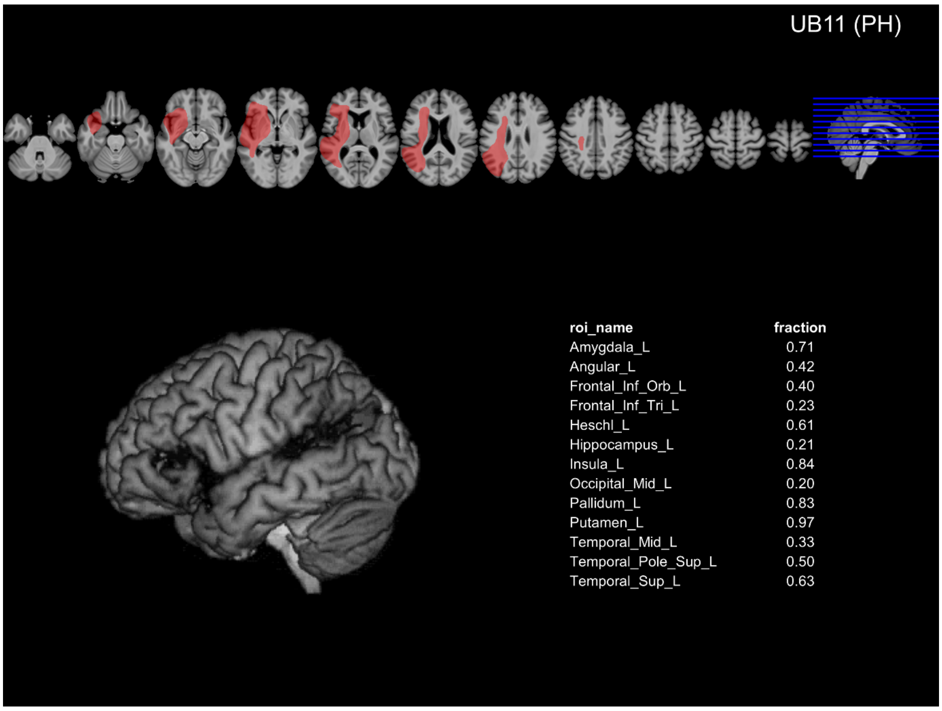
roi_name	fraction
Frontal_Inf_Oper_R	0.56
Heschl_R	0.82
Insula_R	0.88
Pallidum_R	0.23
Putamen_R	0.69
Rolandic_Oper_R	0.67



mu -31.74

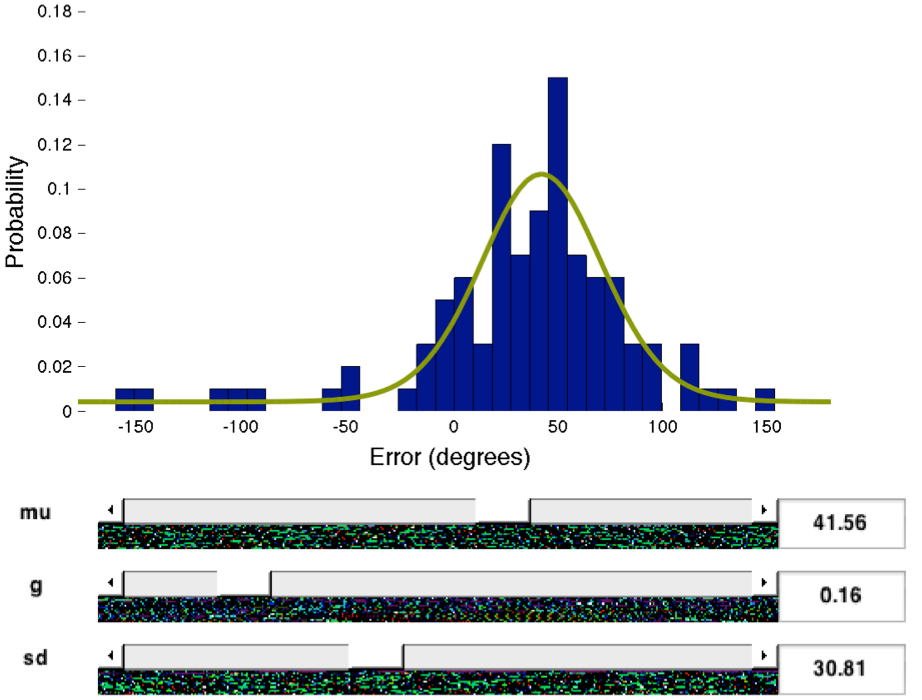
g 0.38

sd 28.31



UB11 (PH)

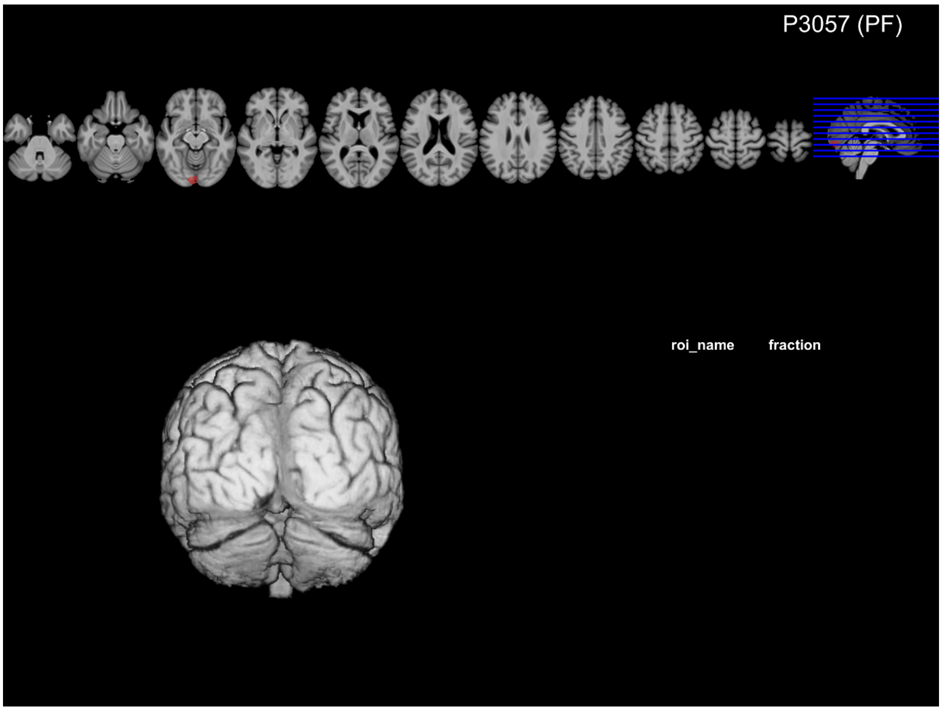
roi_name	fraction
Amygdala_L	0.71
Angular_L	0.42
Frontal_Inf_Orb_L	0.40
Frontal_Inf_Tri_L	0.23
Heschl_L	0.61
Hippocampus_L	0.21
Insula_L	0.84
Occipital_Mid_L	0.20
Pallidum_L	0.83
Putamen_L	0.97
Temporal_Mid_L	0.33
Temporal_Pole_Sup_L	0.50
Temporal_Sup_L	0.63

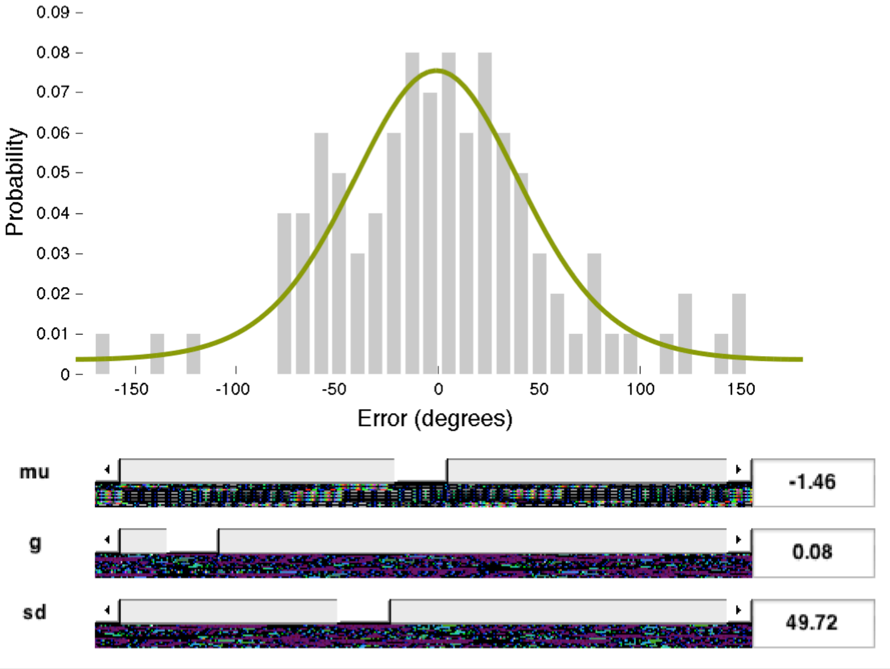


mu 41.56

g 0.16

sd 30.81

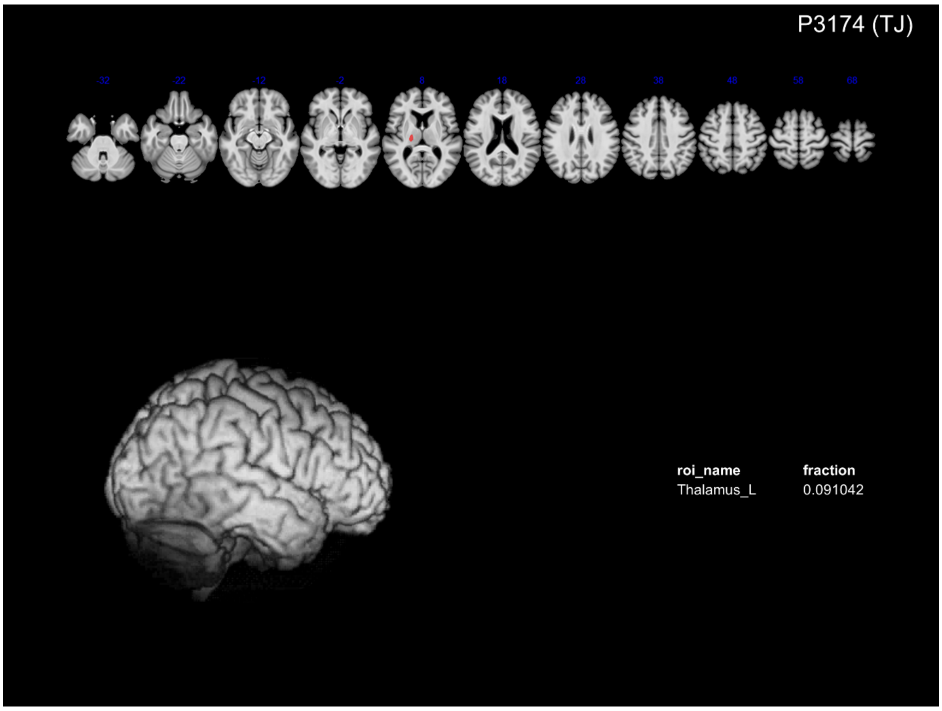


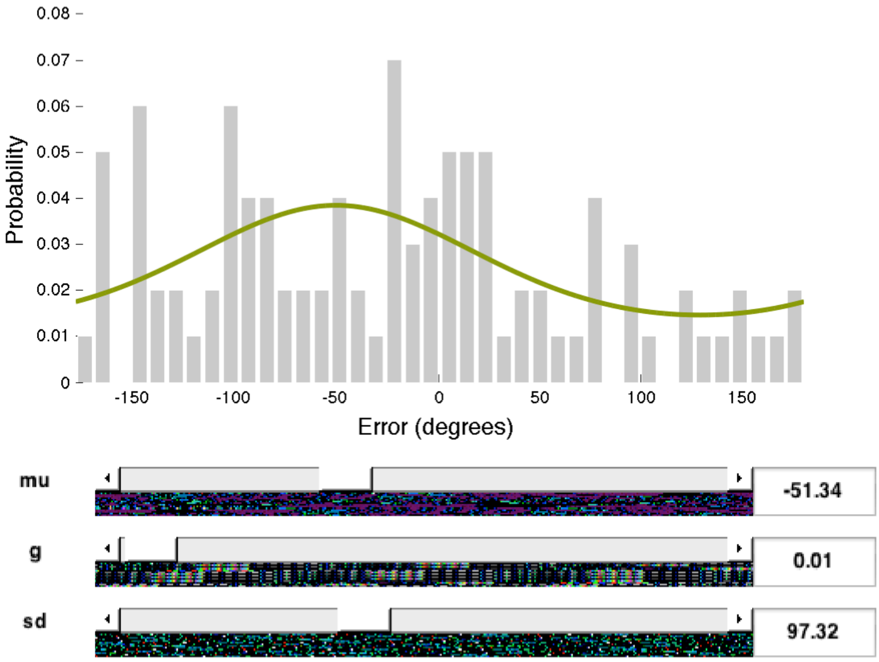


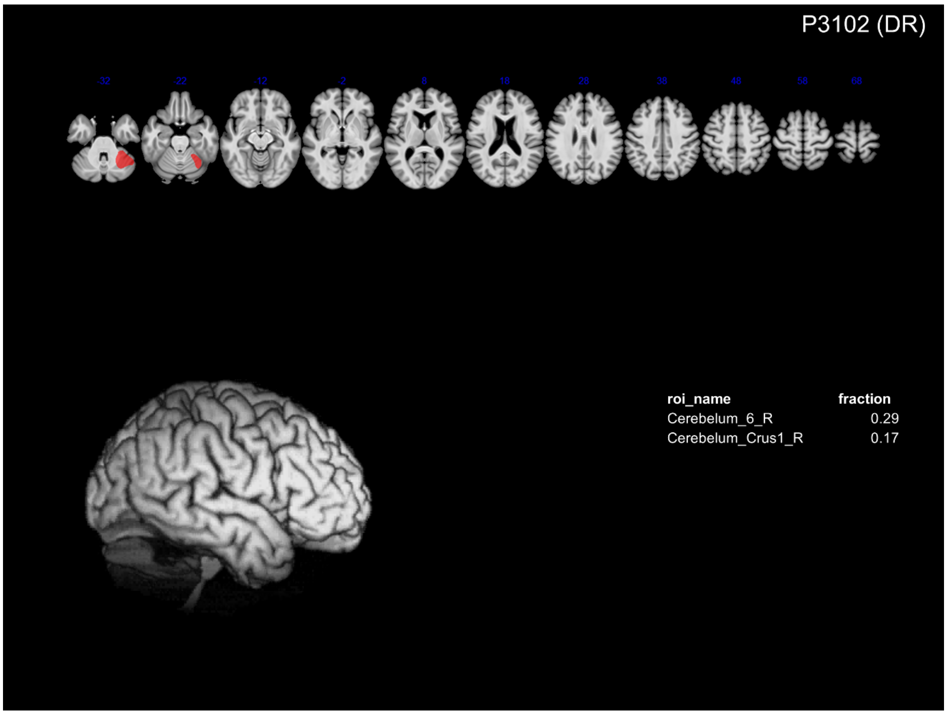
mu -1.46

g 0.08

sd 49.72

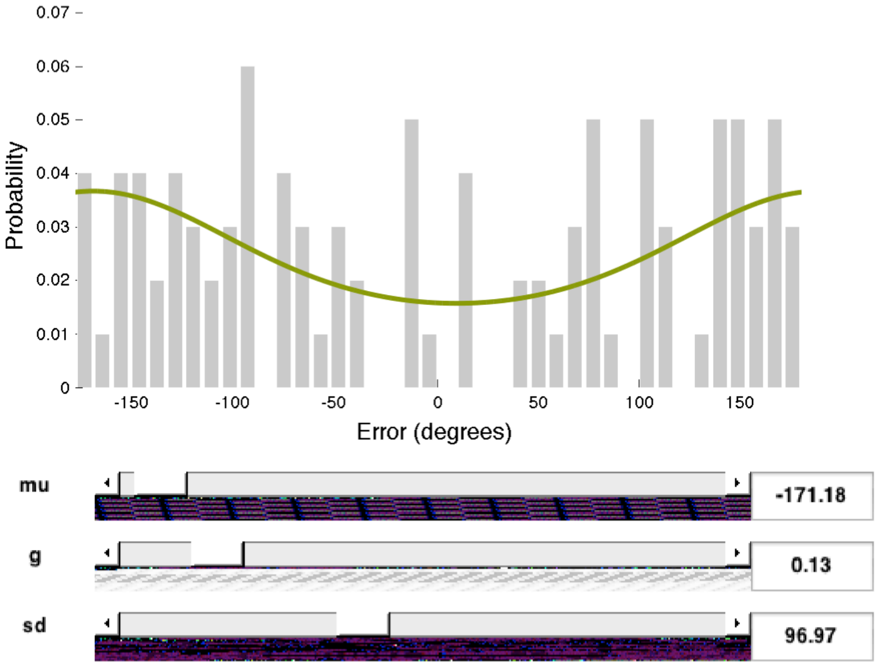

P3174 (TJ)
-32
-22
-12
-2
8
18
28
38
48
58
68
roi_name
fraction
Thalamus_L
0.091042


0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
Probability
-150
-100
-50
0
50
100
150
Error (degrees)
mu
-51.34
g
0.01
sd
97.32



P3102 (DR)

roi_name	fraction
Cerebelum_6_R	0.29
Cerebelum_Crus1_R	0.17



mu -171.18

g 0.13

sd 96.97

Discussion

In this (ongoing) experiment I replicated in older controls the basic feature tracking results found in younger participants, including the associated forward displacement effect. However, about five times as many older participants had to be excluded for simply not being able to do the task (responding uniformly). This suggests that there is an age-related decline in the ability to track a changing feature of a moving object at all. For the older controls who could do the task, there was no difference along other performance parameters compared to younger participants.

The evidence so far is also consistent with the interpretation that most patients do not show the normal forward displacement behavior found in older controls, since only 38% of patients exhibited a forward displacement. Furthermore, after only 8 patients there is already a potential trend toward lower precision and more of a negative mean error in patients vs. older controls. To the extent that the forward bias may serve an adaptive purpose (see General Discussion), this lack of a forward bias in patients could impair their ability to track and anticipate changing features in the real world.

In ongoing work, I am investigating what is responsible for the difference in performance between the two groups, especially whether there is an interesting lesional cause for this difference, while continuing to gather more patient data.

8. Conclusion

The current experiments investigated how the mind tracks the changing feature of a moving object. Experiments 1 and 2 found that observers were capable of doing this for various speeds of motion, although their estimates grew less precise as the speed of the stimulus increased. The experiment also found that observers reliably misperceived the feature to be further ahead in time than it truly was.

Experiments 3 and 4 then investigated the extent to which the tracking process is object- vs. feature-specific, finding that tracking was not impaired for moving vs. stationary objects (Experiment 3), nor object-incongruent vs. -congruent feature changes (Experiment 4). This suggests a highly separable process that is able to hone in on the changing feature information.

I next investigated whether this separable tracking process is discrete or continuous. Using both a manipulation of temporal expectations (Experiment 5), and eye tracking as a window into observer's mental representations, I found that the feature was continuously tracked, even during occlusion. Further, eye positions suggested that a visual image of both the orientation and spatial location of the feature was continuously transformed throughout occlusion. I also found that eye movements led the feature throughout the occlusion period, and that the amount of leading predicted the extent to which observers displaced the feature forwards. This result suggests that the forward displacement effect was caused by an acceleration in the rate of mental transformation during occlusion. This interpretation is consistent with a central rate controller that speeds up the rate of mental transformation during occlusion (Makin & Bertamini, 2014; Makin & Chauhan, 2014).

Since 1) the forward displacement effect was only observed during free eye movements but not during fixation, and since 2) observers' estimates were less precise in the fixation condition, it is possible that the stimulus was not continuously tracked during fixation, but rather, estimated discretely or only partially tracked with covert attention. Another possibility is that the stimulus was processed in a more integral fashion during peripheral vision, preventing separable tracking of the feature, as well as the occurrence of the accompanying feature-specific bias. These possibilities remain to be tested more directly.

Finally, I found that there is a substantial decrease in feature tracking ability with age increase, although those adults who can track the feature do not differ from younger adults along other performance parameters. I also found that a majority of patients showed a negative displacement effect. Ongoing work will assess whether these patients are more likely to have lesions in the posterior parietal lobes, since this would be consistent with my hypothesis that these regions are involved in temporal updating of the feature transformation (which I think is likely to be employed in the current experiments).

Why does the perceptual system track a changing feature continuously? One possibility is that continuous tracking places the system in a better position to react swiftly to unexpected deviations in a target's behavior, such as a sudden change in a featural state (more likely to occur when tracking animate agents). There might also be a computational and/or memory storage advantage associated with tracking dynamic features continuously versus otherwise, and future work can investigate this possibility using dual-task and memory recall paradigms. Another question, of course, is whether tracking also behaves this way in real-world environments, where additional information might be incorporated to guide prediction. The fact that observers employed the continuous tracking mechanism in these experiments despite repetitive task parameters may suggest so, yet ultimately this possibility would need to be tested in more ecological settings.

I have concluded that the forward displacement effect may be driven by the acceleration of a central rate controller during occlusion. But of course, this naturally raises another question: why would this acceleration occur in the first place? I speculate that when observers try to predict the future states of changing features that temporarily go out of sight, they often benefit from conservatively anticipating the arrival of these future states, such as when the features are action-guiding. One adaptive way to gain this benefit would be to see (in the mind's eye) such a future state before it actually emerges.

9. References

Alexander, I., Cowey, A., & Walsh, V. (2005). The right parietal cortex and time perception: back to Critchley and the Zeitraffer phenomenon. *Cognitive Neuropsychology*, *22,* 306–315.

Alvarez, G. A., & Cavanagh, P. (2004). The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychological Science 15*, 106–111.

Barborica, A., & Ferrera, V. P. (2003). Estimating invisible target speed from neuronal activity in monkey frontal eye field. *Nature Neuroscience*, 6, 66–74.

Barborica, A., & Ferrera, V. P. (2004). Modification of saccades evoked by stimulation of frontal eye field during invisible target tracking. *Journal of Neuroscience*, 24, 3260–3267.

Battaglini, L., Campana, G., & Casco, C. (2013). Illusory speed is retained in memory during invisible motion. *i-Perception*, 4, 180–191.

Baylis, G. C., Simon, S. L., Baylis, L. L., & Rorden, C. (2002). Visual extinction with double simultaneous stimulation: what is simultaneous? *Neuropsychologia*, *40*, 1027–1034.

Bays, P. M., Catalao, R. F. G., & Husain, M. (2009). The precision of visual working memory is set by allocation of a shared resource. *Journal of Vision*, *9*, 1–27.

Benguigui, N., & Bennett, S. J. (2010). Ocular pursuit and the estimation of time-to-contact with accelerating objects in prediction motion are controlled independently based on first-order estimates. *Experimental Brain Research*, 202, 327–339.

Benguigui, N., Broderick, M., & Ripoll, H. (2004). Age differences in estimating arrival-time. *Neuroscience Letters, 369,* 197–202.

Blaser, E., Pylyshyn, Z. W., & Holcombe, A. O. (2000). Tracking an object through feature space. *Nature*, *408*, 196–199.

Blaser, E., & Sperling, G. (2008). When is motion ‘‘motion’’? *Perception*, *37*, 624–627.

Brady, T. F., Konkle, T., & Alvarez, G. A. (2011). A review of visual memory capacity: Beyond individual items and toward structured representations. *Journal of vision*, *11*, 1–34.

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436.

Chechlacz, M., Rotshtein, P., Hansen, P. C., Deb, S., Riddoch, M. J., & Humphreys, G. W. (2013). The central role of temporo-parietal junction and the superior longitudinal fasciculus in supporting multi-item competition: evidence from lesion-symptom mapping of extinction. *Cortex*, *49,* 487–506.

Cohen, M. S. *et al.* (1996). Changes in cortical activity during mental rotation: a mapping study using functional MRI. *Brain, 119*, 89–100.

Cornelissen, F., Peters, E., & Palmer, J. (2002). The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behavior Research Methods, Instruments, & Computers, 34,* 613–617.

Coull, J. T., Nobre, A. C. (1998). Where and When to Pay Attention: The Neural Systems for Directing Attention to Spatial Locations and to Time Intervals as Revealed by Both PET and fMRI. *The Journal of Neuroscience*, *18,* 7426–7435.

Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. *Psychological Bulletin, 104*, 163–191.

Danckert, J., Ferber, S., Pun, C., Broderick, C., Striemer, C., Rock, S., & Stewart, D. (2007). Neglected time: impaired temporal perception of multisecond intervals in unilateral neglect. *Journal of Cognitive Neuroscience*, *19*, 1706–1720.

De Freitas, J., Liverence, B. M., & Scholl, B. (2014). Attentional rhythm: A temporal analogue of object-based attention. *Journal of Experimental Psychology: General,* 143, 71–76.

DeLucia, P. R., & Liddell, G. W. (1998). Cognitive motion extrapolation and cognitive clocking in prediction motion tasks. *Journal of Experimental Psychology: Human Perception and Performance, 24,* 901–914.

DeLucia, P. R., Tresilian, J. R., & Meyer, L. E. (2000). Geometrical illusions can affect time-to-contact estimation and mimed prehension. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 552–567.

de'Sperati, C., & Deubel, H. (2006). Mental extrapolation of motion modulates responsiveness to visual stimuli. *Vision Research*, *46*, 2593–2601.

de'Sperati, C., & Santandrea, E. (2005). Smooth pursuit-like eye movements during mental extrapolation of motion: The facilitatory effect of drowsiness. *Cognitive Brain Research*, *25*, 328–338.

Driver, J., & Mattingley, J. B. (1998). Parietal neglect and visual awareness. *Nature Neuroscience*, *1,* 17–22.

Egly, R., Driver, J., & Rafal, R. D. (1994). Shifting visual attention between objects and locations: Evidence from normal and parietal lesion subjects. *Journal of Experimental Psychology: General, 123,* 161–177.

Finke, R. A. (1989). *Principles of mental imagery*. Cambridge: MIT Press.

Finke, R. A., & Shepard, R. N. (1986). *Visual functions of mental imagery*. In K. R. Boff, L. Kaufman, & J. P. Thomas (Eds.), Handbook of perception and human performance (pp. 37.1–37.55). New York: Wiley.

Fougnie, D., & Alvarez, G. A. (2011). Object features fail independently in visual working memory: Evidence for a probabilistic feature-store model. *Journal of Vision*, *11*, 1–12.

Garner, W. R. (1974). *The processing of information and structure*. Potomac, MD: Lawrence Erlbaum.

Gilden, D., Blake, R., & Hurst, G. (1995). Neural adaptation of imaginary visual-motion. *Cognitive Psychology*, *28*, 1–16.

Gillebert, C. R., & Humphreys, G. W. (2010). The decomposition of visual binding over time: Neuropsychological evidence from illusory conjunctions after posterior parietal damage. *Visual Cognition*, *18*, 954–980.

Gould, I. C., Nobre, A. C., Wyart, V., & Rushworth, M. F. (2012). Effects of decision variables and intraparietal stimulation on sensorimotor oscillatory activity in the human brain. *The Journal of Neuroscience*, *32*, 13805–13818.

Hecht, H., & Savelsburgh, G. (2004). Theories of time-to-contact judgment. In H. Hecht & G. Savelsburgh (Eds.), Time-to-contact (pp. 1–11). Amsterdam, The Netherlands: Elsevier.

Holcombe, A. O. (2009). Seeing slow and seeing fast: two limits on perception. *Trends in Cognitive Sciences, 13,* 216–221.

Howard, C. J., Bashir, N., Chechlacz, M., & Humphreys, G. W. (2015). Neural Mechanisms of Temporal Resolution of Attention. *Cerebral Cortex*, bhv101.

Howard, C. J., & Holcombe, A. O. Tracking the changing features of multiple objects: Progressively poorer perceptual precision and progressively greater perceptual lag. *Vision Research, 48,* 1164–1180.

Isaak, M. I., & Just, M. A. (1995). Constraints on the processing of rolling motion: The curtate cycloid illusion. *Journal of Experimental Psychology: Human Perception and Performance, 21,* 1391–1408.

Jordan, K., Heinze, H. J., Lutz, K., Kanowski, M. & Jancke, L. (2001). Cortical activations during the mental rotation of different visual objects. *Neuroimage*, *13,* 143–152.

Jupp, P. E., & Mardia, K. V. (1980). A general correlation coefficient for directional data and related regression problems. *Biometrika*, *67*, 163–173.

Kahneman, D., & Henik, A. (1981). Perceptual organization and attention. In M. Kubovy, & J. Pomerantz (Eds.), *Perceptual organization* (pp. 181 - 211). Hillsdale, NJ: Erlbaum.

Karnath, H. O., Himmelbach, M., & Küker, W. (2003). The cortical substrate of visual extinction. *Neuroreport*, *14*, 437-442.

Kosslyn, S. M. (1973). Scanning visual images: Some structural implications. *Cognitive Psychology, 8*, 441–480.

Kosslyn, S. M. (1994). *Image and brain*. Cambridge: Harvard University Press.

Kosslyn, S. M., DiGirolamo, G., Thompson, W. L. & Alpert, N. M. (1998). Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. *Psychophysiology, 35*, 151–161.

Kosslyn, S. M., Ganis, G., & Thompson, W. L. (2001). Neural foundations of imagery. *Nature Reviews Neuroscience, 9*, 635–642.

Kosslyn, S. M., Thompson W. L., Kim, I. J., & Alpert, N. M. (1995). Topographic representations of mental images in primary visual cortex. *Nature, 378*, 496–498.

Kwon, O. S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. *Proceedings of the National Academy of Sciences*, *112*, 8142–8147.

Laeng, B., & Teodorescu, D. S. (2002). Eye scanpaths during visual imagery reenact those of perception of the same visual scene. *Cognitive Science*, *26*, 207–231.

Lee, D. N. (1976). Theory of visual control of braking based on information about time-to-collision. *Perception*, 5, 437–459.

Levine, D. N., Warach, J. & Farah, M. J. (1985). Two visual systems in mental imagery: dissociation of 'what' and 'where' in imagery disorders due to bilateral posterior cerebral lesions. *Neurology*, *35* 1010–1018.

Liverence, B. M., & Scholl, B. J. (in press). Object persistence enhances spatial navigation: A case study in smartphone vision science. *Psychological Science*.

Luck, S., & Vogel, E. (1997). The capacity of visual working memory for features and conjunctions. *Nature, 390*, 279–281.

Lyon, D. R., & Waag, W. L. (1995). Time-course of visual extrapolation accuracy. *Acta Psychologica*, *89*, 239–260.

Makin, A. D. J., & Bertamini, M. (2014). Do different types of dynamic extrapolation rely on the same mechanism? *Journal of Experimental Psychology: Human Perception and Performance, 4,* 1566–1579.

Makin, A. D. J., & Chauhan, T. (2014). Memory-guided tracking through physical space and feature space. *Journal of Vision*, *14*, 1–15.

Makin, A. D. J., & Poliakoff, E. (2011) Do common systems control eye movements and motion extrapolation? *The Quaterly Journal of Experimental Psychology, 64,* 1327–1343.

Makin, A. D. J., Poliakoff, E., & El-Deredy, W. (2009). Tracking visible and occluded targets: Changes in event related potential during motion extrapolation. *Neuropsychologia, 47,* 1128–1137.

Mast, F. W., & Kosslyn, S. M. (2002). Eye movements during visual mental imagery. *Trends in Cognitive Sciences, 6,* 271–272.

Ng, V. W. *et al.* (2001). Identifying rate-limiting nodes in large-scale cortical networks for visuospatial processing: an illustration using fMRI. *Journal of Cognitive Neuroscience, 13,* 537–545.

Nobre, A. C. (2010). *How can temporal expectations bias perception and action?* In A. C. Nobre and J. T. Coull (eds), Attention and time. Oxford, UK: Oxford University Press, pp. 371–392.

Nobre, A. C., Rao, A., & Chelazzi, L. (2006). Selective attention to specific features within objects: Behavioral and electrophysiological evidence. *Journal of Cognitive Neuroscience, 18,* 539–561.

O'Craven, K., Downing, P., & Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature, 401*, 584–587.

O’Craven, K. M. & Kanwisher, N. (2000). Mental imagery of faces and places activates corresponding stimulus-specific brain regions. *Journal of Cognitive Neuroscience, 12,* 1013–1023.

Olivers, C. N. L, & Humphreys, G. W. (2004). Spatiotemporal segregation in visual search: Evidence from parietal lesions. *Journal of Experimental Psychology: Human Perception and Performance*, *30*, 667–688.

Orban de Xivry, J.-J., Missal, M., & Lefèvre, P. (2008). A dynamic representation of target motion drives predictive smooth pursuit during target blanking. *Journal of Vision*, *8*, 1–13.

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics transforming numbers into movies. *Spatial Vision, 10,* 437–442.

Peterken, C., Brown, B., & Bowman, K. (1991). Predicting the future position of a moving target. *Perception*, *20*, 5–16.

Pinker, S. (1999). *How the Mind Works*. New York: Oxford University Press.

Posner, M. I., Snyder, C. R. R., & Davidson, B. J. (1980) Attention and the detection of signals. *Journal of Experimental Psychology: General, 109,* 160–174.

Proffitt, D. R., Kaiser, M. K., & Whelan, S. M. (1990). Understanding wheel dynamics. *Cognitive Psychology, 22,* 342–373.

Rao, S. M., & Mayer, A. R., & Harrington, D. L. (2001). The evolution of brain activation during temporal processing. *Nature Neuroscience*, *4*, 317–323.

Rensink, R. A. (2000). The dynamic representation of scenes. *Visual Cognition, 7*, 17–42.

Richter, W. *et al.* (2000). Motor area activity during mental rotation studied by time-resolved single-trial fMRI. *Journal of Cognitive Neuroscience, 12*, 310–320.

Roberts, K. L., Lau, J. K. L., Chechlacz, M., & Humphreys, G. W. (2012). Spatial and temporal attention deficits following brain injury: A neuroanatomical decomposition of the temporal order judgement task. *Cognitive Neuropsychology*, *29*, 300–324.

Rorden, C., Mattingley, J. B., Karnath, H-O., & Driver, J. (1997). Visual extinction and prior entry: impaired perception of temporal order with intact motion perception after unilateral parietal damage. *Neuropsychologia*, *35*, 421–433.

Rosenbaum, D. A. (1975). Perception and extrapolation of velocity and acceleration. *Journal of Experimental Psychology: Human Perception and Performance*, *1*, 395–403.

Scholl, B. J. (2001). Objects and attention: The state of the art. *Cognition, 80,* 1–46.

Scholl, B. J., & Flombaum, J. I. (2010). Object persistence. In B. Goldstein (Ed.), *Encylopedia of Perception, Volume 2* (pp. 653–657). CA: Sage Press.

Scholl, B. J., & Pylyshyn, Z. W. (1999). Tracking multiple items through occlusion: Clues to visual objecthood. *Cognitive Psychology, 38,* 259–290.

Shepard, R. N., & Cooper, L. A. (1986). *Mental images and their transformations*. Cambridge: MIT Press.

Shepard, R. N. and Metzler, J. (1971). Mental rotation of three-dimensional objects. *Science, 171*, 701–703.

Sheth, B. R., Nijhawan, R., & Shimojo, S. (2000). Changing objects lead briefly flashed ones. *Nature Neuroscience*, *3*, 489–495.

Suchow, J. W., Brady, T. F., Fougnie, D., & Alvarez, G. A. (2013). Modeling visual working memory with the MemToolbox. *Journal of Vision*, *13*, 1–8.

Tresilian, J. R. (1995). Perceptual and cognitive processes in time-to-contact estimation: Analysis of prediction-motion and relative judgment tasks. *Perception & Psychophysics*, 57, 231–245.

Vallar, G., & Perani, D. (1986). The anatomy of unilateral neglect after right hemisphere stroke lesions. A clinical/CT-scan correlation study in man. *Neuropsychologia*, *24*, 609–622.

Wassle, H., Grunert, U., Rohrenbeck, J., & Boycott, B. B. (1989). Cortical magnification factor and the ganglion cell density of the primate retina. *Nature, 341*, 643–646.

Xiao, Q., Barborica, A., & Ferrera, V. P. (2007). Modulation of visual responses in macaque frontal eye field during covert tracking of invisible targets. *Cerebral Cortex*, *17*, 918–928.

Xu, Y. (2002). Encoding color and shape from different parts of an object in visual short-term memory. *Perception & Psychophysics, 64*, 1260–1280.

Xu, Y., & Franconeri, S. L. (in press). Capacity for visual features in mental rotation. *Psychological Science.*

Zhang, W., & Luck, S. J. (2008). Discrete fixed-resolution representations in visual working memory. *Nature*, *453*, 233–235.