RESEARCH ARTICLE

Involuntary cueing effects during smooth pursuit: facilitation and inhibition of return in oculocentric coordinates

David Souto · Dirk Kerzel

Abstract Peripheral cues induce facilitation with short cue-target intervals and inhibition of return (IOR) with long cue-target intervals. Modulations of facilitation and IOR by continuous displacements of the eye or the cued stimuli are poorly understood. Previously, the retinal coordinates of the cued location were changed by saccadic or smooth pursuit eye movements during the cue-target interval. In contrast, we probed the relevant coordinates for facilitation and IOR by orthogonally varying object motion (stationary, moving) and eye movement (fixation, smooth pursuit). In the pursuit conditions, cue and target were presented during the ongoing eye movement and observers made a saccade to the target. Importantly, we found facilitation and IOR of similar size during smooth pursuit and fixation. The results suggest that involuntary orienting is possible even when attention has to be allocated to the moving target during smooth pursuit. Comparison of conditions with stabilized and moving objects suggest an oculocentric basis for facilitation as well as inhibition. Facilitation and IOR were reduced with objects that moved on the retina both with smooth pursuit and eye fixation.

Keywords Smooth pursuit · IOR · Attention · Exogenous orienting · Reference frames

Introduction

When a peripheral location is cued by a transient event (i.e., a luminance change) and the cue-target interval is shorter than 200–300 ms, responses are faster to targets appearing at the cued location than to targets appearing at an uncued location. Facilitation of responses was attributed to involuntary shifts of attention to the cued location. With longer cue-target intervals, responses are slower to targets appearing at the cued location (Posner and Cohen 1984), which is referred to as inhibition of return. IOR is often understood as an adaptive mechanism by which previously attended objects are less likely to be attended later on. In agreement with this interpretation, IOR has been proposed to operate as a visual foraging facilitator (Klein and MacInnes 1999; Gilchrist and Harvey 2000; but see Hooge et al. 2005): IOR optimizes the distribution of saccades over the whole visual scene by avoiding repeated selection of a salient location.

One important question is how inhibition is updated after an eye movement. Is the retinal location, the object, or the location in the environment inhibited? To answer this question, Posner and Cohen (1984) asked their subjects to make a saccade in the interval between cue and target presentation, which changed the retinal (but not environmental) location of the cue. Unimpaired IOR indicated it was coded in environmental coordinates. More recently, Abrams and Pratt (2000) confirmed a dissociation between manual and saccadic responses. While manual IOR was coded in environmental coordinates, saccadic IOR was coded in retinal[1] coordinates. Observers were asked to pursue a moving fixation mark during the cue-target interval and to foveate the peripheral target by making a saccade. Saccades were

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[1] We use the term "retinal" synonymous to "oculocentric". In keeping with general usage, we oppose this reference frame to "environmental" that is synonymous to "spatial". We would like to point out that "environmental" is inexact because a head-centric (egocentric) reference frame cannot be ruled out, as the head was fixed. The term "non-retinotopic" would be more exact.

slower when the target appeared in the same retinal location as the cue, but not when it appeared in the same spatial location (see Exp. 2, Abrams and Pratt 2000). Therefore, Abrams and Pratt concluded that saccadic IOR operates in retinal coordinates. They gave the following reason for using smooth pursuit rather than a saccade during the cue-target interval: "We used a smooth-pursuit movement to change the position of the participant's gaze because the sudden onset of a saccade target, or possibly even the production of an endogenous saccade, might be expected to attract or otherwise activate the attention system and thus disrupt the inhibition that had been established by the initial cue" (p. 780). The rationale seems to suggest that using smooth pursuit does not implicate the attention system.

In light of research on the connection between smooth pursuit and attention, this conclusion seems quite wrong and warrants further research. First, previous studies have shown that attention is bound to the pursuit target during steady-state pursuit (Kerzel and Ziegler 2005; Khurana and Kowler 1987; Madelain et al. 2005; Schutz et al. 2007). For instance, observers were unable to shift attention to a distractor while correctly pursuing the target (Khurana and Kowler 1987), even when target and distractor moved in the same direction, but at slightly different speeds. The allocation of attention was measured by means of a secondary perceptual task. Without incentive to prioritize distractor or target, perceptual performance on the target was much better than perceptual performance on the distractor.

Given the attention-demanding nature of smooth pursuit, that was somewhat downplayed by Abrams and Pratt (2000), one may wonder whether the reduction of IOR when the retinal location of the cue changed was exclusively due to retinal displacement. Second, it seems important to investigate the effects of eye movements because there is little consensus on the coordinate frame of IOR. When retinal- and environment-based coordinates were carefully separated, many experiments have confirmed inhibition that is attached to the object as it moves (Tipper et al. 1991; Tipper et al. 1994). Object-based IOR may even overrule space-based IOR (Tipper et al. 1991). However this effect was elusive with saccadic (Abrams and Dobkin 1994; Ro and Rafal 1999) as well as with manual responses in a different setting (Muller and von Muhlenen 1996). At least with manual responses, it appears that object- and environment-based IOR may vanish after extended training (Weaver et al. 1998). Still, effects of practice on environment-based IOR were not replicated in a series of three experiments (Pratt and McAuliffe 1999).

The purpose of this study was to disentangle the effects of coordinate frame and eye movements. In a previous study, we showed that effects of voluntary attention on manual RTs were similar during fixation and smooth pursuit (Kerzel et al. 2008). Because the peripheral or central cues predicted the upcoming target location, subjects in Kerzel et al. were likely to voluntarily attend to the cued locations. Facilitation was observed with cue-target SOAs as long as 500 ms, and was coupled to a decrease of pursuit gain when the peripheral target did not move along with the pursuit target. In the present study, the cues did not predict the subsequent target location. As a consequence, the best strategy was to ignore them. Any cueing effects that are observed would therefore more likely be involuntary.

There is reason to believe that cueing effects will not occur during smooth pursuit. The strong coupling between attention and smooth pursuit may help observers to filter out irrelevant peripheral events. In some instances, onsets failed to capture attention when attention was narrowly focused on a given location (Theeuwes 1991). If the execution of smooth pursuit induced such a strong attentional focus on the pursuit target, facilitation and IOR may disappear during smooth pursuit. Alternatively, exogenous shifts of attention may still occur under the assumption that only endogenous attention is allocated to the pursuit target. Some authors have proposed that endogenous and exogenous attention are partially independent resources (e.g., Riggio and Kirsner 1997).

To tease apart retinocentric from environmental coordinates, we compared conditions in which cued objects moved on the retina with conditions in which objects were stabilized on the retina. Because object or eye movements were continuous, our paradigm avoids transients between cue and target presentation that may have contaminated effects in previous studies. The comparison between fixation and smooth pursuit is expected to produce similar latencies, as the readiness to make a saccade has been shown to be very similar during pursuit and fixation (Boman et al. 1996; Krauzlis and Miles 1996).

Methods

Subjects

The first author (DS) and 11 students (10 females) of the University of Geneva participated for course credit ($M = 20.5$ years old, $SD = 2.8$). Students were naïve with respect to the purpose of the experiment and the first author's results followed the average pattern.

The experiment was conducted in compliance with the ethical regulations of the University of Geneva and with the Helsinki Declaration of 1964.

Materials and stimuli

Eye movements were recorded with an Eyelink II (Osgood, Ontario, Canada) eye-tracker, in pupil only mode. Sampling

frequency was 250 Hz. A 9-point pseudo-random calibration procedure was run at the beginning of each session, and every two blocks if needed. Experiments took place in a dimly lit room. Head movements were minimized with a chinrest, at a distance of 46 cm from the screen. The luminance of the gray background was 29 cd/m^2. Dark gray placeholders (22 cd/m^2, 1° × 1°), were shown at a vertical eccentricity of 5°. The size of the red fixation cross was 0.2° × 0.2°. The cue was a dimming (to 0 cd/m^2) and thickening (from 0.04° to 0.21°) of the horizontal lines of the placeholders. The target was a black circle (0 cd/m^2) of 0.4° diameter.

Figure 1 depicts the relative motion conditions, in which the pursuit target and peripheral boxes moved relative to each other at 10.8°/s. After a random time interval, from 600 to 1,060 ms after start of the trial, the cue was displayed for 20 ms. After a variable time interval, the target appeared in the cued (valid condition) or opposite location (invalid condition) for 40 ms. The stimulus onset asynchrony (SOA) between cue and target was set to either 130 or 600 ms to maximize saccadic facilitation and IOR, respectively (Briand et al. 2000). In two stabilized conditions, the fixation cross and peripheral boxes were static or moved together, and were therefore approximately stabilized on the retina by fixation or pursuit eye movements, respectively. Cue onset was as unpredictable in the relative motion as in the stabilized conditions. In stabilized conditions the placeholders were exactly above and below the fixation target. In relative motion conditions, horizontal eccentricity of the cue relative to the fixation target varied randomly around 0° of eccentricity (−2.5° to 2.5°).

A potentially important point about the cue is that it avoided perceptual interference with the target because only the upper and lower bars were highlighted (see Fig. 1a, b). If the vertical lines had been dimmed, the flashed box could be perceived as overlapping the target due to the mislocalization of flashed objects during smooth pursuit (e.g., Kerzel et al. 2006) or because of the flash-lag effect during fixation (e.g., Nijhawan 2002).

Procedure

Subjects were asked to accurately track or fixate the red cross until they saw a black dot, which they had to fixate as fast as possible, while avoiding anticipatory responses. The experimental design was within-subjects with the factors relative motion (with or without relative motion), eye movement (fixation or pursuit), validity (valid or invalid) and SOA (130 or 600 ms). Relative motion, eye movement, and SOA were blocked. SOA was blocked to maximize IOR (Tipper and Kingstone 2005) and help subjects maintain smooth pursuit after presentation of the exogenous cue. With uncertainty about the SOA, subjects tended to stop
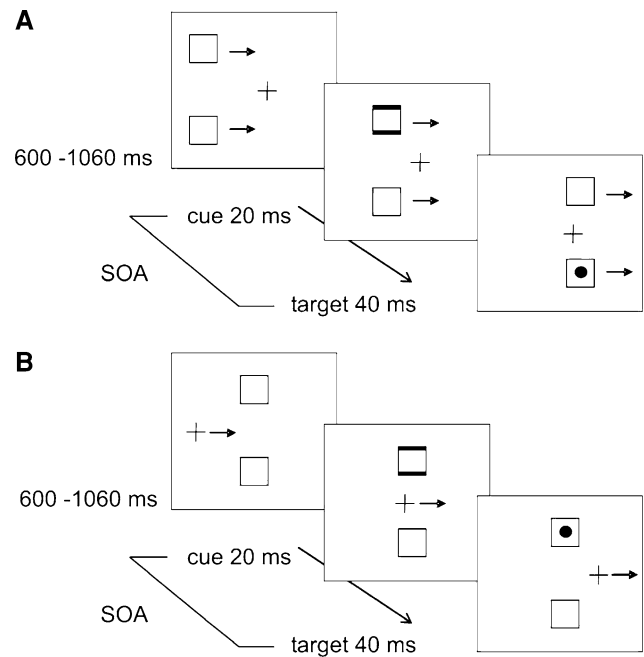

Fig. 1 Time-course for relative motion conditions with eye fixation (**a**) and smooth pursuit (**b**). The cue appeared at the same horizontal eccentricity in both conditions and could be invalid (**a**) or valid (**b**) with equal probability. In stabilized conditions, which are not shown, everything was static or moved together. The stimulus onset asynchrony (SOA) was either 130 or 600 ms. The response was a saccade to the target disk

pursuit after the exogenous cue, because they were getting ready to make a saccade. This reduced pursuit gain considerably in the long SOA condition. The direction of eye or object motion was randomized. There were 48 repetitions for fixation trials, 96 for eye movement trials because we assumed that the dual task situation would increase variability. Each subject completed at least 1,152 trials in three sessions. Erroneous trials were repeated. An error message and a tone was displayed whenever any of the following events was detected: a blink between 100 ms before cue onset to 500 ms after target onset, an anticipatory saccade (latencies shorter than 100 ms), a late saccade (latencies longer than 500 ms which are more than ~3 SD away from the median latency), a saccade in the wrong direction, or bad pursuit. The online criterion for smooth pursuit was that the eye had to travel a distance corresponding to a pursuit gain of 0.8–1.2 during the cue-target interval. A small proportion of trials was repeated because of anticipations (4%), timed-out responses (2%), saccades in the wrong direction (2%), or low pursuit gain (6%).

Results

We calculated the gain (eye velocity/target velocity) of smooth pursuit after removing saccades from the eye movement

traces. We then retained trials in which pursuit gain was between 0.8 and 1.2 in the cue-target interval. Figure 2a–d shows pursuit gain. Indeed, there was a tendency for most of the subjects to slow down in anticipation of target presentation when the target was stationary, notably for the long SOA (see Fig. 2a, b). As shown in Fig. 2e, f, the proportion of trials with gain below cut-off is only substantial in the relative motion conditions with the long SOA (11%). Overall, 3% of trials were removed in the offline analysis.

We calculated median saccadic reaction times for each condition and participant. Mean of median saccadic latencies for all conditions are graphed in Fig. 3. A repeated-measures ANOVA (relative motion × eye movement × validity × SOA) was run on median saccadic reaction times. Most importantly, we found a three-way interaction between relative motion (stabilized vs. relative motion), SOA, and validity, $F(1,11) = 10.44$, $P < 0.01$, but no effects including eye movement. This means that cueing effects were as strong during smooth pursuit as during fixation. The only factor that modulated cueing effects was relative motion. To follow up on the significant interaction, we calculated cueing effects (i.e., the difference between invalid and valid trials) for each relative motion condition and SOA. For short SOAs, cuing effects were not significantly

different in relative motion and stabilized conditions (facilitation of 12 vs. 17 ms, respectively), $P = 0.14$. For long SOAs, cueing effects were significantly smaller with relative motion than without (inhibition of -9 vs. -23 ms), $t(11) = 4.28$, $P < 0.001$. Further, we ran separate three-way ANOVAs (eye movement × validity × SOA) for each relative motion and stabilized condition.

Stabilized conditions

The similarity of fixation and pursuit is remarkable when the peripheral objects were stabilized (see Fig. 3a, b). The classic facilitation and inhibitions effects were found in both conditions and no significant interaction with eye movement was observed. A repeated-measures ANOVA (eye movement × validity × SOA) showed a significant interaction of validity and SOA, $F(1,11) = 45.89$, $P < 0.001$, not modulated by eye movement, $F < 0.4$. Eye movement interacted with validity, $F(1,11) = 11.59$, $P < 0.01$, indicating longer latencies (across SOAs) with valid cues during fixation than during pursuit (239 vs. 229), $t(11) = 5.9$, $P < 0.05$.

For the short SOA, facilitation was of 14 ms for the static condition (valid vs. invalid: 231 vs. 245 ms),

Fig. 2 Analyses of pursuit gain. **a–d** show pursuit gain (eye velocity/target velocity) averaged over the 12 subjects from 200 ms before cue presentation until 100 ms after target presentation. Relative motion (**a**, **b**) and stabilized (**c**, **d**) conditions are shown on different panels. The short cue-target stimulus onset asynchrony (SOA) is shown on the *left* (**a**, **c**) and the long SOA on the *right* (**b**, **d**). *Thin lines* represent the between-subjects standard error of the mean. **e**, **f** Histograms of pursuit gain in the cue-target interval for short (**e**) and long (**f**) SOAs. *Vertical lines* show the cut-off used for inclusion of trials in our analyses
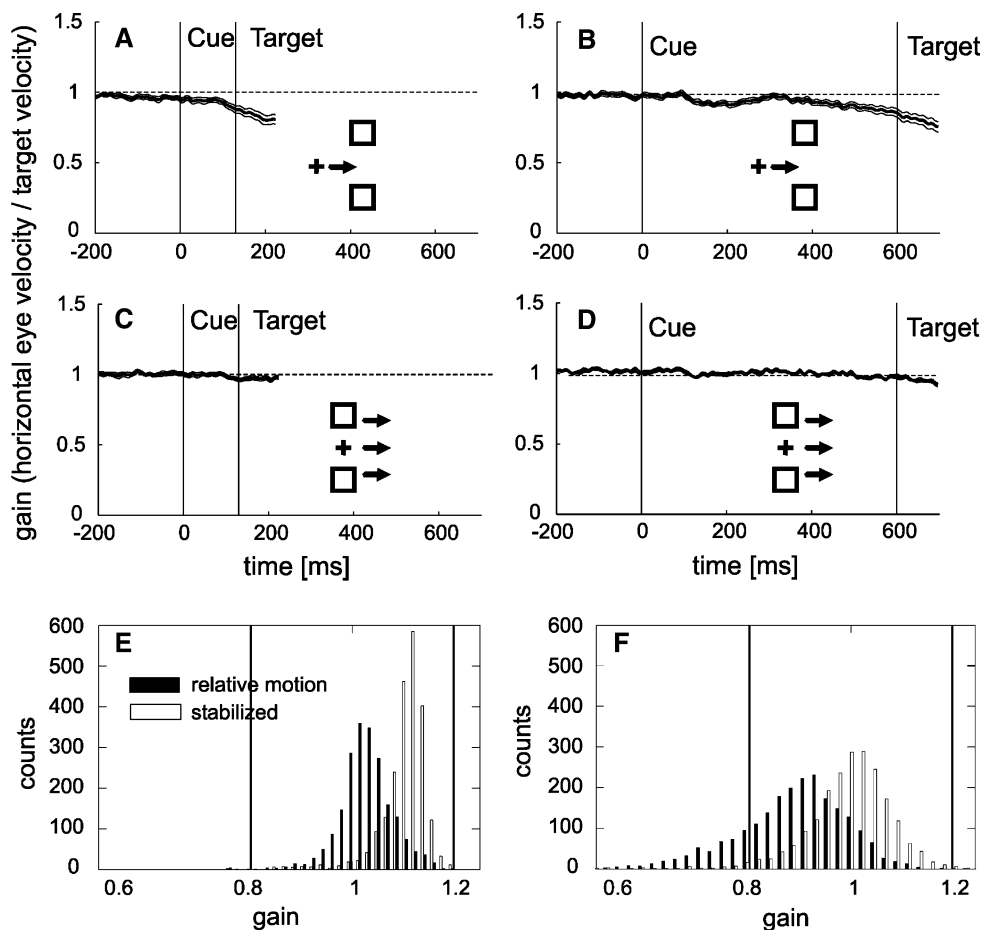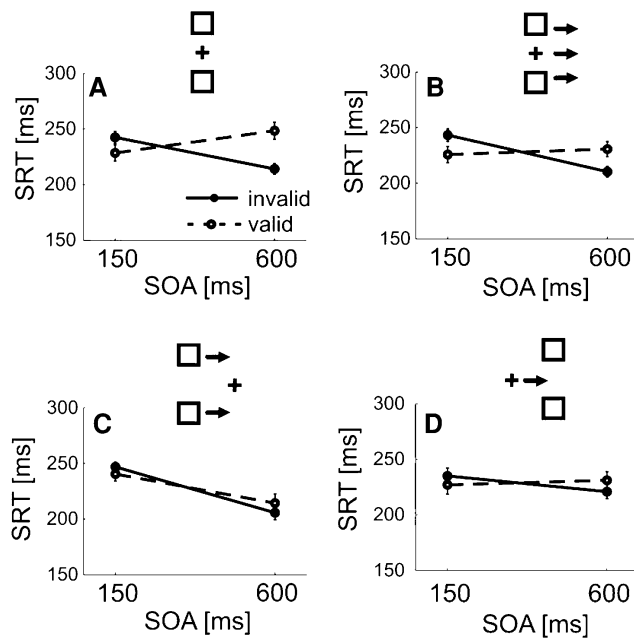
Fig. 3 Mean of median saccadic reaction times (SRT). The *upper* panels show the conditions with stabilized peripheral objects during fixation (**a**) or smooth pursuit (**b**). The *lower* panels show the condition with relative motion during fixation (**c**) or smooth pursuit (**d**). *Error bars* represent between-subjects standard error of the mean

Fig. 4 Effects of eccentricity on median saccadic reaction time (SRT). Facilitation was observed at short stimulus onset asynchronies (**a**, **b**) and inhibition of return at long stimulus onset asynchronies (**c**, **d**). The *left* and *right* columns show fixation and pursuit conditions as shown in the *insets* at the *top*. *Error bars* represent between-subjects standard error of the mean

$t(11) = 6.07$, $P < 0.05$, and of 20 ms for the pursuit condition (224 vs. 244 ms), $t(11) = 15.2$, $P < 0.01$. For the long SOA, an IOR effect of −29 ms (248 vs. 219 ms) was found during fixation, $t(11) = 21.46$, $P < 0.001$, and of −17 ms during pursuit (233 vs. 216 ms), $t(11) = 10.2$, $P < 0.01$.

Relative motion conditions

With relative motion between fixation cross and peripheral boxes, the cue could be presented with a variable horizontal eccentricity (between −2.5° and 2.5°). To rule out that the reduction of the cueing effects with relative motion was due to target eccentricity, we calculated median saccadic reaction time in three eccentricity bins that were 0.8° wide (0°–0.8°, 0.8°–1.6°, and 1.6°–2.4°). Figure 4 shows that the differences between valid and invalid (short or long SOA) were stable over eccentricities ranging from 0° to 1.6°. It also indicates that the reduction of IOR and facilitation with relative motion was not due to decreasing cueing effects with increasing eccentricity. If anything, the opposite was the case. We then tested cueing effects for trials with eccentricities smaller than 1°. A repeated-measures ANOVA (eye movement × validity × SOA) confirmed an interaction between SOA and validity, $F(1,11) = 20.35$, $P < 0.001$, indicating that facilitation with the short SOA turned into inhibition with the long SOA. Again, the interaction of SOA and validity was not qualified by eye movement, $F < 0.02$. Further, there was an interaction of eye
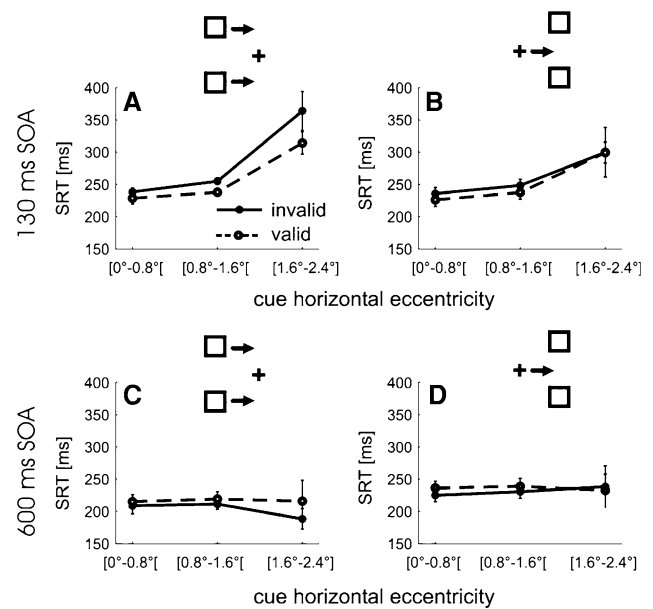
movement and SOA, $F(1,11) = 7.3$, $P < 0.05$, indicating shorter latencies during fixation compared to pursuit with the long SOA (209 vs. 227 ms), $t(11) = 2.17$, $P = 0.05$, but longer latencies during fixation compared to pursuit with the short SOA (244 vs. 235 ms). We then tested the reliability of cueing effects for each combination of SOA and eye movement. *T* tests showed tendencies in the predicted direction for facilitation effects (Ps > 0.19), and statistically significant or nearly significant effects for inhibition. Facilitation with the short SOA was of 8 ms (240 vs. 248 ms) during fixation and of 3 ms (233 vs. 236 ms) during pursuit. Inhibition with the long SOA was of −8 ms during fixation (214 vs. 206 ms), $t(11) = 2.11$, $P = 0.06$, and of −11 ms during pursuit (233 vs. 222 ms), $t(11) = 3.13$, $P = 0.01$.

Discussion

We wanted to know how smooth pursuit affects involuntary cueing effects and in which reference frame these effects operate. We measured the facilitation and IOR effects during pursuit and fixation with peripheral objects that either moved on the retina or remained on the same retinal location. We found similar effects with a static display during fixation as with objects that moved at the same velocity as the pursuit target. The size of these effects is comparable to those previously reported in the literature, which confirms the existence of automatic orienting and inhibition by peripheral cues during

smooth pursuit. This finding complements our earlier study on voluntary attention during smooth pursuit (Kerzel et al. 2008). Involuntary cuing effects occur even if instructions required participants to focus on the pursuit task until the peripheral saccade target appeared. Pursuit with a high gain requires attention on the pursuit target, yet this is not a sufficient condition for filtering out the influence of irrelevant, peripheral transients (i.e., the cue).

With relative motion of fixation cross and peripheral objects, cuing effects were reduced to half of those in stabilized conditions. A decrease of pursuit gain was observed when a static target was cued, indicating anticipatory preparation of fixation in response to cue onset. Nonetheless, cuing effects were smaller than in the stabilized condition.

One might argue that perception of the cue was hampered because of motion smear in conditions with retinal motion. If this was true, saccadic latencies with relative motion should be increased relative to the stabilized conditions. However, responses were not delayed with relative motion.

The smaller effects when the cued object moved only 5° (long SOA) or 1.1° (short SOA) on the retina before target onset suggest a retinal basis of saccadic facilitation and IOR. Consistent with Abrams and Pratt (2000), these results confirm that facilitation and inhibition of saccades are anchored in retinal coordinates. In contrast, IOR with manual responses was found to be environment- (Maylor and Hockey 1985; Posner and Cohen 1984) and object-based (e.g., Tipper et al. 1991). The idea of more than one mechanism underlying IOR may explain differences between manual and saccadic responses (e.g., Kingstone and Pratt 1999). First, there is inhibition of saccadic responses to the cued location (i.e., a motor component), with a presumed neural substrate in the superior colliculus (Sapir et al. 1999; Sumner et al. 2004). The superior colliculus is known to have a retinotopic organization (e.g., Cynader and Berman 1972). Second, there is inhibition of attention shifts to the cued location, with a presumed cortical substrate (Sapir et al. 1999; Sumner et al. 2004). Cortical maps may either be space-based or retinotopic (e.g., Duhamel et al. 1997). The two mechanisms do not necessarily share the same coordinate frame. For instance, patients with cortical lesions in the parietal lobe showed impaired environmental, but preserved retinotopic IOR (Sapir et al. 2004). Although IOR of similar size is sometimes found with saccadic and key-press responses (Reuter-Lorenz et al. 1996), it appears that saccadic IOR depends more strongly on the motor component (Hunt and Kingstone 2003; Kingstone and Pratt 1999; Taylor and Klein 2000). Thus, stronger IOR with stabilized stimuli in the present study may be a consequence of the prominence of the retinotopic motor component with saccadic responses.

How can retinotopic IOR with single saccades to cued locations be reconciled with studies indicating space-based IOR in "saccadic search"? (Gilchrist and Harvey 2000; Klein and MacInnes 1999). A possible reason is the need for space-based memory in saccadic search. In order to keep track of object locations and identities after multiple saccades, the retinotopic input has to be recoded in a space-invariant memory representation (see Pouget and Snyder 2000). The need for such a map is much smaller in trials with single saccades that do not require any form of memory. Therefore, it may be that the discrepancy arises from different task demands.

Further, we found no significant facilitation effect when the cued object was moving during fixation. In contrast, previous studies in which object motion started simultaneous with cue presentation found significant facilitation (Abrams and Dobkin 1994; Ro and Rafal 1999). It may be that the simultaneous onsets induced attentional tracking of the cued object. In our study, object motion started well before cue presentation, and object motion was therefore seen as unrelated to cue presentation. Thus, the cue may have attracted attention to a particular location, and not to the moving object.

Our results point to the superior colliculus as the neural substrate of IOR with saccades (see also some early hypothesis by Posner and Cohen 1984), but they are only suggestive. While it is true that the SC happens to code gaze shifts (eye + head) in retinal coordinates (Klier et al. 2001), retinotopic coding schemes are found at multiple levels in the visual pathways. For instance, structures upstream from the SC, like the FEF (e.g., Dassonville et al. 1992; Schlag-Rey et al. 1992), code eye movements to a specific retinal location. Similarly, facilitation was found to be retinotopic and early visual cortical areas that encode space in a retinotopic reference frame (e.g., Gardner et al. 2008) were believed to underlie these effects (Posner and Cohen 1984). Thus, retinotopy is very weak evidence for the involvement of the superior colliculus. Clearly, more neurophysiologic data is needed to pinpoint the neural substrate of IOR.

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