Effect of smooth pursuit direction and screen quadrant on ODTs

We tested whether the direction of the smooth pursuit movement (from horizontal to vertical meridian or vice versa) and the quadrant of the screen across which the smooth pursuit target was moving (upper left or upper right) influenced the subjects' performance.

**AF Figure 1** shows the median ODT values for the four possible combinations of pursuit direction and screen quadrant for both reference frames. Only the data of subjects that were tested in all possible combinations were included in the analysis ($n = 9$). A Kruskal-Wallis ANOVA, conducted separately on the data of each reference frame, showed that neither smooth pursuit direction nor the quadrant of the screen affected ODTs.

**AF Figure 1.** Experiment 1. Median ODT values. The bars represent individual combinations of smooth pursuit direction, screen quadrant and target reference frame (labels on the abscissa). Arrows indicate pursuit direction and angles pursuit quadrants. The number of included staircases (out of a maximum of 36) is indicated on each bar. Some staircases were discarded following the exclusion criteria. The error bars represent the range between the 25th and 75th percentile of the distributions. The $p$ values correspond to Kruskal-Wallis ANOVAs across the four combinations for each reference frame.
Eye position calibration measurements

In order to quantify the measurement error of the smooth pursuit signals and the accuracy of the saccade detection algorithm we conducted calibration measurements in three of the subjects ('jcm', 'rni', 'thl').

METHODS

Procedure

The subjects were instructed to pursue the pursuit spot moving at the same speed and trajectory as in experiment 1 and 2 (AF Figure 2A). During the smooth pursuit period (930-1730 ms after smooth pursuit onset) we presented a small black square (area = 0.4 degrees visual angle²) at one of four possible distances from the pursuit spot (1, 2, 3 and 8.75 degrees visual angle). The targets presented at 1, 2 and 3 degrees visual angle moved at trajectories parallel to the smooth pursuit spot and the target presented at 8.75 degrees visual angle remained fixed at the screen center, resembling the space-centered target of experiments 1 and 2. Similar to experiment 2, smooth pursuits were restricted to the upper left quadrant of the screen and the direction was from horizontal to vertical meridian. During the smooth pursuit movement subjects made a saccade towards the saccade target as soon as they detected it and then a second saccade to return to the smooth pursuit target in order to finish the smooth pursuit movement. We also included trials during which no saccade target was presented and subjects simply performed the smooth pursuit ('no-saccade' trials). Each subject completed ten trials per condition. Trials of the different conditions were randomly intermixed within the experimental block.

Analysis of eye position data

The methods for recording and processing of the eye position data were identical to those described for the original experiments.

Results

Saccade velocity

The main point of this experiment was to define a velocity threshold for the detection of saccades that might have contaminated the smooth pursuit data. AF Figure 2B shows the spatial traces of example trials of one subject ('rni') for the different saccade/no-saccade conditions. The eye position trace of the 'no-saccade' trial (light blue) superimposes the trajectory of the smooth pursuit dot (black), indicating that the subject pursued the target with high spatial accuracy. The spatial traces of the saccade trials (dark blue, purple, orange, green) clearly show the amplitude of the saccades on top of the smooth pursuit. All saccade end points are located near the respective saccade target trajectory (grey), revealing the degree of spatial precision of the saccadic eye movement.

For each trial we computed the velocity as described in the article. AF Figure 2C illustrates the velocity profiles of the trials shown in AF Figure 2B. The velocity of the 'no saccade' trial (light blue, upper panel) oscillates around the smooth pursuit target velocity (dashed line). However, the fluctuations do not
seem to show a clear bias to lower or higher velocities. These small fluctuations may indicate intrinsic noise in the eye movement measurements. Their maximal velocity was always lower than 20 degrees/sec (see AF Figure 2D). This may be taken as an indication of how noisy our eye movement measurements were and was taken into account for choosing a threshold criterion for our saccade detection method.

The velocity profiles of the saccade trials (lower panel) contain two peaks. The first one belongs to the saccadic eye movement towards the target and the second one to the saccade returning from the target to the smooth pursuit spot. We determined the peak velocity of individual trials and averaged those across trials with identical saccade distances (we did this also for ‘no saccade’ trials, see above). AF Figure 2D shows the typical relationship between saccade amplitude and peak velocity (Van Gisbergen, Van Opstal, & Ottes, 1984) for each of the three subjects.

Since we were mainly interested in the detection of small saccades, we restricted the statistical analysis to the smallest saccade distance of 1 degree. In those trials the saccade target appeared close to the smooth pursuit spot (which had a diameter of 0.6 degrees).

The average peak velocities of the three subjects are remarkably similar (jcm = 28.25; rni = 28.93; thl = 29.8 degrees/s; p = 0.68, one-way ANOVA). Importantly, all of them were higher than 20 degrees/s (p < 0.0001, t-test), which was subsequently defined as the threshold criterion for our saccade detection algorithm.

Using the 20 degrees/s criterion, we could detect saccades in the saccade trials at a perfect score for all subjects. In the ‘no-saccade’ trials we detected none in two of the subjects and one (out of ten) in subject ‘jcm’. We therefore conclude that our threshold criterion is appropriate for detecting saccades in our experiments.

**Velocity during ‘no-saccade’ trials**

In order to assess the measurement error of the smooth pursuit signals, we determined the subjects eye velocity during ‘no-saccade’ trials. Here, the subjects only pursued the dot. Therefore the standard deviation of the eye movement measurements provide a baseline measurement for comparison against trials where subjects performed a second task, i.e., covertly attended to the target grating(s). The average eye velocities during ‘no saccade’ trials are illustrated in AF Figure 2D.

We tested, for the three subjects, whether eye velocities during the no-saccade task were different from those during trials that required covertly attending to a grating, i.e. those in experiments 1 and 2 (AF Table 1). We computed an unpaired t-test for each subject using the gains of all available trials in the former two experiments and compared them to the gains of the ‘no-saccade’ trials. The following table summarizes the results:
AF Table 1. Comparison of smooth pursuit gains during trials of experiments 1 and 2 and ‘no-saccade’ trials of the present experiment. Data represent mean ±1Std.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Experiments 1 &amp; 2 (n &gt;100)</th>
<th>‘No-saccade’ (n = 10)</th>
<th>P unpaired t-test</th>
</tr>
</thead>
<tbody>
<tr>
<td>jcm</td>
<td>1.023 ± 0.055</td>
<td>1.0 ± 0.028</td>
<td>0.18</td>
</tr>
<tr>
<td>rni</td>
<td>1.014 ± 0.06</td>
<td>0.989 ± 0.095</td>
<td>0.2</td>
</tr>
<tr>
<td>thl</td>
<td>1.032 ± 0.063</td>
<td>1.002 ± 0.049</td>
<td>0.13</td>
</tr>
</tbody>
</table>

These data suggests that covertly attending to the target grating or simply pursuing the target did not have a major influence on our measurements of smooth pursuit performance. We believe that the training provided to the subjects at the beginning of the sessions may have made the pursuit almost ‘automatic’ in our subjects (see also experiment 2 in the manuscript).
AF Figure 2. Saccade detection experiment. A) Task design. During smooth pursuit subjects made a saccade towards a target (squares) at one out of four possible locations at different distances from the smooth pursuit target (black disc). For three distances (1, 2 and 3 degrees) the target moved on a circular trajectory (grey curved lines) while for the largest distance (8.75 degrees) the target remained stationary at the screen center. In the ‘no saccade’ condition, only the smooth pursuit movement was required. B) Spatial eye position traces of example trials in the different conditions. The grey curved lines indicate the distances of the saccade target trajectories. C) Velocity profiles of the example trials in ‘B’ for the ‘no-saccade’ trial (upper panel) and the saccade trials (lower panel). The red dashed line indicates the velocity criterion (20 degrees/s) of the saccade detection algorithm and the black solid line the velocity of the smooth pursuit target. Color-coding follows conventions in ‘B’. D) Average peak velocity. The error bars represent Std.
Effect of target retinal velocity on orientation discrimination performance

In this experiment, we tested whether the differences in ODTs found in experiment 1 for targets centered in the two reference frames could be caused by differences in the targets’ retinal velocity. We designed an experiment that allowed us to change target velocity while keeping the eccentricity of a target grating constant and changing the target position in space and on the retina. We then measured the ODTs for different velocities of the target grating.

METHODS

Apparatus and Stimuli

Apparatus, viewing conditions, target grating and smooth pursuit dot were the same as in the previous experiment.

Subjects

One of the authors (‘law’) and two undergraduate students (‘dim’, ‘jon’) participated in the experiment.

Procedure

During trials, two stimuli, a pursuit dot and a sinusoidal target grating identical to those used in experiment 1, were presented. Upon trial initiation, the smooth pursuit dot appeared directly above the target and started moving horizontally across the screen at a velocity of 5.75 deg/s (AF Figure 3A). During trials, the target grating and the pursuit dot kept a constant distance of 8.75 degrees. Different target velocities were achieved by varying the orbiting (angular) displacement of the grating per time unit (AF Figure 3B). The observers’ task was to pursue the dot while attending to the orbiting target and report, at the end of the trial, a change in its orientation (clockwise or counterclockwise, see previous experiment). Seven different target velocities were tested (in deg/s): 0; 1.0; 1.9; 2.9; 3.8; 4.8; 5.75. The task was run in blocks of 160 trials. Within a block, two different orbiting target velocities were presented (in deg/s): 0/1.9; 1.0/2.9; 2.9/4.8; 3.8/5.75. These velocities represent the target retinal velocity. The number of trials per target retinal velocity within a block was balanced and their occurrences randomized. Every subject completed the same block at least twice.

Measurements and analysis

We measured ODTs using the staircase method described in the previous experiment. Starting values for all staircases were between 3° and 9°. In each block, separate staircases were run for every combination of target velocity, starting value, and orientation change direction (clockwise or counter-clockwise). In order to calculate the average ODT for a specific target velocity, we pooled data from similar staircases. Staircases with insufficient reversal points (< 5) were discarded (‘law’: 6.2%; ‘jon’: 7.8%; ‘dim’: 1.6%).

RESULTS

AF Figure 3C shows the three subject’s ODTs as a function of target retinal velocity. We fitted regression lines to these data. The lines have significant positive non-zero slopes (‘dim’: slope ± 95% confidence interval (CI) = 1.2 ± 0.55, \( R^2 = 0.79 \); ‘jon’: slope ± CI = 0.78 ± 0.39, \( R^2 = 0.76 \); ‘law’: slope ± CI = 0.89 ± 0.32, \( R^2 = 0.86 \)). In all cases the 95% confidence interval does not include zero,
demonstrating that ODTs increased linearly as a function of the target retinal velocity.

Interestingly, for one of the subjects (‘law’) who also participated in experiment 1, the ODTs for the lowest retinal velocity (0 deg/s) was 5°, while for the highest retinal velocity (5.75 deg/s) it was 10°. These values are close to those obtained in experiment 1 for the retina centered target (5°), which also had a retinal velocity of 0 deg/s, and for the space centered target (14°), which had a retinal velocity of 5.75 deg/s. The small increase in ODTs in experiment 1 relative to those predicted by our measurements in this experiment may be due to at least two factors. First, the smooth pursuit trajectories in experiment 1 were circular, introducing an extra-level of difficulty relative to the present experiment where pursuit trajectories were straight. Second, in experiment 1 two target gratings were presented, while here only one grating was displayed, making the latter display less crowded and the task easier.

A factor that may explain this increase in ODTs is motion blur (Chung, Levi, & Bedell, 1996; Kelly, 1979; Land, 1999), which causes retinal images to spread over a spatiotemporal area thereby reducing the visibility of the stimulus’ features. An orientation change in a stimulus moving on the retina might therefore be harder to perceive. Blurring can occur at velocities as low as 1 deg/s for high spatial frequency images (Land, 1999), matching our observation of ODT elevation at velocities of 0.95 deg/s. For lower retinal speeds such as those used by Khurana and Kowler (1987) — 0.42 deg/s or 0.83 deg/s, only comparable to the lowest velocity used in our study — this may not apply. Another factor that may contribute to our results is the use of low-level stimuli (sinusoidal gratings), which are likely represented in retinotopic brain areas with comparably small receptive fields, such as V4 (Gardner, Merriam, Movshon, & Heeger, 2008). Letters (used by Khurana and Kowler, 1987) on the other hand, are likely represented in higher-level brain areas, such as left occipito-temporal cortex (Grainger, Rey, & Dufau, 2008), or the posterior parietal cortex (Cattaneo, Rota, Vecchi, & Silvanto, 2008), where neurons show position invariance for stimuli inside their receptive field (Duhamel, Bremmer, BenHamed, & Graf, 1997; Galletti, Battaglini, & Fattori, 1993). In the latter case visual representations might be less susceptible to changes in retinal image velocity, at least within the spatial limits of their position invariance.
Figure 3. A) Experimental layout. Observers pursued the black dot while attending to the orbiting grating. See text for details. The dotted line shows the constant distance between the pursuit dot and the target grating. The straight grey arrow represents the trajectory of the smooth pursuit dot, and the circular arrow the orbiting trajectory of the grating. B) Different final positions of the target grating depending on its orbiting velocity (numbers represent degrees/s). Each position is depicted relative to the smooth pursuit dot (upper right corner). The grey arrow depicts the target trajectory on the retina. C) ODTs as a function of target retinal velocity for the three subjects. Data represent mean ODTs ±1SEM. The lines illustrate the best linear regression models fitted through the data.
References


