

Dynamics of attention during the initiation of smooth pursuit eye movements

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Many studies indicate that saccades are necessarily preceded by a shift of attention to the target location. There is no direct evidence for the same coupling during smooth pursuit. If smooth pursuit and attention were coupled, pursuit onset should be delayed whenever attention is focused on a stationary, non-target location. To test this hypothesis, observers were instructed to shift their attention to a peripheral location according to a location cue (Experiments 1 and 2) or a symbolic cue (Experiment 3) around the time of smooth pursuit initiation. Attending to static targets had only negligible effects on smooth pursuit latencies and the early open-loop response but lowered pursuit velocity substantially about the onset of closed-loop pursuit. Around this time, eye velocity reflected the competition between the to-be-tracked and to-be-attended object motion, entailing a reduction of eye velocity by 50% compared to the single task condition. The precise time course of attentional modulation of smooth pursuit initiation was at odds with the idea that an attention shift must precede any voluntary eye movement. Finally, the initial catch-up saccades were strongly delayed with attention diverted from the pursuit target. Implications for models of target selection for pursuit and saccades are discussed.

Keywords: attention, smooth pursuit eye movements, catch-up saccades, open-loop smooth pursuit, covert and overt attention, endogenous and exogenous attention

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Introduction

Foveation and tracking of moving targets for full acuity perception is achieved by a coordination of smooth pursuit and saccadic eye movements. Pursuit serves the purpose of reducing retinal motion of objects we look at. Initiation of smooth pursuit differs from saccadic initiation in many ways. Among other things, pursuit is initiated with shorter latencies and is mainly driven by a velocity signal (Rashbass, 1961). Smooth pursuit is initiated by an open-loop phase that precedes the onset of functional pursuit by about 100 ms, which is mainly controlled by a negative feedback loop to ensure that the eye velocity closely matches the target velocity (Tychsen & Lisberger, 1986). Only recently researchers have unveiled that saccades and smooth pursuit share many common neural substrates and similar mechanisms of target selection and initiation (for a review, Krauzlis, 2004). However, it is not well understood if attention plays the same role in the initiation of smooth pursuit and saccades.

Visual selective attention is believed to play a mandatory role in the initiation of voluntary saccades (e.g., Deubel & Schneider, 1996, 2003). This relation led some authors to suppose a pre-motor origin to covert shifts of attention (Kustov & Robinson, 1996; Müller, Philiastrides,

& Newsome, 2005; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Smith, Rorden, & Jackson, 2004). The extent of the overlap between covert attention and saccade programming is still under debate (e.g., Thompson, Biscoe, & Sato, 2005). Nonetheless, covert attention allocated to the saccade goal seems necessary for the initiation of voluntary saccades (Crawford & Muller, 1992; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995; Posner, 1980; Reuter-Lorenz & Fendrich, 1992; Shepherd, Findlay, & Hockey, 1986).

Various lines of research suggest that a similar coupling exists for smooth pursuit. Evidence for this coupling is solid for steady-state pursuit and sparse for open-loop initiation. During the steady-state phase, selective attention is tightly coupled to the pursuit target, as shown by very poor perceptual performance for untracked targets moving in the same direction (Khurana & Kowler, 1987), and by the sensitivity of pursuit gain to the size of the attentional window used to track the target (Madelain, Krauzlis, & Wallman, 2005). Furthermore, spatial attention during smooth pursuit seems necessary to override OKN, which could theoretically be triggered by self-induced background motion during smooth pursuit (Lindner & Ilg, 2006; Lindner, Schwarz, & Ilg, 2001). The role of locking attention to the pursuit target may therefore be to filter out disrupting motion signals from the background (Spering & Gegenfurtner, 2007).

The relationship between spatial attention and open-loop pursuit is less clear. Recent studies suggest that pursuit and saccades share mechanisms of target selection (Krauzlis & Dill, 2002; Liston & Krauzlis, 2003, 2005). For example, spatial cuing (endogenous or exogenous) shortens pursuit as well as saccadic latency considerably (~30 and ~50 ms respectively) in the presence of a distractor. In addition, cues indicating the location of the upcoming pursuit target were more effective in reducing pursuit latencies than cues indicating motion direction, which should *a priori* directly prime the pursuit system (Adler, Bala, & Krauzlis, 2002). Those latter findings lend support to the idea of a common attentional selection mechanism.

Other lines of research suggest that spatial attention plays a privileged role well after movement initiation, corresponding to the beginning of the closed-loop phase. A number of studies suggest that attention for smooth pursuit is locked to the endpoint of the first catch-up saccade. This may explain why pursuit velocity is enhanced synchronous to saccade execution (Lisberger, 1998; Ogawa & Fujita, 1998; Schoppik & Lisberger, 2006) as well as when the pursuit target is spatially close to the saccade endpoint (Schoppik & Lisberger, 2006). Conversely, these findings may be taken to indicate that focused attention is not involved in pre-saccadic pursuit. Erkelens (2006) proposed that pursuit latencies in the classic step-ramp paradigm (Rashbass, 1961) are shorter than saccadic latencies because pursuit can be initiated before the target is selected. Target selection is made at the same time for pursuit and saccades. Before that time, pursuit follows the available motion signals, not the voluntarily planned movement.

Ferrera and Lisberger (1995) showed that smooth pursuit latency was strongly delayed (~60 ms) when monkeys were instructed to pursue a target indicated by a color cue in the presence of a distractor moving in the opposite direction (Ferrera & Lisberger, 1995, 1997). However, the dynamics of pursuit were unaffected. Importantly, the delay was reduced but still present if a location cue preceded target and distractor onset by up to 800 ms (Ferrera & Lisberger, 1995), showing that advance target selection by selectively attending to the target is imperfect for smooth pursuit, in striking contrast to target selection for regular saccades.

Our brief summary shows that previous studies are not conclusive about the *effective* involvement of attention in smooth pursuit initiation and do not answer the question whether pursuit and saccades exhibit the same coupling of selection for perception and selection for eye movements (Deubel & Schneider, 1996). This question is of particular interest to understand how attention contributes to the necessary coordination of saccadic and pursuit target choice. Single pursuit target conditions can reveal whether allocation of attention to the pursuit target is mandatory, quite similar to classic studies requiring saccades to non-attended locations. Therefore, we assessed the dynamics and strength of the coupling between spatial attention and

smooth pursuit in a series of three experiments. To shift the focus of attention from the pursuit target location, we used a dual-task paradigm in which spatial attention was summoned at a distant (7°) location, orthogonal to the direction of pursuit target motion. The onset asynchrony between the cue (a location or symbolic cue, also referred to as an *exo-* or *endogenous* cue, respectively) and the pursuit target motion (SOA) was varied from 0 to 500 ms (50 to 550 ms in the third experiment). Similar manipulations have shown that shifting attention in a direction opposite to the saccade goal caused saccadic latency to be delayed by some 20–50 ms (Crawford & Muller, 1992; Reuter-Lorenz & Fendrich, 1992; Shepherd et al., 1986; Shepherd & Müller, 1989).

When summoned by a cue flashed in the periphery, attention takes some 150 ms to be maximally allocated at the cued location, and about 300 ms to return to the fixated location, as indicated by perceptual performance (e.g., Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). The same displacements of attention take a little longer with endogenous cues. Therefore, spatial attention should be maximally diverted from the pursuit target with SOAs of 0–200 ms. In contrast, with an SOA of 500 ms attention should have time to return to the pursuit target location. As a control, we ran a single task condition in which observers were instructed to perform pursuit while ignoring the peripheral events. If attention was coupled to the location of the pursuit target at specific points in time, we should expect an interaction with task load (dual task vs. single task) and SOA, indicating that pursuit parameters (latency or/and speed) change as a function of SOA in the dual task condition, but not in the single task condition. While this approach does not tell us how spatially specific the coupling must be, it will tell us whether spatial attention at the target location is necessary for the initiation of the eye movement. Allocation of attention to the peripheral location was assessed by a perceptual discrimination task (e.g., Deubel & Schneider, 1996).

We contrasted a condition in which to-be-attended perceptual targets remained static with a condition in which they moved along with the pursuit target. The condition with static peripheral targets produced potentially conflicting retinal motion whereas the moving peripheral targets condition did not. Only the former condition required attentional filtering, but both conditions imposed similar dual task demands (pursuit + perceptual discrimination).

Method

Observers

There were 8 participants (age: $M = 23.4$, $SD = 2.7$) in the first experiment: five experienced psychophysical

observers and three naïve observers. In **Experiment 2**, there were 7 participants (age: $M = 22.0$, $SD = 3.0$) and 6 were naïve. In **Experiment 3** there were 8 participants (age: $M = 22.0$, $SD = 2.8$), 7 were naïve, and 2 participated in one of the previous experiments. The first author participated in the three experiments. Naïve observers were undergraduate students from the University of Geneva. They were paid or received credit for an undergraduate class. All participants had normal or corrected-to-normal vision.

Apparatus

Eye movements were recorded with a head mounted EyeLink II eyetracker (EyeLink II, SR Research Ltd., Osgoode, Ontario, Canada). The signal was sampled at 250 Hz and eye position was estimated from pupil centroid and corneal reflection, but on many occasions, only the pupil centroid was used, with a small loss of spatial resolution. The CRT monitor had a refresh rate of 100 Hz and a resolution of 1280×1024 pixels. To display the stimuli, we used a custom C program with SDL (<http://www.libsdl.org/>).

Experiment 1: Ramp target, exogenous cue

In the first experiment, we contrasted conditions in which the to-be-attended discrimination stimuli presented in the periphery remained stationary and conditions in which the discrimination stimuli started to move at the same time and in the same direction as the pursuit target (see **Figure 1A**). The same manipulation was run during fixation to tease apart decrements in perceptual performance due to motion blur from those due to reorientation of attention to the pursuit target location. The comparison of static and moving peripheral targets further assessed how attention adjusts the weight given to the input of conflicting (relative motion) or synergistic peripheral motion (no relative motion) signals during pursuit initiation.

Stimuli

Stimuli were displayed on a uniform gray background (average luminance: 29 cd/m^2). The viewing distance was 46 cm and the visible screen area 29.7×37 deg. The time course of a given trial is schematized in **Figure 1A**. A red cross (0.4×0.4 deg) had to be fixated or pursued after a random period of fixation, ranging from 0.3 to 1.3 s, when it started to move at 7.2 deg/s . Placeholders 7° above or below fixation cross were present throughout the trial, that is during 2 s. To cue one of the two possible target locations, the placeholder was dimmed to 0 cd/m^2 for 50 ms. The cue indicated the correct position (valid cue) of the upcoming discrimination target (an “E” or its mirror

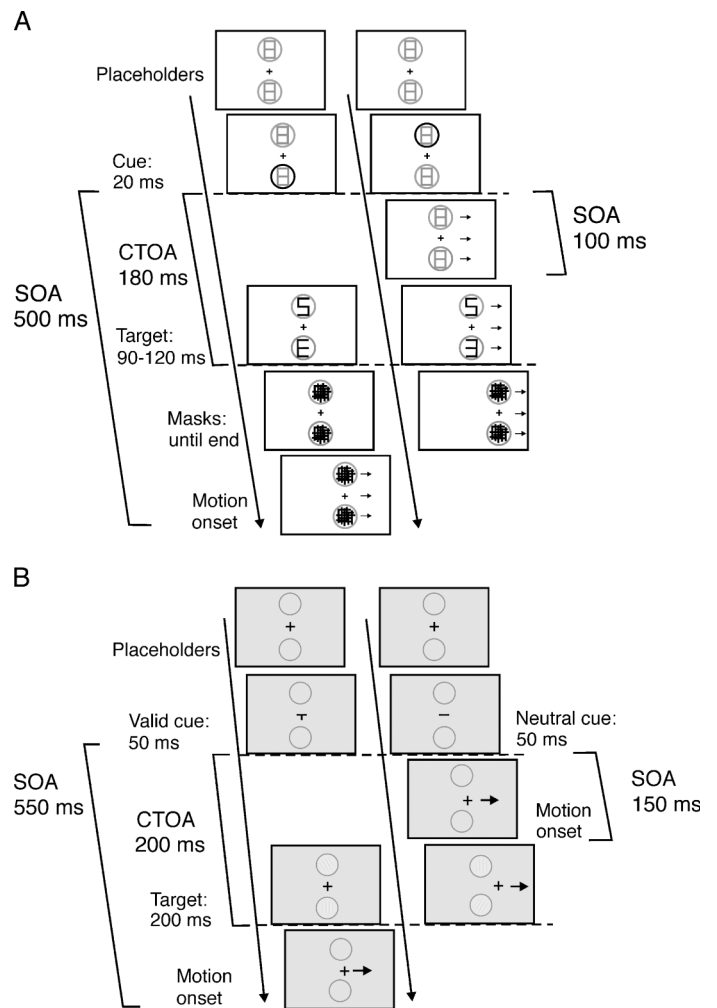


Figure 1. Panel A: Time course in **Experiments 1 and 2**. Placeholders appeared on the screen, and then a luminance increment cued the location of the subsequent discrimination target in 80% of trials (valid trials). The SOA between cue onset and motion onset was varied from 0 to 500 ms. The cue-target onset asynchrony (CTOA) was fixed at 180 ms. The left side of the graph shows a valid cue, and an SOA of 500 ms, with the consequence that the discrimination target is presented before pursuit target motion. Subjects had to discriminate the “E” from its mirror image. The duration of the presentation of the discrimination target was set to threshold. The right side shows an invalid trial, in which the cue indicates the distractor location, and an SOA of 100 ms, implying that the discrimination target was displayed 80 ms (CTOA-SOA) after motion onset. Panel B shows the time course of a trial in **Experiment 3**. The valid symbolic cue (i.e., endogenous cue) always indicated the position of the upcoming target. Disappearance of the upper or lower branch of fixation cross indicated that the target was located above or below, respectively. Peripheral discrimination targets remained static on the screen (relative motion condition).

image) in 80% of the trials. On invalid cue trials (20%), the location of the distractor (an “S” or its mirror image) was cued. In dual task conditions, observers had to report

whether an “E” or a mirror “E” had been displayed at the end of the trial, without any time pressure. The cue appeared 180 ms before the onset of the discrimination target and distractor (e.g., Cameron, Tai, & Carrasco, 2002; Cheal & Lyon, 1991). The asynchrony between the location cue onset and pursuit target onset (SOA) was varied from 0 to 500. An effective allocation of attention should improve discrimination performance of validly over invalidly cued trials.

Procedure

The calibration of eye position preceded each trial block and was achieved by fixation of a dot appearing in 9 pseudo-random locations. The within-subjects design for was: task load (dual or single) eye movement (fixation or smooth pursuit) \times cue (valid or invalid) \times relative motion (relative motion or no relative motion) \times SOA (500, 200, 100, 0 ms or catch) \times direction (left or right). There were 64 repetitions for valid and 16 for invalid cues by condition. In catch trials, neither target nor cue was present. No catch trials were presented during fixation. Each combination of task load, relative motion, and eye movement was blocked. The other factors were randomized within a block. There were four dual task and two single task sessions. Each session was made up of four blocks, each comprising 100 pursuit trials and 80 fixation trials. Block order was balanced across subjects according to a Latin square design. The six sessions were run on different days. A threshold procedure following the UDTR rule (Macmillan & Creelman, 1991) determined the presentation time of the discrimination target at the beginning of each session. The threshold value obtained was the presentation time that yielded 71% of correct discrimination responses (Experiment 1: $M = 94$ ms, $SD = 25$ ms; Experiment 2: $M = 82$ ms, $SD = 28$ ms). Participants triggered each trial by pressing a designated button on a gamepad. A drift correction was performed after the button press. Discrimination responses were made by left or right mouse clicks. At the end of each trial, acoustic feedback was given if the discrimination response was wrong. Visual feedback was displayed on the screen when blinks or saccades (amplitude $>1^\circ$) occurred. Participants were told to perform equally well the perceptual and the pursuit task in the dual task sessions, and that they had to maintain gaze on the red cross during the entire trial.

Experiment 2: Step-ramp target, exogenous cue

In the second experiment, a step-ramp paradigm was used. Step-ramp target motion allows for pursuit initiation without corrective saccades on a relatively large number of trials. We will therefore be able to test effects of

attention on pursuit gain. Further, we added intermediate SOAs (300 and 400 ms) to better trace the time course of attention shifts.

The method was the same as for the Experiment 1 except for the following modifications. The within-subjects design was task load (dual or single) \times relative motion (no relative motion or relative motion) \times cue (valid or invalid) \times SOA (500, 400, 300, 200, 100, 0 ms or catch) \times direction (left or right). There were 32 invalid and 128 valid cue trials per condition. The pursuit target followed a step-ramp trajectory (Rashbass, 1961). The step, i.e., the time it took the target to cross its initial position, was set to the approximate mean latency of pursuit initiation in Experiment 1, i.e., 120 ms. The peripheral stimuli could not follow a step-ramp trajectory without perceptual performance being strongly disrupted; therefore, the peripheral stimuli started to move when the pursuit target reached its initial position.

An additional feedback error message was displayed on the screen if the eye traveled less than 2° degrees during target motion. The purpose of this feedback was to provide a supplementary incentive to perform well on the two tasks at the same time.

Experiment 3: Step-ramp target, endogenous cue

Some concerns may be raised against our interpretations because we used a location (exogenous) cue. First, most of the studies that have tested the allocation of attention to the saccade goal used symbolic cues (e.g., Deubel & Schneider, 1996; Kowler et al., 1995). Second, in one study (Reuter-Lorenz & Fendrich, 1992), endogenous cuing was found to be more strongly coupled to eye movements than exogenous cuing (but see Kustov & Robinson, 1996). Third, one could argue that the small differences between dual and single task conditions for pursuit onset could be attributable to a purely exogenous orienting of attention in the single task condition. Attention may have been automatically summoned by the abrupt peripheral onset of the cue even when it was task irrelevant. Some studies support this idea by finding cuing effects on discrimination tasks with non-informative exogenous cues (e.g., Liu, Pestilli, & Carrasco, 2005). However, with our paradigm, the cue could probably be ignored in the single task condition by adjusting the size of the attention spotlight (see Eriksen & St James, 1986). Even onsets and singletons, thought to shorten RTs by capturing attention in some automatic manner, do not affect RTs when attention is focused on another location (Theeuwes, 1991). This may have been the case in the single task condition.

To address the latter concerns, we ran a similar experiment in which attention was summoned by a symbolic cue. This time, we presented low-contrast, unmasked Gabor patches and asked observers to report

the orientation of the tilted grating (following Liu et al., 2005). These stimuli were expected to reduce effects of the mere onset of the stimuli used in the perceptual discrimination task, as they are much less salient and unmasked. Furthermore, we added a control condition in which only the pursuit target was shown. Only the condition with relative motion was tested, as it was the condition in which attentional modulations of pursuit were largest.

Figure 1B shows the time course of a trial and the stimuli used. In valid cue trials, the upper or lower part of the fixation cross disappeared for 50 ms. The direction of disappearance of the branch always indicated the position of the upcoming discrimination target. The neutral cue was the disappearance of the upper and lower branches of the cross. The discrimination stimuli remained static on the screen (cf. relative motion condition of Experiments 1 and 2). We used five SOAs: 550, 350, 250, 150, 50 ms intermingled with catch trials, with neither cue nor discrimination target. Half of the trials containing a cue were valid and the other half neutral. In single task blocks, only neutral cues were presented. Because of the step-ramp dynamics of the pursuit target, there was no SOA of 0 ms. A pre-test showed that perception of the central cue was degraded if it was presented at the same time as the pursuit target step onset. The cue-target asynchrony was increased from 180 to 200 ms, as maximum cuing benefits are reached later with central than with peripheral cues (Cheal & Lyon, 1991). The threshold procedure estimated the orientation of the Gabor patches that yielded 71% of correct responses during fixation ($M = 3.2^\circ$, $SD = 0.8^\circ$). Sine-wave gratings of 2 and 4 cpd were randomly alternated to avoid visual adaptation. The standard deviation of the Gaussian was 0.9° , and the placeholders had a diameter of 1.7° .

There were 4 sessions comprising four blocks. The block order was balanced across subjects. The within-subjects design was task load (dual or single) \times SOA (550, 350, 250, 150, 50 ms or catch) \times cue validity (neutral or valid) \times direction (left or right). There were 40 trials for each condition. Single and dual task conditions were blocked. Additionally, a single task condition was run in a separate block (abbreviated single/no distractor), in which neither cue nor discrimination target was displayed.

Data analysis

Saccades were detected online by the Eyelink II parser with an acceleration threshold set at ± 9500 deg/s². Offline, a period of 12 ms (3 samples) before and after a saccade was removed from the eye traces before averaging. Traces contaminated by eye-blinks or with vertical saccades (amplitude $>1^\circ$) were excluded from analysis. With a ramp target, closed-loop smooth pursuit is systematically preceded by a catch-up saccade, but open-loop

pursuit did not always occur before the catch-up saccade. Thus, the first corrective saccade (henceforth CS1) latency was used as an exclusion criterion to ensure that the target was pursued. Then, only in the Experiment 1, we excluded trials in which no CS1 with amplitude greater than $1/3^\circ$ was detected from 100 to 400 ms after motion onset. Effects were tested by running repeated measures analysis of variance (rmANOVA). When running multiple post hoc comparisons, we applied the Benjamini–Hochberg correction (Benjamini & Hochberg, 1995); offering the advantage over Bonferroni’s correction of a higher statistical power with a large number of comparisons.

To determine the pursuit onset, two regression lines separated by 75 samples were moved by a sample increment along the filtered velocity trace from target onset until the CS1 onset; the first regression line was a baseline that encompassed 60 samples (240 ms) and the second one comprised 15 samples (60 ms). If the difference of the two slopes, that is acceleration, was above a threshold set to 20 deg/s² the intersection of the two regression lines was taken as an estimation of the pursuit onset. To avoid false detections, 80% of velocity samples of the second regression line had to be above/below baseline. False onsets were removed manually after visual inspection. Velocity traces were smoothed by the application of a second order Butterworth filter with a 60-Hz cutoff frequency. Pursuit onset latencies shorter than 52 ms or longer than 400 ms were excluded as anticipations and timed-out responses, respectively.

Results

Error analysis

Table 1 shows the proportion of trials removed from further analysis for Experiments 1–3. Overall, CS1 and pursuit latencies overlap to some extent such that CS1 can start before smooth pursuit. With pursuit of a ramp target

	Experiment 1	Experiment 2	Experiment 3
Blinks	0.80%	0.30%	0.60%
Vertical saccades	1.35%	0.30%	0.90%
Visual inspection	0.82%	1.10%	1.30%
Pursuit anticipations or timed-outs (<52 ms or >400 ms)	2.10%	0.60%	0.80%
CS1 anticipations or timed-outs (<100 or >500 ms)	18.9%	–	–
Pursuit online criterion	–	2.60%	2.60%

Table 1. Percentage of eliminated trials in the Experiments 1–3.

at 6–20 deg/s, Kimmig, Biscaldi, Mutter, Doerr, and Fischer (2002) reported 27% of movement initiation with a catch-up saccade. This is very close to the overall 33% without pre-saccadic pursuit found in the ramp experiment. In Experiments 2 and 3, the pursuit onset was not detected before a saccade in about 10% of the trials, far less frequent than in the ramp experiment.

Perceptual performance

Cuing effects, indexed by higher discrimination for valid than invalid/neutral trials, remained high at every SOA, with the exception of short SOAs when peripheral stimuli were moving on the screen.

Ramp, exogenous cue (Experiment 1)

Percent correct discrimination responses showed impaired performance for the shortest SOA when the discrimination target moved on the screen (during fixation or pursuit) but not when it remained stationary on the screen. A four-way rmANOVA (eye movement \times cue validity \times relative motion \times SOA) confirmed a significant interaction between eye movement, relative motion and cue validity, $F(3,21) = 5.56$, $p < .01$, and a marginally significant four-way interaction, $F(3,21) = 2.85$, $p < .06$. Importantly, valid cues produced 17% better discrimination performance than invalid cues (80 vs. 63%), $F(1,7) = 42.4$, $p < .001$, confirming that subjects allocated attention to the peripheral target.

Step-ramp, exogenous cue (Experiment 2)

A three-way rmANOVA (cue validity \times relative motion \times SOA) showed that performance was 23% better with valid than with invalid cues (82 vs. 59%), $F(1,6) = 42.25$, $p < .001$. Overall discrimination performance decreased somewhat with smaller SOAs, $F(5,6) = 3.49$, $p < .02$. However, there was no indication that the cuing effects (valid vs. invalid) were modulated by SOA, $F < 0.04$.

Step-ramp, endogenous cue (Experiment 3)

A two-way rmANOVA (cue validity \times SOA) confirmed 9.8% higher performance with a valid than with a neutral cue (79 vs. 70%), $F(1,7) = 21.61$, $p < .002$. Cue validity and SOA did not interact, $F(4,28) = .53$, $p = .74$.

Pursuit and catch-up saccade latency

If perceptual performance is maintained at a high level, as shown in the previous section, then some differences in latency should be found as a result of attention shifts away

from the target in the dual task condition. We expect the effect of task to interact with SOA, as attention has time to return to the pursuit target with long SOAs.

Ramp, exogenous cue (Experiment 1)

Figure 2 graphs the mean latency (of median individual latencies) of CS1 (A–B) and of pursuit (C–D), as a function of relative motion and SOA. Trials with valid and invalid cues were pooled in this and subsequent analysis. As described above, with a step-ramp target, smooth pursuit starts often after a catch-up saccade. Even when pre-saccadic smooth pursuit is detected, the first corrective saccade usually marks the beginning of the closed-loop phase of smooth pursuit with a ramp target trajectory. Pursuit latency and the first CS1 latency were analyzed separately in a three-way, rmANOVA (task load \times relative motion \times SOA).

Inspection of Figures 2C–2D show that latency of smooth pursuit in the dual task condition increased compared to the single task with SOAs of 100–200 ms. This increase was smaller for the remaining SOAs. With SOAs of 100–200 ms, latencies increased by 16–19 ms with relative motion and by 10–13 ms without relative motion. However, the interaction of SOA and task load was only marginally significant, $F(4,28) = 2.43$, $p = .07$. Overall, latencies were longer in the dual than in the single task condition (123 vs. 114 ms), $F(1,7) = 6.33$, $p < .04$, and they were longer by 14 ms with than without

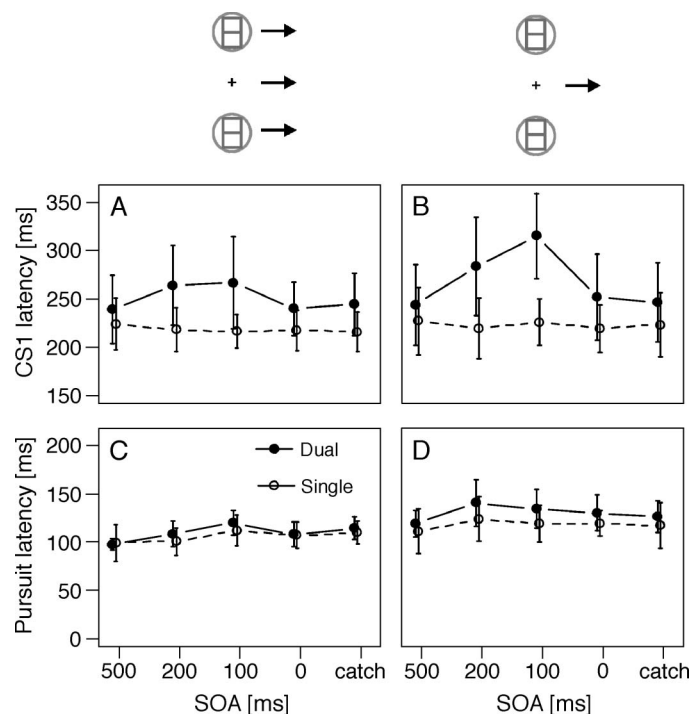


Figure 2. Latency of the first catch-up saccade (CS1, A–B) and pursuit onset (C–D) in Experiment 1, as a function of relative motion, task load and SOA. Error bars represent inter-subject SD.

relative motion (112 vs. 125 ms), $F(1,7) = 39.84$, $p < .001$. There also was a main effect of SOA $F(4,28) = 12.89$, $p < .001$. With SOAs of 100 and 200 ms, latencies were longer than with the SOA of 500 ms and catch trials (121 and 126 ms vs. 110 and 112 ms, respectively; corrected $ps < .05$). Effects of SOA were modulated by relative motion, $F(4,28) = 4.17$, $p < .01$, probably due to a slowing at short SOAs with relative motion that was not present without relative motion.

For the latency of CS1 (Figures 2A and 2B), an interaction between task load and SOA was confirmed, $F(4,28) = 13.42$, $p < .001$, indicating a pronounced increase in latency for SOAs of 200 (+56 ms) and 100 ms (+64 ms) in the dual compared to the single task condition. This increase was somewhat less pronounced for the SOA of 0 ms (+27 ms), $ts(7) = 4$, corrected $ps < .02$. A main effect of SOA showed that latencies were longer for SOAs of 100 and 200 ms, $F(4,28) = 10.29$, $p < .001$. Further, latencies were 37 ms longer in the dual than in the single task condition (248 vs. 211), $F(1,7) = 12.90$, $p < .01$, and 8 ms longer with than without relative motion (233 vs. 225 ms), $F(1,7) = 8.03$, $p < .05$.

Step-ramp, exogenous cue (Experiment 2)

Figure 3 graphs pursuit and CS1 latency as a function of relative motion and SOA. Pursuit latencies were 21 ms longer with than without relative motion (144 and 123 ms), $F(1,6) = 178.47$, $p < .001$. Effects of relative motion were

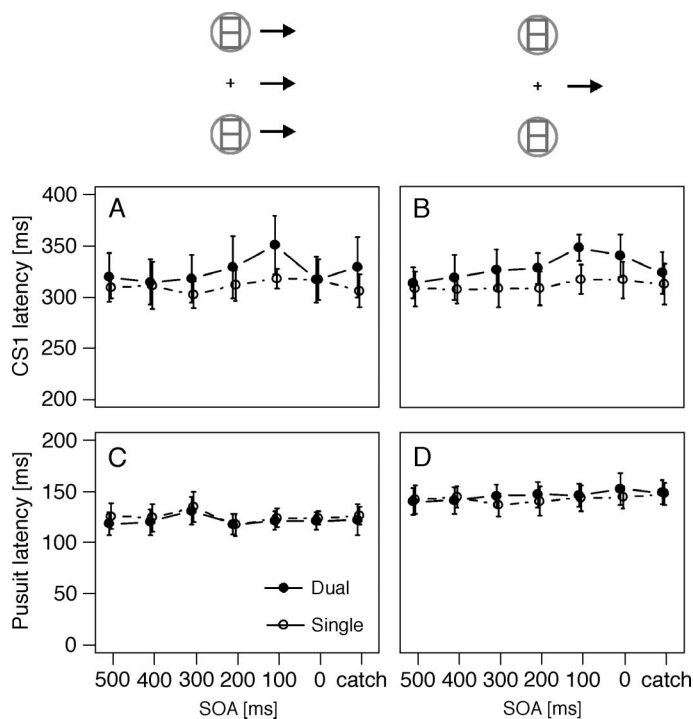


Figure 3. Latency of the first catch-up saccade (CS1, A–B) and pursuit (C–D) in Experiment 2, as a function of relative motion, task load and SOA. Error bars represent inter-subject SD.

modulated by task load, $F(1,6) = 8.54$, $p < .05$. In the dual task condition, the effect of relative motion was 6 ms larger (146 vs. 122 ms) than in the single task condition (143 vs. 125 ms). There was a main effect of SOA, $F(6,6) = 2.65$, $p < .05$, modulated by relative motion, $F(6,36) = 7.13$, $p < .001$. This is probably due to the increase of pursuit latencies with the SOA of 300 ms without relative motion. Post hoc comparisons showed significantly longer latencies for the SOA of 300 ms compared to the SOA of 200 ms (difference of 15 ms), $t(7) = 6.95$, $p < .001$. There was no interaction between SOA and task load, $F(6,6) = 1.46$, $p = .22$, nor a main effect of task load, $F(1,6) = 0.01$, $p = .92$.

Similar to Experiment 1, pursuit latencies were overall little delayed in the dual compared to the single task condition. However, the dual task condition accentuated the detrimental effect of relative motion, indicating that attention to static peripheral stimuli delays smooth pursuit. This difference was not modulated by SOA, suggesting that task-relevance rather than the timing of the attention shift was important.

As shown in Figures 3A and 3B, effects of attention shifts (dual task compared to single task) on saccadic latency were smaller than in Experiment 1. As a consequence of the step-ramp paradigm, catch-up saccades were triggered some 50 ms later than in the first experiment. A trivial explanation is that critical eye crossing time (see below) for saccade execution was not reached right after target onset as often as with a ramp target motion. Therefore, effects of attention are expected to be smaller. A three-way rmANOVA (task load \times relative motion \times SOA) showed longer latencies in the dual than in the single task condition (324 vs. 308 ms), $F(1,5) = 8.72$, $p < .05$. The effect of task load was modulated by SOA, $F(6,30) = 4.26$, $p < .01$. Post hoc comparisons confirmed that latencies in the dual task were 31 ms longer than in the single task condition with the SOA of 100 ms (345 vs. 314 ms), $t(6) = 4.8$, corrected $p < .02$, and 16 ms with the SOA of 0 ms (328 vs. 312 ms), $t(6) = 4.7$, corrected $p < .02$. Additionally, there was a main effect of SOA, $F(6,30) = 5.10$, $p < .001$, indicating that latencies were longer with SOAs of 300 to 0 ms than with SOAs of 500 to 400 ms.

Step-ramp, endogenous cues (Experiment 3)

Pursuit and CS1 latency are graphed in Figure 4. In the previous experiments, we averaged across valid and invalid cues when we analyzed the eye movement data. The reason was that both valid and invalid cues imply shifts of attention to the peripheral location with the only difference that the target is either presented at the expected or unexpected location. With neutral cues, the situation is less clear. Attention may either stay focused on the pursuit target, or it may be equally spread between possible target locations. The latter interpretation was favored by previous research (de Gonzaga Gawryszewski,

Riggio, Rizzolatti, & Umiltá, 1987). To evaluate effects of cue type (neutral or valid), we first ran separate rmANOVAs (cue validity \times SOA) on pursuit and then on CS1 latencies in the dual task conditions. This analysis could not be run for the single task conditions as only the neutral cue was presented in these trials. Figures 4A and 4C show that latency, of pursuit and CS1, overlaps in valid and neutral cue trials. The main effect of cue validity (valid vs. neutral) was not significant for pursuit and CS1 latencies. Therefore, data were collapsed across valid and neutral trials. A two-way rmANOVA (task load \times SOA) was run separately on pursuit and CS1 latency without single/no distractor trials to increase statistical power. The latency of pursuit onset in dual task conditions was 5 ms longer than in the single task condition (134 vs. 129), $F(1,7) = 11.96$, $p < .02$. Furthermore, there was a significant interaction between task load and SOA, $F(5,35) = 2.59$, $p < .05$. Post hoc comparisons showed a significant 11 ms difference between dual and single task for the SOA of 350 ms, $t(7) = 3.9$, corrected $p < .05$. A main effect of SOA was found, $F(5,35) = 3.28$, $p < .02$, indicating that latency increased with the SOA of 350–250 ms (133–132 vs. 126–130).

Again, CS1 latency was more strongly affected by task load. Latencies were 30 ms longer in the dual than in the single tasks (315 vs. 285 ms), $F(1,7) = 32.97$, $p < .001$. However, interaction between SOA and task load was only marginally significant, $F(5,35) = 2.18$, $p = .08$.

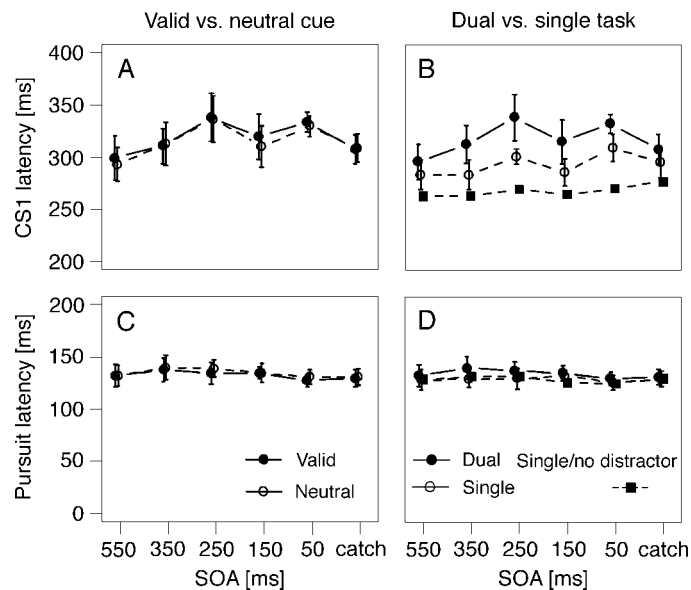


Figure 4. Pursuit and saccadic (CS1) latency in Experiment 3. The left panels (A, C) show latencies in valid compared to neutral endogenous cue trials. The right panels (B, D) show pursuit latencies in dual compared to single task trials. Additionally, data from the condition without peripheral stimuli are shown (single/no distractor). In all conditions, the discrimination target always remained static on the screen (cf. relative motion conditions of the Experiments 1 and 2). Error bars represent inter-subject SD.

Latencies were modulated by SOA, $F(5,35) = 4.02$, $p < .01$, indicating longer latencies for the SOA of 250 and 50 ms compared to the other SOAs, corrected $ps < .01$.

The lack of a significant interaction between SOA and task load can be explained by the fact that even the largest SOA of 550 ms was modulated by task load. Similarly, some effects on closed-loop pursuit velocity were also found at this SOA (velocity analysis below). With the use of endogenous cues, facilitation takes usually longer to develop but also lasts longer (e.g., Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). It may be that an SOA of 550 ms was too short to allow for attention to fully return to the pursuit target, thus explaining the only near-significant interaction of task load and SOA on CS1 latency.

Effect size of the task load \times SOA interaction

The effect-size (η_p^2) of the interaction between SOA and task load for pursuit latency was similar across experiments: 0.25, 0.20, and 0.27 in Experiments 1–3, respectively. This interaction was only significant for the third experiment, presumably as a result of a greater statistical power. For CS1 latency, the effect-size was 0.67, 0.46, and 0.24 in Experiments 1–3. The smaller effect in Experiments 2 and 3 could be accounted for by saccades with much longer latency in the single task condition as a consequence of the step-ramp and the use of endogenous cues (Experiment 3).

ECT analysis

Next, we verified that low-level factors, such as position error and retinal slip resulting from pre-saccadic velocity, did not contribute to the observed increase in saccadic latencies in the dual task conditions. According to the de Brouwer, Yuksel, Blohm, Missal, and Lefèvre (2002) model, the execution of catch-up saccades is mainly predicted by the *eye crossing time* (ECT). Defined as the time it would take the eye to cross the target's path with its actual velocity, ECT is determined by retinal velocity (or retinal slip, RS) and distance between the target from the fovea (or position error, PE): $ECT = PE/RS$ (de Brouwer et al., 2002). Negative values denote that the fovea is lagging behind the target. ECT measures were based on eye velocity and position 124 ms before CS1. In Experiment 1, a three-way rmANOVA (task load \times relative motion \times SOA) was run on ECT values. With relative motion, saccades were triggered at more negative ECTs than without (-122 vs. -111 ms), $F(1,7) = 6.50$, $p < .05$. There were more negative ECTs in the dual task than in the single task condition (-135 vs. -98 ms), $F(1,7) = 14.00$, $p < .001$. The interaction between SOA and relative motion, $F(4,28) = 5.89$, $p < .001$, indicated that the effect of relative motion was maximal at an SOA of 100 ms (with vs. without relative motion: -150 vs. -115 ms), $t(7) = 4.21$, corrected $p < .02$. The expected interaction

between SOA and task load was also confirmed, $F(4,28) = 5.88$, $p < .001$. Post hoc comparisons showed more negative ECTs in the dual than in the single task conditions for the SOA of 200 and 100 ms (difference of 63 and 52 ms, $t(7) = 3.44$ and $t(7) = 3.79$, respectively, corrected $ps < .05$). In sum, the analysis of ECT shows that the different latencies of catch-up saccades are matched by differences of the ECT distributions. The same analysis was run on [Experiments 2](#) and [3](#) and confirmed independence of pre-saccadic ECT values and the delay observed in the dual task.

Analysis of trade-offs

Perceptual performance and eye movement latency suggest that pursuit can be initiated with little selective attention at the pursuit target location. We further asked whether a tradeoff could unveil some incompatibility of the two tasks. Sperling and Melchner (1978) proposed a method to test the strategy used by participants to trade attentional resources between two simultaneously monitored tasks (see also Khurana & Kowler, 1987). They contrasted “shared” or “switch” strategies of attention allocation. Their argument states that if attention is shared between tasks A and B, performance on tasks A and B should decrease by the same amount compared to the single task condition, but A and B may still be independent. On the other hand, if attention is switched between tasks from trial to trial, then performance on the two tasks is expected to depend on each other: good performance on task A should lead to bad performance on task B and vice versa. A chi-test on the contingency table of successes and misses on the two tasks tests this dependence (see [Figure 5A](#)). As a measure of success in the oculomotor task, we used latencies of smooth pursuit and of the first catch-up saccade and divided them into fast or slow by a median split. Only the validly cued trials were considered, as the opposite relation between pursuit and perception may hold in invalidly cued trials. When the cue is invalid, it may be better for discrimination performance to keep attention on the pursuit target rather than shifting attention to the more distant downward or upward locations. Chi-tests on individual contingency tables or across subjects ([Figure 5B](#)) never indicated a significant negative relation between oculomotor and perceptual performance as measured by pursuit or CS1 latency in [Experiment 1](#), supporting the use of a “shared” resources strategy (Sperling & Melchner, 1978). Analysis of [Experiments 2](#) and [3](#) yielded similar results (data not shown).

Velocity traces

Because the manipulations modified CS1 latency, only average velocity traces of pursuit initiation of trials in which no catch-up saccade was executed are shown. This

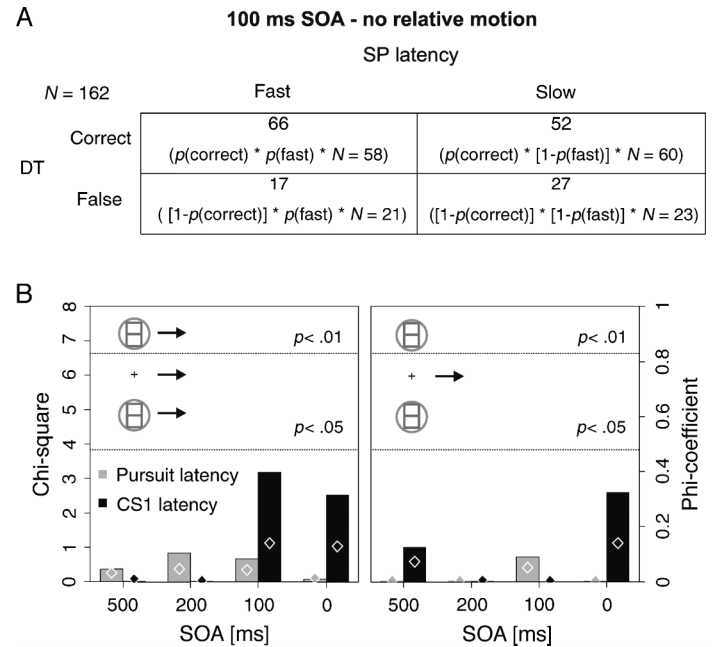


Figure 5. Analysis of trade-offs in [Experiment 1](#). Panel A: Example of a contingency table used to test the compatibility of the oculomotor and discrimination task. The expected number of observations, under the hypothesis of independence, is displayed in parentheses. Panel B: The small values of the chi-square and phi-coefficient (i.e., a measure of effect-size) support a shared resources strategy and not a switch between two different incompatible states. The bars represent the chi-square (left axis), and the diamonds represent the phi-coefficient (right axis). Horizontal lines indicate the p -values for the chi-square statistic. Data was pooled across subjects.

was only possible in [Experiments 2](#) and [3](#). Modulation of horizontal eye velocity during initiation is shown in [Figures 6](#) ([Experiment 2](#)) and [7](#) ([Experiment 3](#)). With moving peripheral stimuli, the pursuit target and the attended discrimination target moved in the same direction ([Experiment 2](#) only, see [Figure 6A](#)). Therefore, any modulation of eye velocity by shifting attention to the periphery resulted from spreading attention across a larger region of space. It cannot be due to conflicting motion signals. Smooth pursuit gain was relatively unimpaired by attention shifts in this condition, suggesting that a small focus of attention around the pursuit target is not necessary for successful pursuit initiation. While attention shifts without relative motion had little effect on pursuit velocity (a maximum of about 5%), eye velocity was strongly modulated about closed-loop initiation with relative motion (about 40%, see [Figure 6B](#)). [Experiment 3](#) (with more observers) confirmed the same pattern, as seen in [Figure 7](#). As with pursuit latency results, velocity traces were very similar for valid and neutral cue trials (see [Figure 7A](#)) and were therefore pooled.

For testing differences between dual and single task, horizontal velocity traces were divided into 40-ms bins

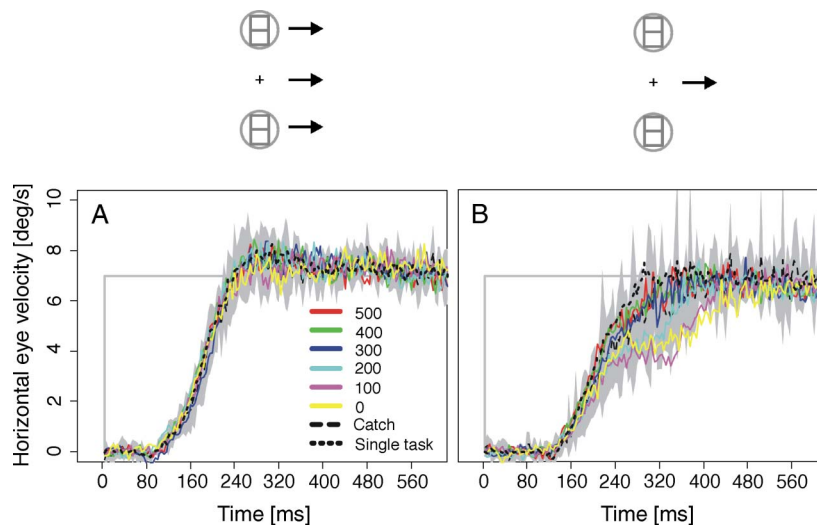


Figure 6. Average horizontal velocity in Experiment 2 ($N = 7$) of trials in which pursuit was initiated without a catch-up saccade for no relative motion (A) and relative motion conditions (B). Gray lines represent pursuit target speed. Dotted lines represent single task performance averaged across SOAs. The gray area represents the inter-subject SD of catch trials.

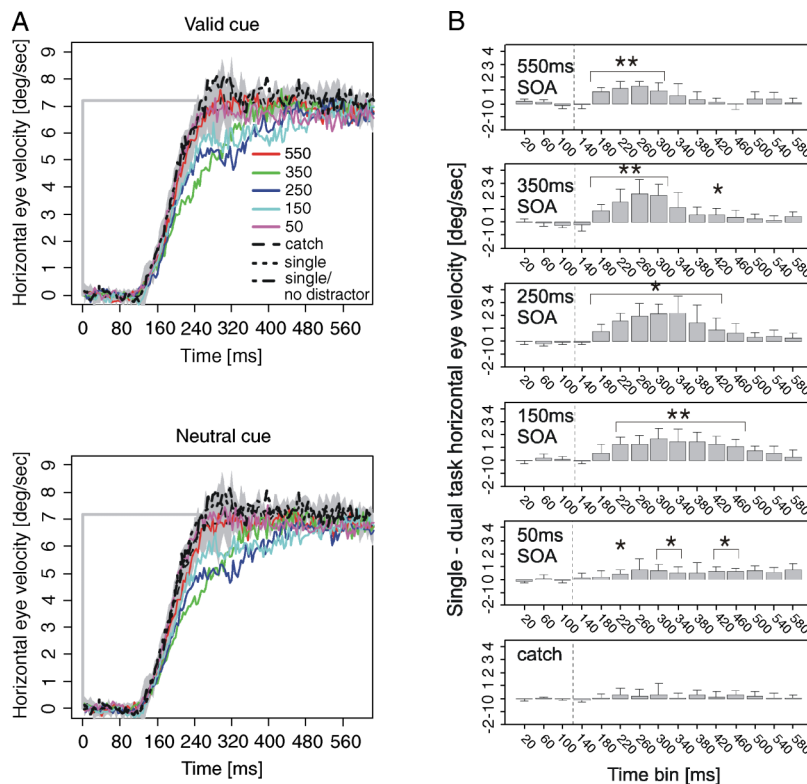


Figure 7. Panel A shows average horizontal velocity in Experiment 3 ($N = 9$) of trials in which pursuit was initiated without a catch-up saccade. Peripheral stimuli were static (relative motion condition). Gray areas represent the inter-subject SD in catch trials. Single task trials are averaged across SOAs. Data from valid and neutral trials are shown in the upper and lower panels. Panel B: Decreased horizontal velocity in dual compared to single task as a function of SOA. On the x-axis, the center values of 40 ms time bins are displayed. Vertical, dashed lines indicate pursuit onset (around 120 ms). When contiguous time bins were significant, the least significant p -value is reported above the respective bracket. The Benjamini–Hochberg correction was applied to the p -values. Note: *** $p < .001$; ** $p < .01$; * $p < .05$.

within a 0- to 600-ms time range (see [Figure 7B](#)). Significant differences were found no earlier than the 160- to 200-ms time bin and lasted until the 400- to 440-ms time bin for the SOA of 150–350 ms, with a shorter time range for the SOA of 550 ms. Maximal differences were found with the SOA of 250 ms and 350 ms. Effects of comparable size and timing were confirmed in the condition with relative motion of [Experiment 2](#).

Discussion

Because spatial attention at the saccade goal is needed for saccade initiation, it cannot be shifted away from the target location without compromising eye movement latency or accuracy (Deubel & Schneider, 1996; Kowler et al., 1995; Posner, 1980). Reductions of pursuit latencies by cues (e.g., Adler et al., 2002; Krauzlis, Zivotofsky, & Miles, 1999) and salient targets (Hashimoto, Suehiro, & Kawano, 2004; Hashimoto, Suehiro, Kodaka, Miura, & Kawano, 2003) suggest a similar involvement of attention in the initiation of pursuit.

Our study assessed the costs associated with shifts of attention away from the pursuit target location and asked whether attention is strictly necessary for pursuit initiation. Attention shifts made to the periphery were indexed by discrimination performance in valid and invalid/neutral cue trials. Cueing effects on discrimination performance were not different from those obtained in a control condition during fixation. The only exception was for the shortest SOAs with physical motion of the peripheral targets, but the observed difference may be entirely due to motion smear. The substantial shifts of attention induced by our cueing procedure had (i) no reliable effect on pursuit latency when the peripheral discrimination targets moved along with the pursuit target (i.e., without relative motion condition). (ii) Small but significant effects on pursuit latency were found only when attention was shifted by means of an endogenous cue to static a target ([Experiment 3](#)). However, lack of statistical power, rather than cue type *per se*, was likely to account for the difference. Effects of similar size were observed in [Experiments 1](#) and [2](#) but failed to reach significance.

We found no evidence for trade-offs between pursuit and perception. Tradeoffs are considered a hallmark of incompatible tasks (Sperling & Melchner, 1978). There was little interference between attention shifts and smooth pursuit latency on a trial-by-trial basis. If a strong coupling existed, pursuit latency should have been traded for perceptual accuracy. Similarly, no significant trial-by-trial trade-off was found for CS1 latencies.

Compared to the initial pursuit response, much larger differences between conditions without and with relative motion were obtained for post-onset pursuit velocity. Without relative motion (iii): moderate effects on pursuit

gain were observed near the onset of steady-state pursuit phase with a ramp target. These effects were even smaller with a step-ramp target presumably because retinal motion was further reduced (~5% difference between single and dual task conditions). With relative motion (iv), attention shifts at the time of pursuit onset strongly reduced (~40%) pursuit velocity in the late open-loop (some 100 ms after movement onset), or near closed-loop pursuit phase, until ~400 ms after movement onset. (iv) Catch-up saccades were strongly delayed (up to 60 ms) in the dual task condition when attention was shifted to stationary objects in the periphery. Thus, catch-up saccades are similar to voluntary saccades in that both are delayed when attention is shifted away from the oculomotor target.

To sum up, the results show that pursuit onset does not depend strongly on the prior allocation of attention on the pursuit target. Some costs on latency are incurred when the attended object competes with the relevant motion signal. Significant attention-dependent latency increases on the order of 10 ms were observed in one experiment. Thus, our results support the notion of a loose coupling of selective spatial attention and pursuit initiation. On the other hand, initial corrective saccades were as much delayed in both competing (relative motion) and synergistic (no relative motion) conditions. The delay was of comparable magnitude as in studies that tested effects of shifts of attention in opposite direction to the saccade goal (Crawford & Muller, 1992; Reuter-Lorenz & Fendrich, 1992; Shepherd et al., 1986; Shepherd & Müller, 1989).

Further, we observed that effects of neutral and valid cue trials are very similar on pursuit latency and velocity, even though it is clear from the discrimination performance that only valid cues resulted in allocation of attention to a specific location. Some studies indicate that with endogenous shifts of attention, cueing effects are more compatible with a “zoom lens” metaphor of attention (as proposed by Eriksen & St James, 1986), with attention initially spread out and then focused on the cued location; whereas exogenous cueing may be more compatible with a “spotlight” metaphor (as proposed by Posner, Snyder, & Davidson, 1980), with attention focused over a zone of constant size moving in space (Shepherd & Müller, 1989). Accordingly, it has been shown that with an incentive to keep attention focused on the fixation point, RTs to peripheral stimuli are longer than in the neutral cue condition, suggesting that the distribution of attention is diffuse in the neutral condition (de Gonzaga Gawryszewski et al., 1987) and not, as often supposed, focused on the fixation cross. Thus, performance in neutral trials may reflect the same mechanisms of endogenous attention as performance in valid trials. In the neutral condition, both peripheral targets received some attention as a result of a broad attentional window. Consequently, less attention was devoted to the pursuit target. Spreading attentional resources over space is probably the best strategy as the discrimination target can appear in two different locations with equal probability.

Finally, the presence of static peripheral objects lengthened pursuit latency by some 20 ms. This effect was poorly modulated by the timing of attention shifts but rather by task-relevance of the peripheral targets. A large reduction of acceleration, of steady-state velocity, and less often a delay in latency is documented in studies in which the pursuit target moves over a stationary structured background (Mohrmann & Thier, 1995; Spering & Gegenfurtner, 2007; but see Keller & Khan, 1986; Kimmig, Miles, & Schwarz, 1992; Masson, Proteau, & Mestre, 1995).

According to some estimations (Lisberger & Westbrook, 1985; Tychsen & Lisberger, 1986), the first 100 ms after pursuit onset can be considered as an open-loop phase. In our experiments, the earliest significant attention-dependent effects were found within the 160- to 200-ms time window (i.e., some 40–80 ms after pursuit onset) and maximal changes of velocities were reached in bins centered on 200 to 320 ms (i.e., some 80 to 200 ms after pursuit onset).

As proposed by Ferrera and Lisberger (1995), the role of attention in target selection for pursuit initiation may be to bias the strength of one over many competing motion signals. With monkeys, latencies were much longer in the presence of a distractor moving in the opposite direction than with a single target. However, the average velocity traces were about the same before and during loop closure (Ferrera & Lisberger, 1995), suggesting a winner-take-all response. Subsequent results suggested that a vector-average is generally the first response but that under the latter circumstances winner-take-all response can be achieved via a delay in latency (Lisberger & Ferrera, 1997). Our manipulations show that pursuit velocity can be modified by giving different weights to the signals of the to-be-attended target and the pursuit target. Our results are not incompatible with Ferrera et al.'s interpretation; they rather add that shifts of attention can modulate the late open-loop or beginning of closed-loop phase of smooth pursuit when there is a competition between the to-be-pursued and to-be-attended motion signals (i.e., between signals prompting fixation and pursuit). We can suppose that the delay found in their first study is due to the time it takes to select the appropriate target among incompatible bottom-up signals.

Our results lend support to the recent “two-stage” model of coordination of smooth pursuit and saccades proposed by Erkelens (2006). The model claims that preparation for saccades and pursuit by engagement of attention to the new target goal is synchronous. In conditions of temporal overlap between the old and new target, latencies of pursuit and saccades are indeed synchronized and highly correlated ($R^2 = 0.91$; Erkelens, 2006). In classic conditions of comparison (i.e., no temporal overlap between pursuit old and new target), pursuit and saccades latencies are not correlated (Erkelens, 2006; Merrison & Carpenter, 1994). The difference between the two systems could then be that pursuit can be “prematurely” disengaged at the oculomotor level when the old target

disappears at the time the new target appears (Erkelens, 2006). But in conditions of temporal overlap, the new target's speed and direction is only selected by the eye at the time when a saccade can be executed. Erkelens further speculated that attentional engagement to the new target is concomitant with movement programming, and that the outcome of this process is allowed to reach the execution level at the same time for pursuit and saccades. This point was suggested by directional changes occurring almost exclusively after saccades in overlap conditions (see also Gardner & Lisberger, 2001, 2002). This interpretation is not too far from our conclusion that attention for pursuit and saccades follow a similar time course, with smooth pursuit starting in some cases without attention being focused on the target, as a result of shorter pursuit latency.

Shared gating and target selection for pursuit and saccades

The role of the rostral superior colliculus (SC) in the gating of pursuit, in addition to its well-established role in release from fixation for saccades, has been recently pinpointed (for a review, Krauzlis, 2004). There is also evidence for shared target selection from studies showing that subthreshold micro-stimulation of SC can manipulate the target choice for saccades and pursuit (Carello & Krauzlis, 2004). Moreover, omnipause neurons which are classically implied in the gating of the impulse burst that trigger saccades (Munoz & Wurtz, 1993a, 1993b) also strongly modulate steady-state pursuit (Missal & Keller, 2002), presumably via excitatory connections with the SC (Gandhi & Keller, 1999). This circuitry leads to the idea that the fixation system that gates saccades can also gate pursuit. Shared gating also offers an explanation for similar latency reductions with the gap paradigm (Kimmig et al., 2002; Knox, 1998; Krauzlis & Miles, 1996a, 1996b, 1996c; Merrison & Carpenter, 1995). That is, smooth pursuit and saccadic latencies are reduced when the fixated stimulus disappears some time before target onset. Further, latencies of saccades and smooth pursuit are prolonged when a remote distractor appears at the same time as the target (Knox & Bekkour, 2004). Interestingly, Ogawa and Fujita (1998) pointed also to the common gating system as a factor contributing to post-saccadic pursuit enhancement: Insufficient inactivation of the fixation system may prevent a saccade but may suffice to release a weak pursuit response. Once the fixation system is fully inactivated, enhanced pursuit and saccades are released.

In a similar vein, Liston and Krauzlis (2003, 2005) proposed a model of shared selection that builds on race to threshold models of decision making (e.g., Carpenter & Williams, 1995). It supposes that initiation of pursuit and saccades share the same signals that accumulate across time but with a different threshold for triggering the movement, leading to different latencies.

Concerning the joint programming of eye movements and attention shifts, recent studies show that microstimulation of either FEF or SC neurons below saccade execution threshold can nonetheless cause an attention shift (Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Müller et al., 2005). We speculate that the strength of the attention shift will depend on the strength of the eye movement signal. As some authors have argued that the necessary signal strength to trigger pursuit is smaller than for saccades (Krauzlis & Dill, 2002), the attention shift preceding smooth pursuit will also be weaker. The present results confirm the flip side of this mechanism: pursuit is far less affected by attention shifts away from the eye movement goal than saccades.

Conclusion

Our study shows that pursuit may be started at little cost when attention is diverted from the pursuit target, unlike the first catch-up saccade. A strong coupling may not emerge until the first steps of steady-state pursuit. We demonstrated that attention to a conflicting motion signal may compromise smooth pursuit in the late open-loop or early closed-loop phase. Some features of the pursuit system are consistent with our results: its susceptibility to bottom-up influences and enhanced gain after the first catch-up saccade. Further studies would be needed to clarify if a time-locked coupling is shared by pursuit and saccades, by evaluating its strength for responses with similar latency.

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