



Research report

Smooth pursuit eye movements and perception share target selection, but only some central resources

Dirk Kerzel*, Sabine Born, David Souto

Faculté de Psychologie et des Sciences de l'Éducation, Université de Genève, 40 Boulevard du Pont d'Arve, CH – 1205 Genève, Switzerland

ARTICLE INFO

Article history:

Received 11 November 2008
 Received in revised form 23 January 2009
 Accepted 26 January 2009
 Available online 2 February 2009

Keywords:

Smooth pursuit
 Flash
 Attention
 Secondary task
 Dual task

ABSTRACT

Smooth pursuit eye movements have been linked to perception by a common attentional mechanism. We investigated whether perceptual performance was traded for smooth pursuit performance. While tracking a red target cross, observers had to discriminate the orientation of a flashed peripheral grating. We manipulated the priority given to the two tasks. Pursuit gain changed according to observers' effort to pursue the target, but perceptual discrimination of the peripheral flash was not affected by these changes, suggesting that smooth pursuit does not use the same resources as perception. Complete resource sharing may be confined to situations involving multiple moving objects. Next, we added a second perceptual task on the foveal pursuit target. Foveal discrimination performance was traded for peripheral discrimination performance and pursuit gain followed the perceptual priorities. Thus, smooth pursuit gain is affected by which target has been selected for enhanced perceptual processing, but that does not imply shared perceptual resources.

© 2009 Elsevier B.V. All rights reserved.

1. Introduction

Performance in dual task situations is often limited by the available central resources [1,2]. Resources refer to effort, capacity, or attention [1]. For instance, two visual tasks, such as a foveal and a peripheral discrimination task, are likely to depend on the same central resource. Therefore, subjects are unable to do the two concurrent tasks as well as each can be done alone. Rather, performance on one task has to be traded for performance on the other task (e.g., [3]). Increasing the weight given to one of the tasks improves performance on this task at the cost of reducing performance on the other task. In multiple resource models [4,5], the idea was introduced that there is not only one pool of resources, but that there are separate resources for spatial and verbal tasks. Therefore, executing a verbal and a spatial task simultaneously will not be as difficult as executing two verbal or two spatial tasks simultaneously [6] because different resources are available. The allocation of central resources to tasks or stimuli is referred to as selective attention.

Studies on saccades have concluded that visual perception and the programming of saccades share a common attentional mechanism [7–9]. For instance, saccadic latency was traded for accuracy of letter identification [9]. In one of their experiments, Kowler et al. [9] asked observers to saccade to a target indicated by a central cue and to report the identity of a letter at a fixed location that was

different from the saccadic goal. The priority given to the two tasks was manipulated. High priority to the saccade task produced faster responses, but decreased accuracy on the letter identification task and vice versa when high priority was given to the letter identification task. Importantly, performance in the equal priority condition was worse than in the respective single task conditions. This pattern of results is strong evidence for shared central resources. In the present study, we will reconsider this question in the context of smooth pursuit eye movements which will complement previous research that confirmed a strong link between attention and steady-state smooth pursuit (reviewed in [10–12]).

Previously, Khurana and Kowler [13] asked whether perceptual and target selection for smooth pursuit share a common attentional mechanism. In their experiments, four rows of horizontally aligned letters moved from left to right in a display of fixed size (see Fig. 1A). Participants were asked to track two non-contiguous rows. That is, either rows 1 and 3, or rows 2 and 4 had to be pursued. The pursued rows moved either faster or slower than the non-pursued rows. During pursuit, a search display that was visible for 200 ms contained one search target (a numeral among letters) in the pursued rows, and another search target in the non-pursued rows. Observers' task was to track the designated rows and report the identity and location of the two numerals at the end of a trial. There were two main results. First, without any particular instruction, search performance on the pursued rows was better than on the non-pursued rows. Second, when observers were asked to attend to the non-pursued rows, their performance for those rows improved, but did not exceed performance for the tracked rows. Smooth pursuit gain

* Corresponding author. Tel.: +41 22 37 99 132; fax: +41 22 37 99 229.
 E-mail address: dirk.kerzel@unige.ch (D. Kerzel).

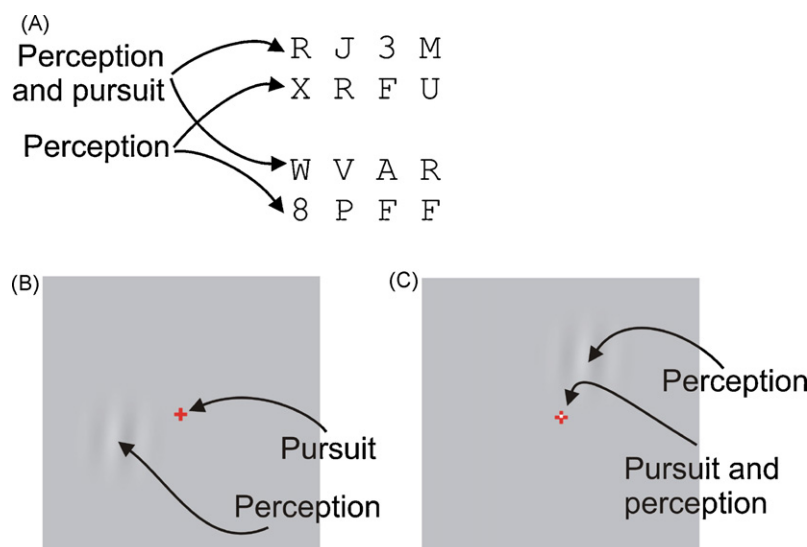


Fig. 1. Experimental paradigms. Panel A Shows a search display from Khurana and Kowler [13]. In the example, observers' task is to track rows 1 and 3 (indicated by arrows). At the same time, they are asked to identify the numeral on the pursued rows as well as on the non-pursued rows 2 and 4. All rows moved from left to right, but the velocity of rows 1 and 3 was different from rows 2 and 4. Panel B shows the dual task conditions of Experiment 1. Observers pursued the red cross and reported the orientation of the flashed peripheral grating. A grating tilted to the right is shown. Panel C shows the triple task conditions of Experiment 2. Observer's task was to pursue the red cross, indicate the position of the single-pixel flash inside the cross and the orientation of the grating. The foveal pixel is shown in its upper position and the grating is tilted to the right.

was hardly affected by instructions to attend to the non-pursued rows. Taken together, these results support the idea that stimuli selected for smooth pursuit are identical to those selected for perception.

These results are consistent with research showing that areas MT/MST are involved in the perception of motion (e.g., [14]) and also provide the principal input for the smooth pursuit system (e.g., [15]; reviewed in [16]). Further, it has been demonstrated that activity in these areas can be modulated by attention [17,18]. Therefore, it is plausible that the stronger neural response to attended stimuli in areas MT/MST will also constrain target selection for smooth pursuit. In fact, when there is more than one moving target, attentional enhancement of the neural response to one of the stimuli may be the mechanism to select the target for smooth pursuit [19,20]. Consequently, the target of smooth pursuit will also be perceived better than the distractor (cf. [13]).

The question addressed in the present paper is whether smooth pursuit will also determine the resource allocation for the perception of motionless stimuli. In this study, we selected stimulus orientation as a feature, because orientation is detected as early as V1 [21] and perception of orientation does not depend on MT/MST [22]. While the concurrent processing of two moving stimuli will cause interference, it may be that smooth pursuit and the perception of a motionless stimulus are relatively independent. Akin to the idea of multiple resources, assigning high priority to the smooth pursuit task will not necessarily decrease the available resources for the perception of a motionless feature, because there are separate resources for the two tasks.

2. Experiment 1

To test this hypothesis, we flashed oriented gratings during pursuit and varied the priority of the pursuit or perceptual task. A single red cross moved horizontally on an otherwise blank screen. The perceptual target was a Gabor patch (a sine-wave grating multiplied by a Gaussian) that was flashed for 10 ms just outside the fovea (see Fig. 1B). Because a flash has zero retinal motion, there were no conflicting motion signals that needed to be separated from target motion. It is known that even irrelevant motion signals change pursuit gain [23–25]. To our knowledge, there are no data to suggest

that irrelevant flashes reduce pursuit gain. Any changes in pursuit gain can therefore be attributed to changes in participant's resource allocation. While the brief presentation time of a flash prevents retinal motion of the discrimination target, visible persistence of the stimulus certainly exceeds 10 ms. A typical estimate of visible persistence is 100 ms [26].

In the dual task conditions, observers were asked to indicate the orientation of the sine-wave grating while pursuing the red cross. They were either told to give priority to the pursuit task, to give priority to the perceptual task, or to give equal priority to both tasks. If the perceptual and the pursuit task shared resources, performance in the two should be traded off. We expect that if processing of the flash uses common resources, pursuit gain will decrease as the "attentional gate" [27] opens. Further, we included single task conditions to evaluate whether the dual task situation itself led to performance decrements. In particular, it is necessary to quantify perturbations of pursuit due to the abrupt onset that may capture spatial attention in a reflexive manner [28,29].

2.1. Methods

2.1.1. Participants

Two of the authors (DK, DS) and four experienced naïve participants with normal or corrected to normal vision participated in the experiment.

2.1.2. Apparatus and stimuli

The stimuli were presented on a 21 in. (diagonal) CRT with a resolution of 1280 (H) × 1024 (V) pixels at a refresh rate of 100 Hz. Participants' head position was stabilized with a chin rest at 46 cm from the screen centre. Eye movements were recorded with a head-mounted, video-based eye tracker (EyeLink II, SR-Research, Osgoode, Ontario, Canada) at a sample frequency of 250 Hz. The experiment was run in a dimly lit room.

A sample stimulus is shown in Fig. 1B. A $0.4^\circ \times 0.4^\circ$ cross was used as pursuit target (three pixel lines = 0.11°). The target moved at $10.8^\circ/\text{s}$ for 2 s. The trajectory was centered on the midpoint of the screen. The perceptual target was a Gaussian-windowed sine-wave (Gabor patch). The sine-wave had a spatial frequency of 1 cycle per degree and a Michelson contrast of 20%. The Gaussian had a standard deviation of 0.9° . The Gabor was presented for a single frame which resulted in a presentation time of less than 10 ms. The flash was presented at an eccentricity of 2° and appeared at one of eight different angles around the smooth pursuit target (from 22.5° to 337.5° of rotation in steps of 45° with 0 denoting the 3 o'clock position).

2.1.3. Task and procedure

At the beginning of each trial, the pursuit target was shown at 10.8° to the left or right. To perform a drift correction, participants pressed a designated button on

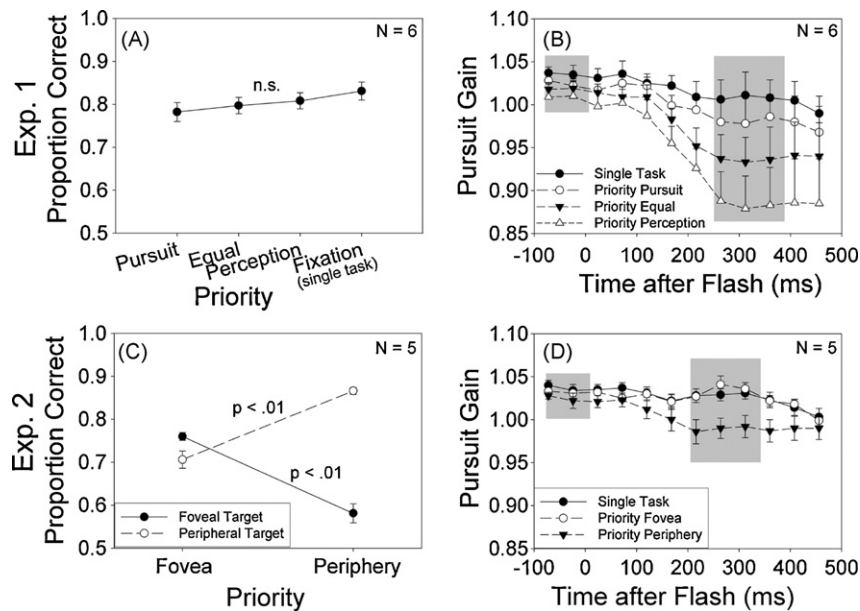


Fig. 2. Results of Experiments 1 and 2. The gray shaded areas indicate the pre- and post-flash intervals that were used in the analysis. Error bars indicate the between-subject error. Panel A shows the mean performance on the peripheral perceptual task in Experiment 1. In the dual task conditions, priority was either given to the pursuit task, to the perceptual task, or equal priority was assigned. In the single task condition, subjects performed the perceptual task without pursuit (fixation). Panel B shows mean horizontal smooth pursuit gain in Experiment 1. For clarity, only one-sided error bars are shown. Panel C shows mean performance on the peripheral orientation discrimination task and the foveal position judgment task as a function of priority in Experiment 2. Panel D shows mean smooth pursuit gain in Experiment 2.

a game pad with their left hand. If the drift correction was successful, the target started to move toward the opposite side of the screen. In the dual task condition, participants' task was to follow the pursuit target with their eyes and to indicate the orientation of the sine-wave grating by pressing one of two mouse buttons with their right hand after target motion stopped. The flash appeared between 500 ms before and 500 ms after the pursuit target passed the center of the screen. Prior to data collection, the grating orientation yielding 79% correct responses during pursuit was determined by a staircase procedure. This value was used in subsequent testing. Across observers, the mean orientation threshold was 3.7° of rotation. To assure a gain close to 1, experimental trials in which pursuit gain was outside 1 ± 0.3 in the interval from 50 ms before to 50 ms after flash presentation were aborted and repeated in the remainder of the experiment. About 5% of the trials had to be repeated.

2.1.4. Design

There were five different conditions. In the dual task conditions, priority was either given to pursuit or perception, or both tasks should be weighted equally. In the "pursuit only" condition, participants tracked the target and were told to ignore the flash. No manual response was elicited at the end of the trial. In the "fixation" condition, the red cross was displayed at the center of the screen and only the perceptual task was performed. Dual or single task conditions were blocked and participants completed 64 trials in each block. Within each block, the direction of motion, position of the flash, and grating orientation were randomized. Each condition was run once in two separate sessions for a total of 128 trials per condition. For each participant, the order of the dual task conditions with unequal priority (priority perception, priority pursuit) and the order of the single task conditions (pursuit only, perception only) were reversed between the first and the second session. The equal priority condition was always run between the dual task conditions and the single task conditions. Finally, half of the participants started with the dual tasks, and the other half with the single tasks.

2.2. Results

To identify saccades, the output of the EyeLink II eye movement parser was used. It classified episodes with acceleration larger than $4000^\circ/s^2$ and velocity larger than $22^\circ/s$ as saccades. Velocity traces were filtered with a 40 Hz low-pass, zero-phase-shift Butterworth filter. After removing saccades and 4 samples (16 ms) before and after each saccade, episodes in which the eye velocity deviated by more than two standard deviations from the average eye movement velocity, as well as 16 ms preceding and following this interval, were discarded. This was done to exclude small saccades not detected by

the EyeLink parser. Visual inspection confirmed that the algorithms worked well. Then, we calculated smooth pursuit gain in 48 ms bins (12 samples). If more than four samples were missing in a bin, the bin was discarded.

Trials with saccades ± 50 ms around flash presentation and trials with extreme variability in the velocity traces were removed (2.7% of all trials). After filtering, at least 120 trials remained per condition and observer. Data were averaged across repetitions for each condition and observer to assure independence of the observations in the statistical tests (e.g., [30]). In other words, only one value was retained per condition and observer for statistical testing.

2.2.1. Perceptual performance

Mean proportions of correct responses are shown in Fig. 2A. The accuracy data were entered into a one-way ANOVA with four factor levels (priority pursuit, equal priority, priority perception, fixation). The effect of condition did not reach statistical significance, $F(3, 15)=2.19$, $p=.13$. We nonetheless ran follow-up *t*-tests between the condition means. Only the difference between the condition with priority to perception and priority to pursuit approached significance (81% vs. 79%), $t(5)=2.13$, $p=.09$. As evident in Fig. 3(bottom panel), only two (S3 and S6) out of six subjects showed a substantial decrease of performance (5–8%) between the priority to perception and the priority to pursuit conditions. Only one of the subjects showed an intermediate level of performance in the equal priority condition (S3).

2.2.2. Smooth pursuit gain

Fig. 2B shows the mean gain for the four conditions across time. Smooth pursuit gain started to decrease about 100–150 ms after flash onset. Importantly, this decrease differed between priority instructions. To assure that pursuit gain before flash presentation was the same across conditions, we ran a two-way, between-subjects ANOVA (2 bins \times 4 priority conditions) on the first two bins centered on -72 and -24 ms before flash onset (left shaded area in Fig. 2B). No significant effects emerged ($p > .1$). To evaluate effects of priority instruction on smooth pursuit performance

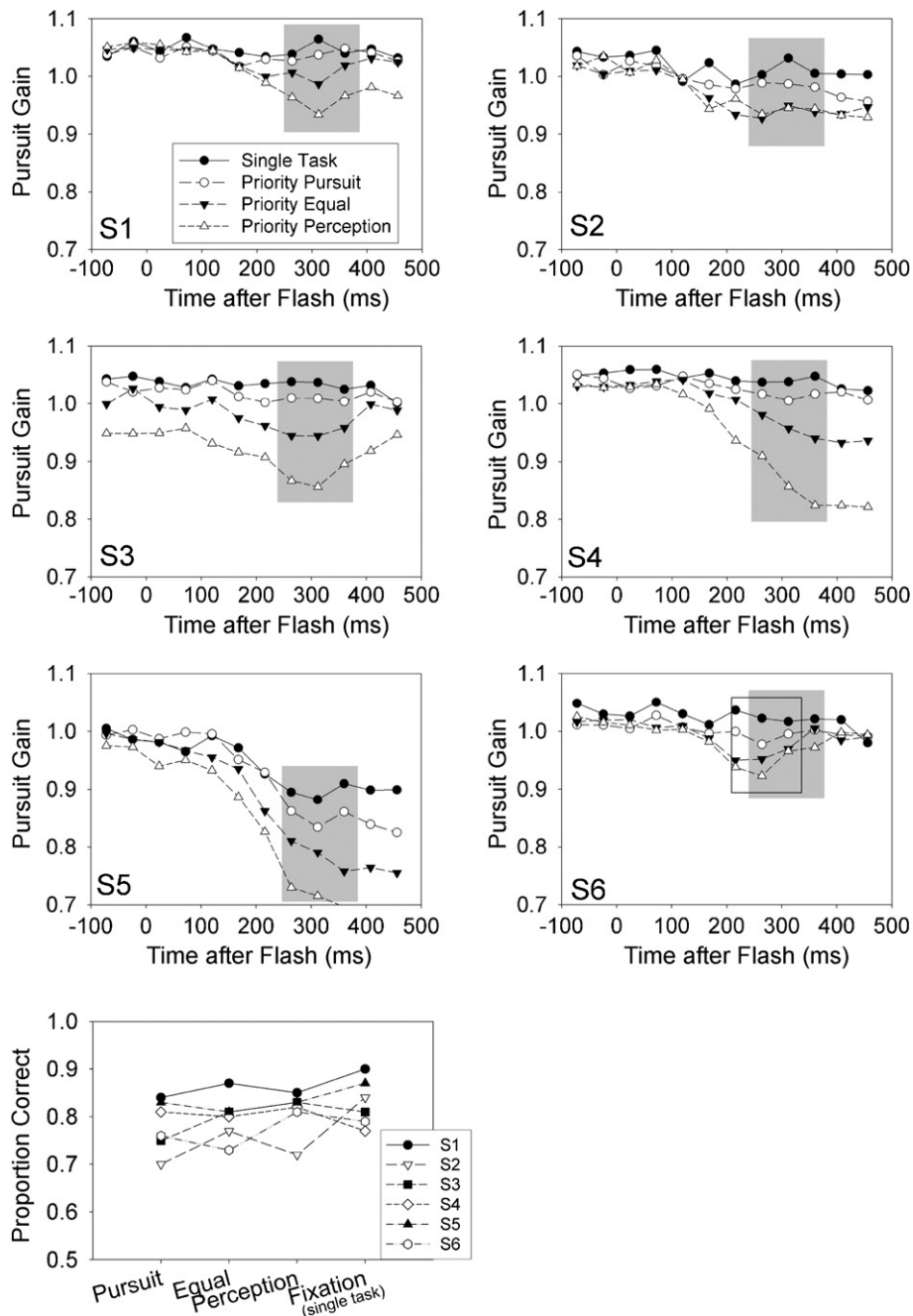


Fig. 3. Individual means in Experiment 1. Horizontal smooth pursuit gain and proportions correct for the six subjects in Experiment 1. The gray shaded area indicates the bins used as estimates of post-flash pursuit. For S6, the bin indicated by the unfilled rectangle was considered more appropriate. The bottom graph shows the mean proportion correct for the six subjects.

after flash presentation, we ran a two-way ANOVA (3 bins \times 4 priority conditions) on the bins centered on 264, 312, and 360 ms (right shaded area in Fig. 2B). For all but one subject, this interval seemed appropriate as it captured either the plateau or the last part of the decrease. For subject S6 (see Fig. 3), however, this period did not seem appropriate and we used data from bins centered on 216, 264, and 316 for this subject (as indicated by the outline rectangle in Fig. 3). A main effect of priority condition emerged, $F(3, 15) = 32.63$, $p < .01$. All pair-wise comparisons (t -tests) between adjacent data points were significant, $ps < .025$. That is, pursuit gain decreased significantly from single task, priority pursuit, equal priority, to priority perception. To quantify the decrease from the pre-flash to the post-flash interval, we subtracted the mean gain in the selected

post-flash interval from the mean gain in the pre-flash interval. The resulting net decrease was 0.027, 0.044, 0.086, 0.128 for the single task, priority pursuit, equal priority and priority perception condition, respectively. In a one-way ANOVA on these differences, a significant effect of priority condition emerged, $F(3, 15) = 27.11$, $p < .01$, and adjacent levels were significantly different from each other, $ps < .05$.

Fig. 3 shows the different individual patterns of smooth pursuit gain and perceptual performance. All observers show effects of priority. The effect is largest for S4 and S5. However, these subjects showed virtually no effect of priority instruction in the perceptual task. Further, the subject with the largest perceptual effect (S3) showed a poor baseline gain (pre-flash bins) in the priority to per-

ception condition. One would expect task priority to be visible in the bins succeeding flash presentation, because there was no secondary task in the bins preceding it. It is therefore not clear why pre-flash gain was so low for this subject. Consequently, the data should be treated with care.

2.3. Discussion

The results show dissociation between perceptual and oculomotor performance. While orientation discrimination was hardly affected by the various priority instructions, smooth pursuit showed a strong effect. Thus, the two tasks are compatible in the sense that performance on one task does not have to be traded for performance on the other. This pattern is at odds with Khurana and Kowler's [13] suggestion of a strong coupling between perception and smooth pursuit performance. Therefore, it seems likely that the perception of motion for pursuit and the perception of motionless features (e.g., orientation) rely on separable resources, whereas perception of motion for pursuit does share resources with the perception of conflicting motion signals. The strong effects of priority instruction on smooth pursuit in our experiment reflect that smooth pursuit eye movements are under voluntary control (e.g., [16]). Therefore, trying hard or not so hard to follow the target results in high and low gain, respectively. In contrast, the perception of orientation is not under voluntary control and the present experiment suggests that it is not traded for smooth pursuit performance either.

A further point worth mentioning is that compared to the single task pursuit condition in which the same stimuli were shown, the gain decreased in the dual task conditions even when high priority was given to the pursuit task. This indicates that top-down attention modulates the perturbation caused by a flash. In a similar vein, Blohm et al. [31] have demonstrated that flashes may act as a position signal to the pursuit system, triggering smooth pursuit in the direction of the flash. However, such an effect was only observed when the flash was selected as the goal of a subsequent saccade. Thus, Blohm et al.'s and our study showed that the behavioral relevance of a flash determines how strongly it affects pursuit gain.

3. Experiment 2

Experiment 1 has demonstrated that performance on the smooth pursuit task was not traded for performance on the perceptual task (cf. Fig. 2A and B). All we saw was an effect of priority instruction on smooth pursuit which probably reflects participants' effort to track the target in the dual task situation (i.e., after flash onset). In the second experiment, we replicated the abstract features of Khurana and Kowler's [13] study using the present paradigm. A second perceptual task was added on the pursuit target (see Fig. 1C). The foveal discrimination task required discrimination of the vertical position of a one-pixel flash inside the red cross. The peripheral discrimination task involved the orientation of the same flashed Gabor as in Experiment 1.

In contrast to the previous experiment, observers were not asked to differentially attend to smooth pursuit and perception. Rather, they were asked to weigh performance on the two perceptual tasks differently while maintaining pursuit performance at its maximum. These instructions resemble those in Khurana and Kowler's [13] experiments.

3.1. Methods

3.1.1. Participants

Five of the six subjects who had participated in Experiment 1 took part in this experiment.

3.1.2. Apparatus, stimuli, design, and procedure

Apparatus and stimuli were identical to the first experiment with the following exceptions. A single gray pixel was lit up inside the red cross for 10 ms at the same time as the peripheral flash (sample stimulus in Fig. 1C). The gray pixel was located either one pixel above or one pixel below the center of the cross. The size of one pixel was 0.036° . Observers' task was to indicate the location of the gray pixel by pressing one of two vertically aligned keys ("8" and "2" on the numerical pad of a standard keyboard) and the orientation of the grating by pressing one of two horizontally aligned keys ("4" and "6" on the numerical pad). The response for the foveal task was always collected before the peripheral task. Prior to the experiment, the orientation of the grating and the luminance of the pixel yielding 79% correct responses during smooth pursuit were determined in two separate blocks. Across observers, the mean orientation threshold was 4.1° of rotation and the mean luminance threshold was ~ 40 cd/m². Participants were told to give priority to the foveal perceptual task ("priority to fovea") or to the peripheral perceptual task ("priority to periphery"). The two priority instructions were run in separate blocks of 96 trials. One block was run per condition in two sessions with counterbalanced order.

3.2. Results

After data filtering, at least 166 of the 192 trials remained per condition and participant. On average, 2.7% of the trials were removed.

3.2.1. Perceptual performance

Mean proportions of correct responses are shown in Fig. 2C. The data were entered in a two-way ANOVA (priority \times target eccentricity). Overall perceptual performance was better for peripheral than for foveal targets (79% vs. 67%), $F(1, 4) = 45.46$, $p < .01$. The interaction between target eccentricity and priority, $F(1, 4) = 116.95$, $p < .01$, showed that performance for peripheral targets increased from 71 to 87% when priority was given to the periphery and conversely, that performance for foveal targets increased from 58 to 76% when priority was given to the fovea. The change in performance of ~ 16 –18% due to priority instructions did not differ significantly between the periphery and the fovea. Fig. 4 shows that all observers showed an approximately symmetrical change in perceptual performance.

The improvement of peripheral discrimination performance when priority was given to the periphery was larger with two perceptual tasks (this experiment) compared to just one (Experiment 1). A *t*-test on the five subjects who participated in both experiments confirmed that the difference in peripheral discrimination performance as a function of priority was larger in this than in the previous experiment (16% vs. 2%), $t(4) = 3.99$, $p < .025$.

3.2.2. Smooth pursuit gain

Fig. 2D shows smooth pursuit gain across time for the three conditions. Again, there was a decrease in pursuit gain about 100–150 ms after flash presentation. We ran a two-way ANOVA (2 bins \times 3 priority conditions) on the two bins preceding flash onset. No significant effects emerged ($ps > .07$). Relative to Experiment 1, pursuit gain after flash presentation stabilized about 50 ms earlier. The reason may be that the decrease was somewhat smaller to begin with (cf. Fig. 2B and D). Therefore, we ran the second ANOVA (3 bins \times 3 conditions) on the three bins centered on 216, 264, and 312 ms (see shaded areas in Figs. 2D and 4). Pursuit gain changed significantly as a function of condition, $F(2, 8) = 13.26$, $p < .01$. Follow-up *t*-tests showed that pursuit gain with priority to the periphery was significantly lower compared to priority to the fovea (0.99 vs. 1.03), $t(4) = 4.63$, $p < .025$, and compared to the single task (0.99 vs. 1.03), $t(4) = 3.95$, $p < .025$. Priority to the fovea and single task conditions did not differ. Further, we estimated the net decrease by subtracting post-flash from pre-flash gain. The decrease was 0.008, 0.003 for pursuit only, priority to fovea and priority to periphery, respectively. Follow-up *t*-tests showed that the condition with priority to the periphery was significantly different from priority to the fovea and single task, $ps < .05$.

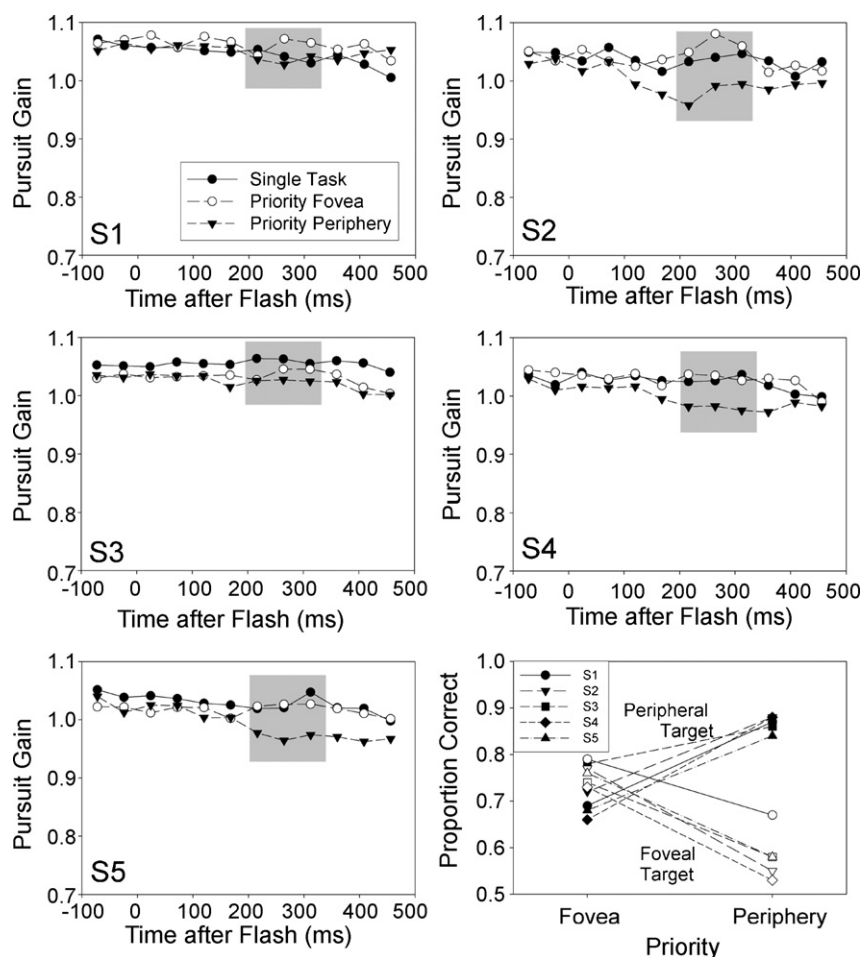


Fig. 4. Individual means in Experiment 2. Horizontal smooth pursuit gain and proportions correct for the six subjects in Experiment 2. The gray shaded area indicates the bins used as estimates of post-flash pursuit. The bottom right graph shows the mean proportion correct for the five subjects.

The decrease of pursuit gain (i.e., the difference pre- vs. post-flash) when priority was given to the peripheral perceptual task was smaller in this experiment than in the previous (0.138 vs. 0.035), $t(4)=3.43$, $p<.05$. This was true for all five subjects who participated in both experiments. Fig. 4 shows that priority to the fovea resulted in a higher gain than priority to the periphery for all five observers. The single task pursuit condition was the same (S4, S5), worse (S1, S2) or better (S3) than with priority to the fovea.

3.3. Discussion

Performance on the foveal discrimination task, was traded for performance on the peripheral discrimination task. This result is consistent with previous reports of flexible allocation of processing resources (e.g., [3]). Attentional priorities were formulated with respect to the two perceptual tasks while observers were asked to keep pursuit performance at its best. However, smooth pursuit was affected by perceptual priorities. If the foveal discrimination task was prioritized, smooth pursuit was better than when the peripheral discrimination task, involving a target that was different from the pursuit target, was prioritized. Note that there were no conflicting motion signals because the stimuli were flashed. Overall, the results of Experiment 2 show that smooth pursuit gain indexed which target was selected for perception. When the “attentional gate” was opened for a non-pursued target, smooth pursuit gain decreased. However, this does not imply that processing resources were shared between smooth pursuit and perception

of non-pursued targets. Remember that Experiment 1 failed to show trade-offs between the two.

Further, smooth pursuit gain in the single task condition was not different from the triple task condition with attention on the foveal target. This is quite surprising as the cognitive load was high. Observers had to make two discrimination judgments at the same time. Thus, when attention was allotted to the foveal flash, neither the high cognitive load nor the occurrence of the peripheral flash had a detrimental effect. Discussion of these findings is deferred to Section 4.

Further, the results of Experiment 2 rule out an alternative interpretation of Experiment 1. In Experiment 1, perceptual performance was unaffected by priorities. One may therefore argue that the perceptual task was not sensitive enough to reflect the allocation of attention, whereas smooth pursuit gain was sufficiently sensitive. However, peripheral orientation discrimination in Experiment 2 clearly improved when it was prioritized over foveal position discrimination, suggesting that the null effect in Experiment 1 was not due to a lack of sensitivity. It was not due to large inter-subject variability either, because the comparison of the effect of priority between Experiments 1 and 2 was significant.

4. General discussion

There are three main results. First, performance on the smooth pursuit task was not traded for performance on a single perceptual task that did not involve conflicting motion signals. Experiment 1 showed that resources (or effort) allotted to the pursuit task

could be changed voluntarily, but this had only negligible effects on peripheral orientation discrimination. Second, performance on the smooth pursuit task followed perceptual priorities. In Experiment 2, pursuit performance decreased if a non-pursued object was prioritized over the pursued object. Third, the triple task situation in Experiment 2 did not compromise smooth pursuit as long as most of the perceptual resources remained focused on the pursuit target.

The results of our study are incompatible with a strong version of resource sharing claiming that smooth pursuit and perception share all central resources. Rather, resource sharing does occur with respect to motion (cf. [13]), but not with respect to motionless features such as orientation. This conclusion is consistent with the underlying neurophysiology. Cortical motion processing for perception and smooth pursuit are intertwined, whereas orientation and motion are processed in partially independent cortical modules. Nonetheless, Experiment 2 showed that the allocation of attention to one of two flashed – and therefore motionless – stimuli affected smooth pursuit gain. Smooth pursuit gain was better when the pursuit target received more perceptual resources than peripheral flashes.

Why would a flashed stimulus that does not produce any retinal slip reduce pursuit gain? In particular, the decrease occurred when perception of the peripheral flash was given a high priority, and virtually absent when the peripheral flash was given low priority (cf. Experiment 2). This pattern suggests that the flash did not disturb pursuit in a purely bottom-up manner, but that the perturbation was modulated by top-down control settings. We believe that the mechanisms underlying the perturbation of smooth pursuit gain are similar to those involved in the remote distractor effect (RDE). When an irrelevant stimulus appears far from the target of a saccadic eye movement, saccadic reaction times are slowed down [32–35]. It has been suggested that the RDE arises from competition between the target and the distractor. A possible neural substrate for such competitive processes is the superior colliculus (SC; [36–39]). Recently, we have demonstrated that the RDE is modulated by top-down settings to particular stimulus features. If observers were asked to saccade to green targets, green distractors were more disturbing than gray distractors and vice versa for gray targets [40]. This is consistent with the notion that activity in the SC may be modulated by top-down as well as bottom-up factors [37,39]. A distractor effect has also been observed for the onset of smooth pursuit [41]. Because the SC plays a role in target selection for smooth pursuit [42], the mechanisms underlying the RDE in pursuit initiation may be similar to those of the saccadic RDE, and may also involve top-down control. In contrast to pursuit initiation, target selection is complete during steady-state pursuit. Nonetheless, a distractor may compete with the target, in particular when it is task-relevant as in the dual task conditions of Experiment 2. The resulting uncertainty (or neural noise) with respect to which target has to be pursued may subsequently decrease pursuit gain.

4.1. Comparison to non-visual dual tasks

There is a debate about whether non-visual dual tasks increase or decrease pursuit gain. With easy auditory tasks, such as listening to a series of letters [43] or auditory oddball detection [44], improvements of pursuit gain have been reported. In contrast, Hutton and Tegally [45] demonstrated that spatial and non-spatial auditory discrimination tasks degraded smooth pursuit compared to a single task condition. Also, they reported that demanding tapping tasks decreased performance (i.e., tapping a certain spatial pattern), but repetitive tapping with the same finger did not affect performance. On the basis of these results, Hutton and Tegally concluded that smooth pursuit performance may change according to

the difficulty of the secondary task. Easy tasks improve or have no effect on smooth pursuit performance, while difficult tasks degrade performance.

The present experiments shed light on the question whether performing visual tasks in addition to smooth pursuit decreases performance. The results suggest that difficulty is not the decisive factor, but rather the location of the visual stimulus. If attention is focused on the pursuit target, performance may be good despite a high load. These results are consistent with studies reporting that a visual task on the pursuit target, such as number reading [46] or letter reading [43,47], improved pursuit performance. Consistent with these reports, pursuit performance in our experiments did not decrease with higher load (Exp. 2), and reductions of pursuit gain due to shifts of attention were smaller than in a situation with only a single perceptual target (Exp. 2 vs. Exp. 1).

In sum, the present results suggest that perception and smooth pursuit do not share all resources. Processing of orientation in the absence of motion is not traded for smooth pursuit gain. However, when a peripheral discrimination task receives more resources than a central discrimination task, smooth pursuit gain suffers. Thus, diverting attention from the foveal pursuit target affects pursuit even in the absence of conflicting motion signals.

Acknowledgments

The three authors were supported by the Swiss National Foundation (SNF 10011-107768/1 and PDFM1-114417/1). We wish to thank Blandine Ulmann for helping to collect the data.

References

- [1] Navon D, Gopher D. On the economy of the human-processing system. *Psychological Review* 1979;86(3):214–55.
- [2] Norman DA, Bobrow DG. On data-limited and resource-limited processes. *Cognitive Psychology* 1975;7(1):44–64.
- [3] Sperling G, Melchner MJ. The attention operating characteristic: examples from visual search. *Science* 1978;202(4365):315–8.
- [4] Wickens CD. The structure of attentional resources. In: Nickerson R, editor. *Attention and performance VIII*. Hillsdale, NJ: Lawrence Erlbaum; 1980. p. 239–57.
- [5] Wickens CD. Multiple resources and mental workload. *Human Factors* 2008;50(3):449.
- [6] Brooks L. Spatial and verbal components of the act of recall. *Canadian Journal of Psychology* 1968;22:349–68.
- [7] Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research* 1996;36(12):1827–37.
- [8] Hoffman JE, Subramaniam B. The role of visual attention in saccadic eye movements. *Perception & Psychophysics* 1995;57(6):787–95.
- [9] Kowler E, Anderson E, Doshier B, Blaser E. The role of attention in the programming of saccades. *Vision Research* 1995;35(13):1897–916.
- [10] Barnes GR. Cognitive processes involved in smooth pursuit eye movements. *Brain and Cognition* 2008;68(3):309–26.
- [11] Kerzel D, Souto D, Ziegler NE. Effects of attention shifts to stationary objects during steady-state smooth pursuit eye movements. *Vision Research* 2008;48(7):958–69.
- [12] Madelain L, Krauzlis RJ, Wallman J. Spatial deployment of attention influences both saccadic and pursuit tracking. *Vision Research* 2005;45(20):2685–703.
- [13] Khurana B, Kowler E. Shared attentional control of smooth eye movement and perception. *Vision Research* 1987;27(9):1603–18.
- [14] Newsome WT, Wurtz RH, Dursteler MR, Mikami A. Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *Journal of Neuroscience* 1985;5(3):825–40.
- [15] Dursteler MR, Wurtz RH. Pursuit and optokinetic deficits following chemical lesions of cortical areas MT and MST. *Journal of Neurophysiology* 1988;60(3):940–65.
- [16] Krauzlis RJ. Recasting the smooth pursuit eye movement system. *Journal of Neurophysiology* 2004;91(2):591–603.
- [17] Treue S, Maunsell JH. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 1996;382(6591):539–41.
- [18] Treue S, Maunsell JH. Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *Journal of Neuroscience* 1999;19(17):7591–602.
- [19] Ferrera VP, Lisberger SG. The effect of a moving distractor on the initiation of smooth-pursuit eye movements. *Visual Neuroscience* 1997;14(2):323–38.

- [20] Ferrera VP, Lisberger SG. Neuronal responses in visual areas MT and MST during smooth pursuit target selection. *Journal of Neurophysiology* 1997;78(3):1433–46.
- [21] Hubel DH, Wiesel TN, Stryker MP. Anatomical demonstration of orientation columns in macaque monkey. *Journal of Comparative Neurology* 1978;177(3):361–80.
- [22] Zihl J, von Cramon D, Mai N. Selective disturbance of movement vision after bilateral brain damage. *Brain* 1983;106(Pt 2):313–40.
- [23] Barnes GR, Crombie JW. The interaction of conflicting retinal motion stimuli in oculomotor control. *Experimental Brain Research* 1985;59(3):548–58.
- [24] Niemann T, Ilg UJ, Hoffmann KP. Eye movements elicited by transparent stimuli. *Experimental Brain Research* 1994;98(2):314–22.
- [25] Suehiro K, Miura K, Kodaka Y, Inoue Y, Takemura A, Kawano K. Effects of smooth pursuit eye movement on ocular responses to sudden background motion in humans. *Neuroscience Research* 1999;35(4):329–38.
- [26] Coltheart M. Iconic memory and visible persistence. *Perception & Psychophysics* 1980;27(3):183–228.
- [27] Reeves A, Sperling G. Attention gating in short-term visual memory. *Psychological Review* 1986;93(2):180–206.
- [28] Posner MI, Cohen Y. Components of visual orienting. In: Bouma H, Bouwhuis DG, editors. *Attention and performance X*. Hillsdale, N.J.: Erlbaum; 1984.
- [29] Yantis S, Jonides J. Abrupt visual onsets and selective attention: evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance* 1984;10(5):601–21.
- [30] Cumming G, Fidler F, Vaux DL. Error bars in experimental biology. *Journal of Cell Biology* 2007;177(1):7–11.
- [31] Blohm G, Missal M, Lefevre P. Direct evidence for a position input to the smooth pursuit system. *Journal of Neurophysiology* 2005;94(1):712–21.
- [32] Benson V. A comparison of bilateral versus unilateral target and distractor presentation in the remote distractor paradigm. *Experimental Psychology* 2008;55(5):334–41.
- [33] Born S, Kerzel D. Influence of target and distractor contrast on the remote distractor effect. *Vision Research* 2008;48(28):2805–16.
- [34] Lévy-Schoen A. Détermination et latence de la réponse oculomotrice à deux stimulus simultanés ou successifs selon leur excentricité relative. *L'Année Psychologique* 1969;69(2):373–92.
- [35] Walker R, Deubel H, Schneider WX, Findlay JM. Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *Journal of Neurophysiology* 1997;78(2):1108–19.
- [36] Findlay JM, Walker R. A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences* 1999;22(4):661–74, discussion 674–721.
- [37] Godijn R, Theeuwes J. Programming of endogenous and exogenous saccades: evidence for a competitive integration model. *Journal of Experimental Psychology: Human Perception and Performance* 2002;28(5):1039–54.
- [38] Munoz DP, Fecteau JH. Vying for dominance: dynamic interactions control visual fixation and saccadic initiation in the superior colliculus. *Progress in Brain Research* 2002;140:3–19.
- [39] Trappenberg TP, Dorris MC, Munoz DP, Klein RM. A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience* 2001;13(2):256–71.
- [40] Born S., Kerzel D., Congruency effects in the remote distractor paradigm: evidence for top-down modulation, submitted for publication.
- [41] Knox PC, Bekkour T. Spatial mapping of the remote distractor effect on smooth pursuit initiation. *Experimental Brain Research* 2004;154(4):494–503.
- [42] Krauzlis RJ, Dill N. Neural correlates of target choice for pursuit and saccades in the primate superior colliculus. *Neuron* 2002;35(2):355–63.
- [43] Van Gelder P, Lebedev S, Liu PM, Tsui WH. Anticipatory saccades in smooth pursuit: task effects and pursuit vector after saccades. *Vision Research* 1995;35(5):667–78.
- [44] Kathmann N, Hochrein A, Uwer R. Effects of dual task demands on the accuracy of smooth pursuit eye movements. *Psychophysiology* 1999;36(2):158–63.
- [45] Hutton SB, Tegally D. The effects of dividing attention on smooth pursuit eye tracking. *Experimental Brain Research* 2005;163(3):306–13.
- [46] Shagass C, Roemer RA, Amadeo M. Eye-tracking performance and engagement of attention. *Archives of General Psychiatry* 1976;33(1):121–5.
- [47] Sweeney JA, Clementz BA, Haas GL, Escobar MD, Drake K, Frances AJ. Eye tracking dysfunction in schizophrenia: characterization of component eye movement abnormalities, diagnostic specificity, and the role of attention. *Journal of Abnormal Psychology* 1994;103(2):222–30.