Attentional constraints on target selection for smooth pursuit eye movements

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ABSTRACT

Saccadic eye movements are strongly influenced by shifts of attention to non-target objects. In contrast, we have shown previously that the initiation of smooth pursuit eye movements is relatively unaffected when attention is shifted to objects that are either stationary or move in the same direction as the pursuit target (Souto & Kerzel, 2008). Here, we asked how attention interacts with target selection when a choice has to be made between objects moving in opposite directions. In a dual-task paradigm, observers had to pursue a designated object while making a perceptual judgment on an object moving in the opposite direction. The perceptual target was briefly presented after motion onset and disappeared before the eye started to move. The priority assigned to the perceptual and pursuit task was varied. When priority of the perceptual task was equal or greater than priority of the pursuit task, observers frequently pursued the wrong target and pursuit was delayed. We conclude that when an oculomotor choice is to be made between two equally salient motion signals, the successful initiation of pursuit eye movements depends on the presence of an attentional bias towards the target location.

1. Introduction

Voluntary control over oculomotor programs allows for the selection of a target object in the presence of distracting information. An important question is whether different target objects may be selected for eye movement programming and perception. Here, we asked observers to perform smooth pursuit and a perceptual task concurrently in order to test if both rely on common attentional resources. Voluntary allocation of attention results in enhanced perceptual performance at the attended location (Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). During saccade programming, allocation of attention is constrained to the saccade target (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel & Schneider, 1996; Montagnini & Castet, 2007), enhancing perception at the target location and degrading perception at non-target locations. The necessary alignment of the "mind's eye" with the eye movement goal is often believed to support the "pre-motor theory of attention" put forth by Rizzolatti and colleagues (Rizzolatti, Riggio, & Sheliga, 1994), assuming that a common system is in charge of overt and covert orienting towards a peripheral location. While the validity of the first assertion is well supported by many different sources of evidence (fMRI: e.g. Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; microstimulation: e.g. Awh, Armstrong, &

Moore, 2006; Cavanaugh, Alvarez, & Wurtz, 2006; Moore & Fallah, 2004; psychophysics: e.g. Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Lovejoy & Krauzlis, 2010; Shepherd, Findlay, & Hockey, 1986) most of it concerns saccadic eye movements. Pursuit eye movements are also voluntarily initiated, although they require either the presence of a visual motion signal or of a predictive signal generated after various presentations of target motion (e.g. Barnes, 2008). Pursuit and saccadic eye movements depend on partially different brain structures and thus the study of pursuit initiation allows us to delve deeper into testing the degree of overlap between spatial selection for perception and selection for an eye movement.

The coupling between saccadic programming and attention orienting is reflected in delayed saccades when attention is not allocated to the saccade target location. The attention operating characteristic (AOC) was originally developed to measure the trade-off in performance on two visual tasks performed at the same time, such as letter identification in the periphery and in the fovea (Kinchla, 1980; Sperling & Melchner, 1978) and was used in various contexts ever since (e.g. Bonnel & Prinzmetal, 1998; Mareschal, Morgan, & Solomon, 2010; Reddy, Wilken, & Koch, 2004). In an oculomotor AOC paradigm, the simultaneous execution of a perceptual and a saccade task is compared to performance in single-task conditions. If perception and eye movements relied on independent selection filters or on a common but capacity-unlimited filter, there should be no difference between performance in the dual and single-task conditions. Otherwise, performance on the eye movement task has to be traded for performance on the

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perceptual task. For instance, Kowler, Anderson, Dosher, and Blaser (1995) showed that the latency of a saccadic eye movement was traded for perceptual performance at a location opposite to the saccade target, providing clear evidence for shared attentional resources. In the present study, we estimated the AOC for perception and the initiation of smooth pursuit.

The execution of smooth pursuit eye movements is influenced by several cognitive processes, such as prediction of target trajectory and allocation of spatial attention (for a review Barnes, 2008). While a number of studies have investigated the efficacy of target selection during the initiation of pursuit (e.g., Ferrera & Lisberger, 1995; Ferrera & Lisberger, 1997; Garbutt & Lisberger, 2006; Spering, Gegenfurtner, & Kerzel, 2006), studies that have investigated whether pursuit target selection is achieved by shifting attention to the target concentrated on maintained pursuit (Kerzel, Born, & Souto, 2009; Kerzel, Souto, & Ziegler, 2008; Khurana & Kowler, 1987; Lovejoy, Fowler, & Krauzlis, 2009).

Pursuit initiation differs substantially from pursuit maintenance with respect to attentional requirements. Our previous studies have suggested that attention does not play a prominent role in the open-loop phase of pursuit initiation (i.e., the first 100 ms of the movement), which may be related to the finding that pursuit maintenance relies more heavily on high-level motion signals than pursuit initiation (Wilmer & Nakayama, 2007). We have shown that attention can be shifted into the periphery without delaying the initiation of smooth pursuit when the to-be-attended peripheral object moves with the pursuit target (Souto & Kerzel, 2008). In contrast, the latency of the first catch-up saccade during pursuit initiation is delayed when shifting attention away from the saccade target location, similarly to what happens with voluntary saccadic eye movements under analogue conditions (Kowler et al., 1995; Reuter-Lorenz and Fendrich, 1992; Shepherd et al., 1986). The small effects of diverting attention to the periphery on pursuit latency suggest that the coupling between perception and the initiation of smooth pursuit is much weaker than for saccades. In support of this view, several studies indicate that target selection during pursuit initiation is poor. When the pursuit target appears at the same time as an orthogonally moving distractor, pursuit is first initiated toward the vector-average direction and subsequently (often after a saccade) to the designated target in a winner-take-all manner (Ferrera & Lisberger, 1997; Lisberger & Ferrera, 1997). Also, studies that tested the ability to pursue a target in the presence of a distractor moving in the opposite direction showed a delay of some 15 ms in humans (Adler, Bala, & Krauzlis, 2002; Krauzlis, Zivotofsky, & Miles, 1999) and of at least some 30 ms in monkeys (Ferrera & Lisberger, 1995). One can interpret that this delay is the consequence of a mandatory averaging of motion signals, as it was postulated for short-latency averaging saccades (Ottes, Van Gisbergen, & Eggermont, 1985), or the consequence of imperfect attentional selection of the target.

As noted above, saccadic movements have been shown to be strongly influenced by distracting attention to non-target objects. In contrast, we have shown previously that pursuit initiation is relatively unaffected by drawing attention to the periphery (Souto & Kerzel, 2008): in a dual-task paradigm, subjects reported the identity of a precued letter presented in the periphery, and at the same time, initiated a pursuit eye movement when the foveal stimulus started to move. In one condition, the peripheral stimuli remained stationary in space. In another condition, it moved at the same speed and in the same direction as the pursuit target. Importantly, this design did not allow us to test whether attention was necessary to *select* the pursuit target, as there was only a single motion direction before the eye movement was initiated. The influence of top-down spatial attention on pursuit target selection can only be investigated when there is more than one motion direction to select from. To this purpose, we used a dual-task paradigm in which

subjects were explicitly asked to divide attention between a pursuit target moving in one direction and a perceptual target moving in the opposite direction. Under these conditions, we should be able to demonstrate whether and to what degree attention is implicated in target choice for pursuit initiation.

2. Methods

2.1. Subjects

Five observers participated in two experiments: two of the authors (DK and DS, marked S1 and S2, respectively) and three students that were naïve to the purpose of the experiments. The latter were paid 20 Swiss francs for each hour. All had normal or corrected to normal vision. Our protocol was approved by the Ethics Commission of the University of Geneva.

2.2. Materials

We used an infrared head-mounted eye-tracker (IRIS, Skalar, Delft, Netherlands) to record eye movements at a sampling rate of 500 Hz. Each sensor allows for the precise measurement of a single dimension. Consequently, we measured the vertical rotation of the right eye and the horizontal rotation of the left eye, exploiting the fact that we were interested in conjugate eye movements. Calibration was made every 1–3 blocks by fixation of three horizontally aligned locations followed by fixation of three vertically aligned locations. A bite bar was used to minimize head movements. Observers' eyes were at a distance of 46 cm from a CRT screen (75 Hz, 1280 × 1024 pixels), on which visual stimuli were displayed. To control the stimulus presentation we used custom C routines, with the SDL library (http://www.libsdl.org/) to generate the graphics.

2.3. Stimuli and procedure

Stimuli and trial time course are shown in Fig. 1. At the beginning of a trial, a black fixation square (0.3 × 0.3°) was displayed in
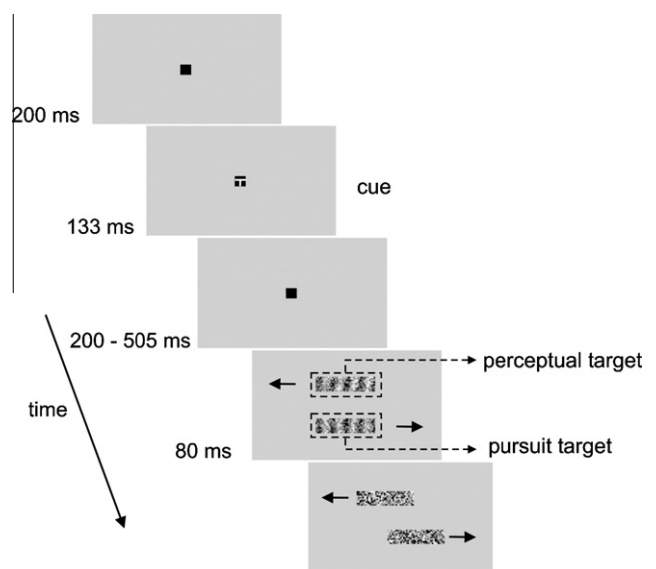
Fig. 1. Time-course of individual trials. The cue consisted of a vertical and horizontal line. In the depicted example, the position of the vertical line instructed observers to follow the stimulus below fixation. A grating tilted by 12° to the right is shown within the upper rectangle at motion onset. In dual-task conditions, observers had to indicate its orientation after motion offset. The stimuli are not drawn to scale.

the middle of the screen for 200 ms before a cue made up of a vertical and horizontal line appeared for 133 ms inside the square. The vertical line indicated the position of the object that was to be pursued. In most conditions, the target for the perceptual discrimination task was on the opposite side. After a random interval of 200–505 ms, two rectangles appeared above and below fixation and started to move horizontally in opposite directions for 1 s, at the velocity of 8.1 deg/s. For 80 ms, the target and the distractor rectangle contained a sine-wave grating embedded in luminance noise. The grating was tilted to the left or to the right in the target rectangle and was vertical in the distractor rectangle. After 80 ms, the sine-wave gratings were replaced by luminance noise of the same mean contrast. At the end of each trial a blank screen was displayed until an orientation response was given by pressing the left or right arrow key on the PC keyboard. The stimulus orientation selected by the participant was then briefly displayed on the screen and auditory feedback (a tone) was given after an error in the perceptual judgment.

The two rectangles of 2.9° width by 0.7° height were located 0.7° above and below the screen center (center-to-center). The stimuli were presented near the fovea as a way to minimize the tendency to execute vertical saccades in anticipation of stimulus presentation. Further, we used wide stimuli to maximize the number of trials in which pursuit is initiated before a horizontal catch-up saccade is made. It would be difficult to do so by using the usual step-ramp paradigm, as the target step would mask the perceptual task target. We reasoned that when the stimulus is wide it is still possible to follow the trailing edge without the need to make a catch-up saccade. The background was medium gray (29 cd/m2). The discrimination targets were 1.5 cpd-gratings of 40% Michelson contrast added to luminance noise that was made of 2-pixel squares with a contrast of 60%. The contrast of the combined stimulus was of 100%. Without the sine-wave grating, the luminance noise had a contrast of 100%. The phase of the sine-wave grating was jittered, such that no single visual detail could be the basis for orientation discrimination across trials.

We manipulated the allocation of voluntary attention by different instructions to prioritize the target of the perceptual task or the pursuit target. The instructions given to the participants are detailed in Table 1. We used an intra-subject factorial design: instruction × target location (up or down) × target direction (leftward or rightward). Instruction was a blocked variable, while location and direction were randomized within a block. Each combination of target location and direction was repeated 12 times per block. There were four experimental sessions, each repeating the six instruction blocks, run on different days, amounting to 192 trials per instruction.

In addition to the acoustic feedback on perceptual performance, subjects received written feedback if their eyes had moved in the wrong direction or if no pursuit was initiated within 500 ms after target motion onset. This was not done in the priority perception condition to keep subjects motivated, as pre-tests showed that direction errors occurred on most trials in this condition. We balanced the order of instructions in single-task and dual-task blocks. Additionally, there were single-task blocks in which only the pursuit target moved on the screen (no distractor stimulus) and

dual-task blocks in which the perceptual target was presented on the pursuit target (termed pursuit = perception) and a distractor stimulus was presented on the other side. Trials with vertical saccades, blinks or pursuit in the wrong direction were repeated at the end of each block. We used a very sensitive velocity criterion (12 deg/s) to detect vertical saccades. In pre-tests, we found that vertical saccades as small as 0.3° were reliably detected with this criterion.

We ran a threshold procedure at the beginning of each session to find the grating orientation that yielded 71% correct responses. Stimuli and task during the threshold procedure were identical to the single task perception condition. Orientation thresholds ranged between 6–11°, 9–11°, 9–17° and 7–12° for observers S1–S4, respectively. Observer S5 had an extreme but stable threshold of 45°. A critical point was that the subjects were able to do the task at their best and that their thresholds were not likely to improve too much within a single session. The perception correct performance in the perceptual single task (performed at the end or at the beginning of the session) was .80 on average (across-subjects); a little higher than the performance targeted by the threshold procedure, .71. To achieve stability of perceptual performance and maximal performance in complying with the different task demands, all subjects completed 4–6 training sessions.

2.4. Data analysis

To detect pursuit onsets, we used an algorithm based on low-pass filtered (de-saccaded) velocity traces (10 Hz low-pass Butterworth filter), obtained by two-point differentiation of the position signal. First, the algorithm searched the first sample that was more than six standard deviations (SD) above the baseline velocity. The mean and SD of the velocity baseline were estimated from samples 100 before to 80 ms after target onset. Then, the algorithm went backwards to find the first sample that was below 20% of the maximum acceleration (obtained by two-point differentiation of the filtered velocity trace). This sample was considered as the pursuit onset. We then fitted a regression line from the estimated onset to the next 80 ms. The slope was used to evaluate whether the subject had pursued the correct target and was used as the estimate of acceleration during the initial open-loop smooth pursuit (e.g., Braun et al., 2008).

We applied the attentional operating characteristic (AOC) analysis to our results (Kinchla, 1980; Sperling & Melchner, 1978). The standard procedure was adapted by Kowler et al. (1995) to examine tradeoffs between perceptual and saccadic performance.

Because the stimulus was presented for 80 ms we excluded the trials in which pursuit was initiated less than 80 ms and after more than 500 ms after target onset. In total, 20–54% (31% on average) of trials were excluded in the first experiment, with 1082–1457 trials analyzed per subject. In the second experiment, 20% and 23% of trials were excluded, with 1190 and 1209 trials analyzed per subject.

The reported *t*-values are the result of multiple post hoc comparisons with Fischer's LSD method. Before statistical testing, proportions (the proportion of correct responses in the perceptual task and the proportion of trials in which pursuit was initiated in the wrong direction) were arcsine-transformed, with $p' = \sin^{-1}\sqrt{p}$.

Table 1
The different instructions that were given at the beginning of each block of trials in the first experiment.

Condition	Instruction
Equal priority	To pay an equal amount of attention to the pursuit target and to the opposite target
Priority perception	To pay attention to the discrimination target, but try nonetheless to follow the pursuit target
Priority pursuit	To pay attention to the pursuit target, but try nonetheless to report the discrimination target's identity
Pursuit single task	To pay only attention to the pursuit target
Perception single task	To pay only attention to the discrimination target
Pursuit = perception	To attend only to the discrimination target, which is the same as the pursuit target

For clarity, however, untransformed proportions are reported in the text.

3. Results

To justify comparisons between selected conditions, we first ran one-way, repeated-measures analysis of variance (ANOVA) to test for effects of task priority. The conditions priority perception, equal priority, priority pursuit, and the respective single-task condition were included in the analysis. The ANOVA revealed a significant effect of instruction on arcsine-transformed proportion correct performance, $F(3, 12) = 7.54$, $p < .01$, pursuit latencies, $F(3, 12) = 6.30$, $p < .01$, acceleration, $F(3, 12) = 8.41$, $p < .01$, and direction errors, $F(3, 12) = 14.92$, $p < .001$. In the following, we will examine whether there was a trade-off between smooth pursuit and perceptual performance. Then, we will examine differences between the priority pursuit and various control conditions.

We first looked at the way pursuit latency was traded for perceptual performance. AOC plots are shown in Fig. 2 for each individual and for the group average. If both tasks rely on a different set of resources or on a capacity-unlimited resource, dual-task performance should be at the intersection between the single-task performances in an AOC plot. As individual and group performance was far from the intersection, we conclude that target selection for perception and smooth pursuit are strongly coupled. Observers were unable to maintain the same level of perceptual and oculomotor performance in the dual-task conditions as in the single-task conditions.

There were clear effects of the weight given to the two tasks. When priority was given to perception, proportion correct responses were higher than when priority was given to pursuit

(.71 vs. .58), $t(4) = 2.92$, $p < .05$. Conversely, pursuit performance was better when priority was given to pursuit than when priority was given to perception. Latencies were shorter (122 vs. 172 ms), $t(4) = 3.07$, $p < .05$, and acceleration was higher (62 vs. 52 deg/s^2), $t(4) = 6.66$, $p < .01$, as shown in Fig. 3. Weaker pursuit acceleration with longer latencies may occur because the target had already moved away when the eye started to move, resulting in a more peripheral location of the motion signal. It is known that that pursuit acceleration is smaller in response to more peripheral motion signals (Tychsen & Lisberger, 1986).

While the trade-off between the priority to perception and priority to pursuit conditions was present in all observers, the situation was less clear for the equal priority condition. If the trade-off between pursuit and perceptual performance was linear, the 50/50 condition should fall on a line connecting the two extreme instructions. While this was true in the group average AOC plot (see Fig. 2), individual patterns diverge strongly from linearity (in particular, results of S3 and S5). Previous studies investigating tradeoffs between perception and pursuit have also noted non-linearities (Khurana & Kowler, 1987; Kowler et al., 1995). However, our small sample does not allow us to draw strong conclusions about the linearity of the underlying process. Regarding perceptual performance, the unequal distances between priority perception and priority pursuit conditions to equal priority condition indicates that the subjects were not able to divide attentional resources exactly as instructed, presumably because own performance is difficult to judge on the pursuit task, as it is a matter of tenths of milliseconds rather than correct or wrong.

We went on to test whether subjects truly divided attention between the two tasks, as the same average performance can theoretically be achieved by means of different strategies. Sperling and
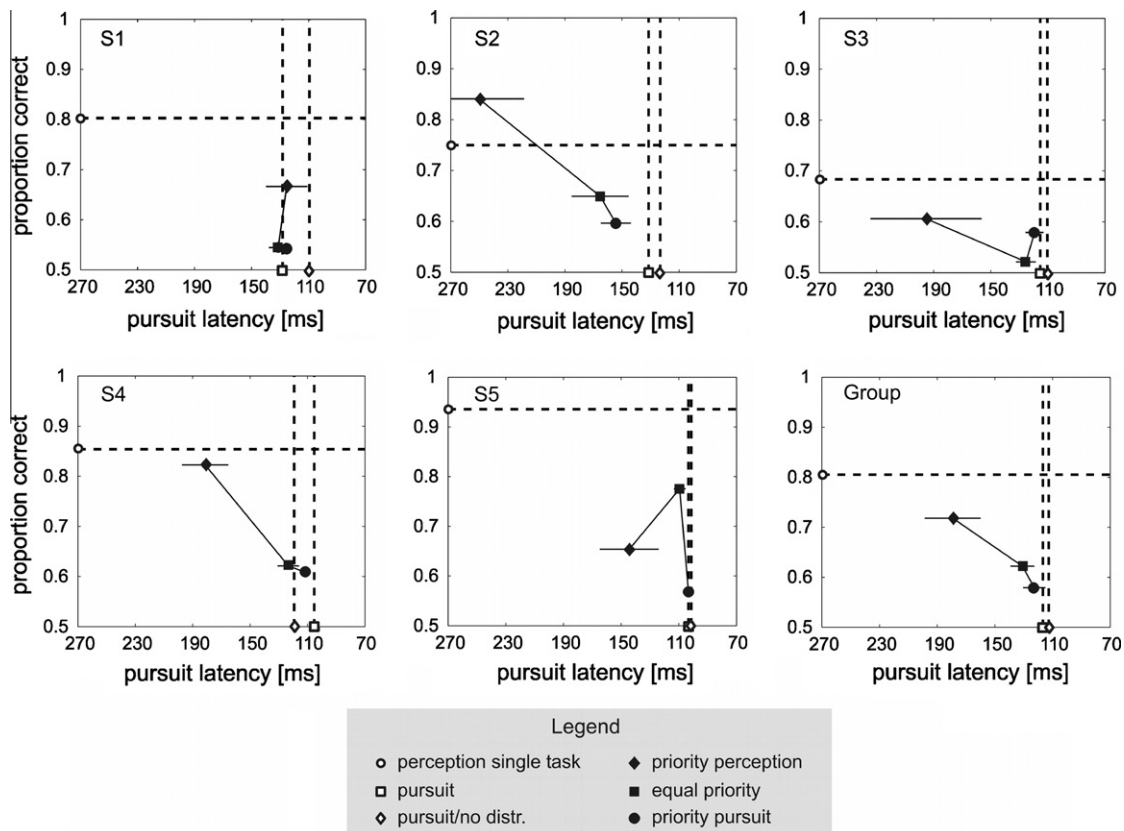
Fig. 2. Plots of the "attention operating characteristic". For each observer, perceptual performance is plotted against median pursuit latency in three dual-task conditions (perceptual priority, equal priority and pursuit priority). Group means are plotted in the bottom right panel. Error-bars represent the between-subjects standard error of the mean.
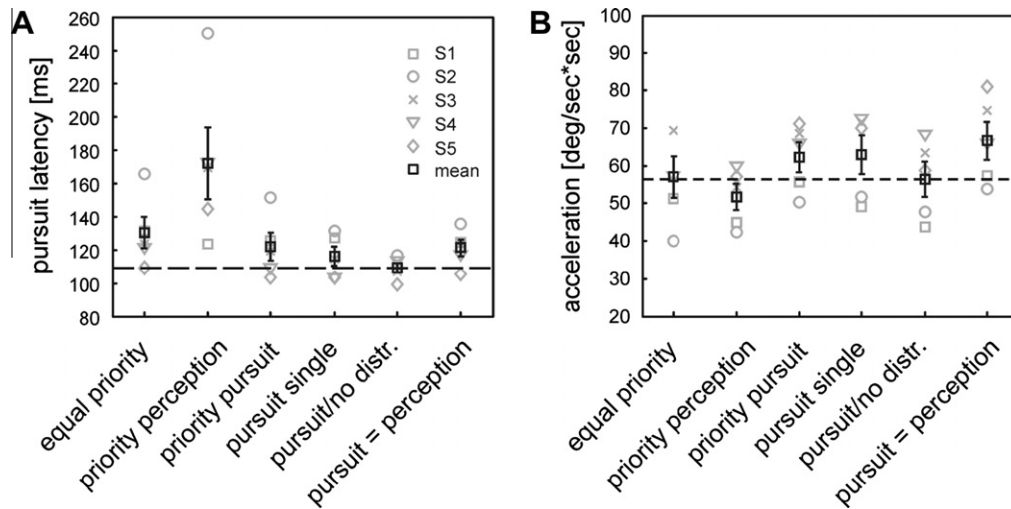
Fig. 3. The left panel (A) shows pursuit latency (re-plotted from Fig. 2) and right panel (B) shows acceleration during the first 80 ms of smooth pursuit initiation, as a function of instruction. The black square indicates the mean across subjects and error-bars represent the between-subjects standard error of the mean. The dotted lines represent the mean latency and mean acceleration of pursuit with no distractor.

Melchner (1978) suggested that resources allocated in two visual search tasks may either be truly shared or may result from switching priorities between trials. In our case, average performance may represent an imbalanced number of trials in which attention was focused on the perceptual or on the pursuit target. To determine whether a "switch" or a "share" strategy was employed, we tested the null hypothesis that the number of fast/slow pursuit trials (pursuit latencies were divided into two bins by a median latency split) and correct/incorrect responses was as predicted by the combined probabilities of each response (see Khurana & Kowler, 1987; Souto & Kerzel, 2008; Sperling & Melchner, 1978). If subjects switched between task A and task B, bad performance on B should be associated more often with good performance on A and inversely. This should not happen if resources are shared on any single trial. Concretely, a chi-square test was run on the difference between expected and actual observations for the priority perception, equal priority and priority pursuit instructions (see Souto & Kerzel, 2008). The test was based on a total of 28 observations in the worst of cases, for subject 1 in the priority perception condition, but over 80 observations in most occasions. The null hypothesis could only be rejected for subject 5 in the equal priority condition, $X^2 = 8.96$, $p < .001$. For this particular case, there was a medium size association as indicated by a phi-coefficient of .30 (Gravetter & Wallnau, 2006). As an illustration, for one cell of this subject's contingency table, 40 observations were expected in which fast pursuit would be associated with incorrect perceptual responses, while 47 were actually observed. Across subjects the phi-coefficient was of .12 on average, indicating a small relation. Therefore participants may have shared resources rather than switched attention between one task to the other on different trials.

Consistent with the large variability of performance in the equal priority condition, statistical comparisons with the priority pursuit and priority perception conditions were not always significant. Numerically, perceptual performance was intermediate in the equal priority condition (.58, .63, and .71 for priority pursuit, equal priority and priority perception, respectively), but not significantly different from the other conditions. Pursuit latencies were slightly, but significantly longer with equal priority than with priority pursuit (130 vs. 122 ms), $t(4) = 4.33$, $p < .02$, and shorter with equal priority than with priority perception (130 vs. 172 ms), $t(4) = 2.79$, $p < .05$. Acceleration was also intermediate with equal priority (62, 57, and 52 deg/s² for priority pursuit, equal priority and priority perception, respectively), but only the difference be-

tween priority pursuit and equal priority approached significance, $t(4) = 2.69$, $p = .055$.

Inspection of Fig. 2 shows that there is one participant, S1, who shows only very small effects of task priority on pursuit latencies. Even when attending more to the perceptual than to the pursuit task, latencies remain basically unchanged, suggesting that S1 does not trade off performance. However, a tradeoff is evident when looking at the proportion of direction errors in Fig. 4. When prioritizing the pursuit task (single task pursuit, priority pursuit), S1's error rate is below 2%, but rises dramatically to 26% with equal priority and 75% with priority to perception. Thus, instead of compromising latency, the accuracy of smooth pursuit was reduced. To confirm this pattern statistically, we ran the same one-way ANOVA as above (equal priority, priority perception, priority pursuit, single task pursuit) on the proportion of direction errors, after applying an arcsine transformation. A significant effect of condition emerged, $F(3,12) = 14.92$, $p < .001$. More direction errors occurred with priority to perception than with priority to pursuit (60% vs.
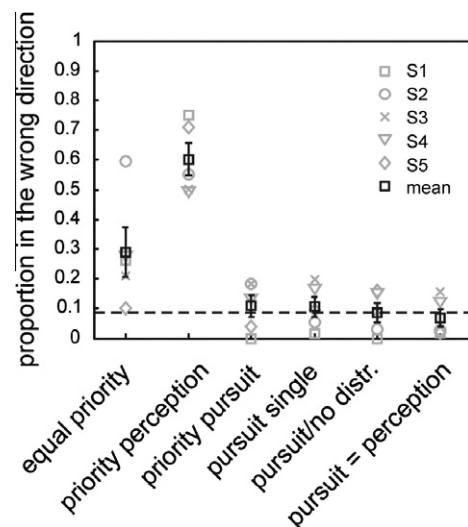
Fig. 4. Proportion of trials in which the subjects did not follow the pursuit target. In the equal priority, priority perception, and priority pursuit conditions, direction errors resulted from pursuing the perceptual target. Symbols represent different subjects. The black square represents the mean. Error-bars represent one standard error of the mean.

11%), $t(4) = 4.30$, $p = .02$. The equal priority condition was intermediate (29% errors), but was just not significantly different from the priority pursuit, $t(4) = 2.70$, $p = .054$, and priority perception conditions, $t(4) = 2.73$, $p = .052$.

The direction errors in the priority perception condition show that observers followed the perceptual target more often than the pursuit target. However, in order to minimally comply with the instruction to pursue the target that moved in the opposite direction, observers followed the pursuit target in 40% of the trials. We suggest that the withdrawal of attention from the perceptual target that was necessary to achieve 40% correct pursuit responses led to a strong reduction of perceptual performance in subjects who only moderately slowed down pursuit (less or equal to 50 ms in S1, S3, and S5). Only subjects who showed an extreme slowing of pursuit (99 ms in S2 and 63 ms in S4) were able to maintain perceptual performance at a level similar to the single task (perception) condition. Thus, the way pursuit and perception was traded off varied between individuals, but the tradeoff was always present in one measure or the other.

One could expect smooth pursuit performance in the dual-task condition to be worse than smooth pursuit performance in the single-task condition with the same stimuli. Similar to the priority pursuit condition, the single-task condition required observers to select the appropriate object. In contrast to the priority pursuit condition, the perceptual target was completely irrelevant. The comparison showed that latencies (122 vs. 116 ms for priority pursuit and single task, respectively), acceleration (62 vs. 63 deg/s²), and direction errors (11% vs. 11%) were statistically identical. Thus, the additional perceptual task did not change smooth pursuit performance when it was given low priority.

Similarly, we could expect that in a single-task condition, the presence of an object moving in the opposite direction would slow down responses compared to a condition with only a single object. We compared the single task pursuit condition to single-element displays and found small and non-significant effects on latencies (116 vs. 109 ms for two-elements vs. one-element displays, respectively) and direction errors (11% vs. 9%). Our participants' ability to filter out the irrelevant stimulus based on the central pre-cue was close to perfect. Somewhat surprisingly, acceleration was higher in two-element than in single-element displays (63 vs. 56 deg/s²), $t(4) = 4.71$, $p = .01$. It may be that participants paid more attention to the pursuit target when there was a risk of pursuing the wrong object, trying to avoid errors.

Finally, when the pursuit target equaled the perceptual target (pursuit = perception condition) we may expect enhanced performance because attention is better focused on the pursuit target (Shagass, Roemer, & Amadeo, 1976; Sweeney et al., 1994). However, the priority pursuit and the pursuit = perception condition, in which the only difference was the location of the perceptual target, led to similar latencies (121 vs. 121 ms) and direction errors (11% vs. 7%). Acceleration was only slightly higher when the perceptual target was also the pursuit target (67 vs. 62 deg/s²), $t(4) = 2.41$, $p = .074$.

3.1. Single instruction experiment

The frequent changes of instruction in the same session could have made it more difficult to dissociate perceptual from oculomotor decisions than if we had asked subjects to do the same tasks repeatedly. To test for this possibility, subjects S2 and S4 did six additional sessions with the same instruction. Each session was initiated by a threshold procedure aiming at 71% correct responses and followed by 4 blocks of at least 48 trials. The instruction was to perform as well as during the threshold block (that is to reach 71% correct), to approach the latency that was measured individually in the previous experiment when pursuing the target in the absence

of a distractor, as well as to minimize the number of pursuit errors. Thus participants were required to give equal priority to both tasks. Detailed performance feedback was given after each block (i.e., four times per session): median pursuit latency, the histogram of latencies, and the number of errors due to pursuit in the wrong direction were displayed. Thresholds measured at the beginning of the session ranged from 8 to 9° for S2, and were constant at 8° for S4.

To look for improvements across sessions we show performance separately in the first and last three sessions. Fig. 5 shows performance in each block for the two subjects. Improvements in dual-task performance would be indicated by displacement of the ellipses toward the independence point, the intersection between single-task performances. The plot shows no evidence for improvement despite extensive training. Therefore, frequent task-switching is not a limiting factor when trying to dissociate attentional from oculomotor selection. Another noteworthy outcome of this control experiment is that even though subjects received feedback about pursuit errors (which was not the case in the priority perception condition of the previous experiment), the proportion of trials in which they pursued the wrong target remained very high (10–30% for S4 and 30–50% for S2), reflecting the tendency to follow the perceptual target on a great proportion of trials. Nevertheless, there was no significant positive correlation between perceptual performance and the proportion of pursuit errors, which would indicate a trade-off between perception and pursuit (high proportion of correct perceptual responses traded for many errors). Rather, there was a tendency in the opposite direction. We correlated the proportion of pursuit errors and perceptual performance in each block of trials ($N = 25$ blocks). A negative correlation emerged for subject S2, r $-.35$, $p = .09$, and S4, $r = -.11$, $p = .60$, suggesting the effect of a spatially unspecific resource, like alertness. The wrong stimulus may be pursued because no attention is paid to either stimulus, and then a correct response in the orientation task will also be less likely. Thus, an increase in the proportion of direction errors goes with lower perceptual performance if subjects lose their concentration.

4. Discussion

We examined the extent to which target selection for perception and pursuit can be dissociated in situations in which the objects associated with each task move in opposite directions. The way pursuit performance was traded for perceptual performance indicates that target selection for smooth pursuit depends strongly on the allocation of attention to one of the moving objects. In particular, when the target of the perceptual task was successfully selected (high perceptual performance) the pursuit latencies where strongly delayed. In contrast, a previous study showed that pursuit initiation is almost unaffected by shifting attention to the periphery (Souto & Kerzel, 2008). Thus, the present study adds that perceptual priorities are strongly linked to target selection for pursuit when the target has to be selected among competing motion signals. Successful oculomotor performance depends on a bias of attentional resources towards the designated target. In addition we showed that performance was not limited by frequent task-switching or the absence of oculomotor feedback. In general, the data is compatible with the idea that under these conditions smooth pursuit eye movements follow the most attended target, but selection may not linearly improve when more attentional resources are allocated to the target.

The current results complement studies on the link between attention and target selection for saccades (e.g., Castet et al., 2006; Deubel & Schneider, 1996; Montagnini & Castet, 2007). For
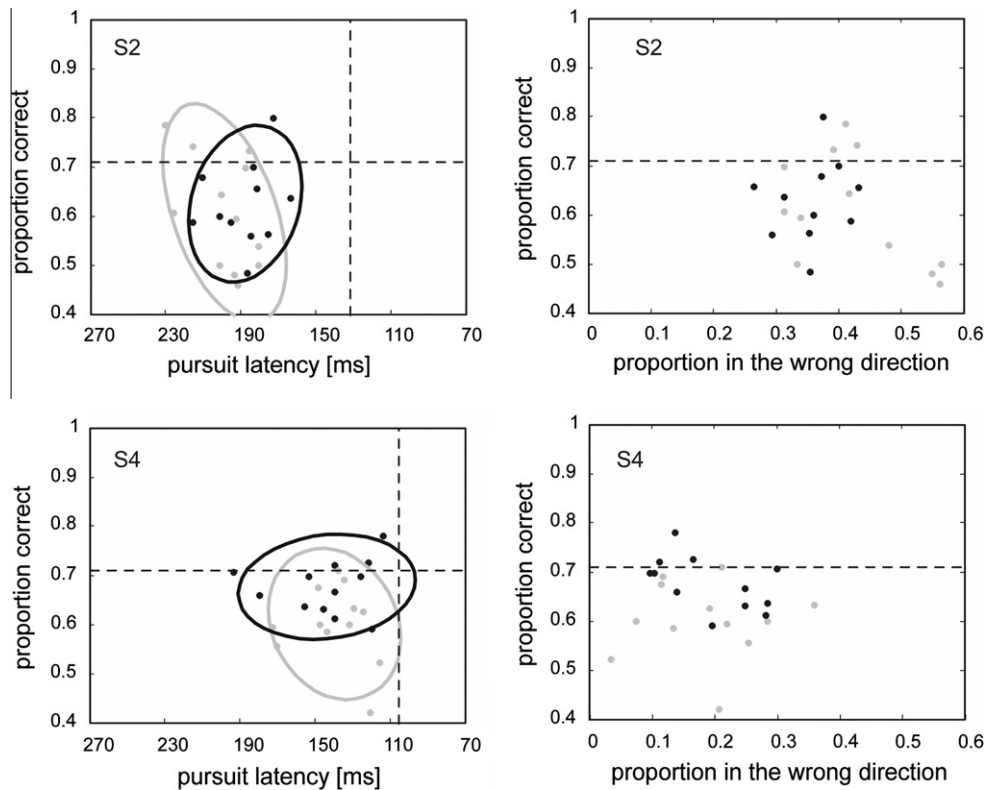
Fig. 5. Black symbols indicate performance (mean proportion correct and median latency) for each block in the first three sessions. Gray symbols indicate data from the last three sessions. Confidence ellipses are shown separately for the first and last sessions. Panel B shows direction errors as a function of perceptual performance. Each data point in the graph represents the average over a block of 48 trials. Vertical and horizontal lines represent single-task performance for the pursuit and perceptual task, respectively.

both saccades and smooth pursuit, action and perception depend on shared filters. Similarities between pursuit and saccades in the way their input is selected is to be expected from recent evidence that pursuit and saccades share similar selection and gating signals at the neural level (Carello & Krauzlis, 2004; Case & Ferrera, 2007; Krauzlis, 2003; Krauzlis & Dill, 2002; Liston & Krauzlis, 2003, 2005).

Ferrera and Lisberger (1995) have proposed that attention is able to select the pursuit target by biasing the outcome of the neural competition that ultimately results in a winner-take-all response. Within this framework the time it takes to converge on a given response depends on the bias strength and on whether motion signals compete or cooperate (Ferrera & Lisberger, 1995). Monkey behavior suggested that the attentional bias (which could be the result of stimulus saliency or of a perceptual decision, as in our experiments) is able to modulate but not suppress the delay that is observed in the presence of opposite motion signals. However, human observers show a delay that depends strongly on the type of cues that point to the target, with very little delay or none at all when the target is cued by location (Krauzlis et al., 1999), while monkeys always showed substantially longer latencies in the presence of a conflicting motion signal, even when selection was facilitated by blocking the target direction (Ferrera & Lisberger, 1995). Consistently with the former study on humans, we found that pursuit was not systematically delayed in the presence of a distractor when sufficient attention was paid to the target (single-element displays vs. single task with two-element displays). Assuming shared selection signals between pursuit and saccades, poor selectivity of pursuit may be explained by the fact that attention takes longer than typical pursuit latencies to suppress the influence of the distractor and to focus on the target. If this were the case we expect that selectivity will be enhanced by instructions to increase attentional resources at the target location

to prepare for target onset. Conversely, the spread of attention to non-target signals would be responsible for delayed responses with two-element displays. Therefore, in a situation when no location cue is provided in advance or when a target search has to be performed after motion onset, the slow deployment of attention can cause pursuit to appear more unselective than saccadic responses of longer latency.

Our previous study showed that in the absence of conflicting motion signals, latencies of smooth pursuit and catch-up saccades were differently affected by shifting attention to the periphery. We observed that attention could be endogenously or exogenously summoned to the periphery with almost no effect on pursuit latency, while catch-up saccades were strongly delayed (Souto & Kerzel, 2008). Other studies have shown decrements in perceptual performance in the periphery during pursuit initiation which suggest that attention was shifted to the pursuit target (Schutz, Braun, & Gegenfurtner, 2007; Schutz, Braun, Kerzel, & Gegenfurtner, 2008). Both results can be accommodated by supposing that while some amount of attention is required at the target, attentional requirements for pursuit initiation are much smaller than what is needed for saccade execution.

Finally, we observed that instructions to give priority to the perceptual target led to a very large number of direction errors. The direction errors may have gone unnoticed, as shown for fast involuntary saccades in the antisaccade task (Mokler & Fischer, 1999) or in the oculomotor capture paradigm (e.g., Godijn & Theeuwes, 2003). It may be that pursuit direction errors go unnoticed because they can often be initiated and corrected within less than 100 ms (Krauzlis et al., 1999). We may therefore lack a reliable estimate of where our eyes are heading over small periods of time. Additionally, unlike saccadic eye movements, initial pursuit velocity is very low, and thus rapidly corrected pursuit errors may be harder to detect.

As pointed out by Kowler et al. (1995; see also Khurana & Kowler, 1987) it may be a desirable feature of the oculomotor system to share object selection mechanisms with the perceptual system to prevent a conflict between motor and perceptual preparedness, but at the same time not to depend linearly on the amount of attentional resources allocated to the target, thus allowing motor performance to be relatively unaffected by continuous concurrent internal and external demands.

Acknowledgments

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