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Differential effect of a distractor on primary saccades and perceptual localization

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Abstract

A distractor presented nearby the target of a goal-directed short latency saccade leads to spatial averaging, that is, the saccade lands between the target and the distractor. This so-called global effect is a characteristic feature of the spatial processing underlying the programming of saccadic eye movements. To determine whether this effect of near distractors on saccade metrics is also reflected in perceptual localization, subjects performed a saccade task and a perceptual localization task using identical, briefly flashed visual stimuli. To make the available visual processing time for saccades and perception more similar, we followed the target with a mask.

Without the mask, primary saccades with short latency landed between target and distractor. The distractor had less effect on primary saccades with longer latencies (>200 ms) and did not affect the final eye position after late secondary saccades in the dark. This indicates that the oculomotor system can correctly use information about the target location 200 ms after the target flash even if no visual stimulus is present during this period. Likewise the presence of a distractor did not affect perceptual localization.

Under the masking condition a similar global effect occurred for primary saccades with short latencies, but the latency dependence of the global effect was weakened. Secondary saccades and perceptual localization still did not show a global effect. The results suggest that the primary saccade is based on a specific target acquisition process that differs from that used for spatial perception and for the programming of memory-guided corrective saccades.

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1. Introduction

When a visual distractor is presented near to and simultaneously with a saccade target, the primary saccade tends to be directed to a location between the target and the distractor. This so-called global effect is observed in a variety of visual tasks, for example, during rapid automatic tracking, scanning for target detail, and comparison of target configurations. Early studies attributed the global effect to low-level mechanisms during early visual processing (Findlay, 1982). However, more recent explanations hold that higher level processing also plays a role in the occurrence of the global effect (Findlay & Gilchrist, 1997; He & Kowler, 1989). Whereas low-level visual processes are most probably shared by motor and perceptual systems, higher-level processes may be specific for each system.

Therefore, we investigated in this study whether the global effect concerns not only the saccadic response but also the perceived location of the target in space. Both saccadic response and perceived location can be subsumed under the term *localization*. Localization, as we define it, is the processing of visual spatial information from the retinal input to the motor or perceptual output. This processing runs in different stages, some of which are influenced by the global effect. These stages will hereafter be summarized as “*target acquisition*”. The question is whether the process of target acquisition is common or separate for saccades and perception. If the process of target acquisition were shared between perception and saccades, a similar global effect should occur for saccades and for perception. Thus, we infer the existence of common or separate target acquisition processes from measuring saccadic and perceptual localization.

To quantify perceptual localization we measured the point of subjective alignment of two sequentially presented peripheral targets (position comparison task).

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A distractor was presented simultaneously but closer to the fovea than the second target. Similar global effects in this perceptual task as in the saccade task would be indicated by the second target being perceived more centrally with the distractor than without it.

Differential effects of the distractor on saccadic and perceptual localization are more difficult to interpret, because they may have different reasons. Differences in the coordinate systems underlying saccadic and perceptual localization may account for differential effects of the distractor. Programming a saccade to a target flashed in darkness requires coding of the target location with respect to the position of the eye, i.e., an egocentric reference frame. In contrast, most perceptual localization tasks involve exocentric visual reference frames, i.e., with respect to other visual stimuli. Thus, a differential effect of the distractor on perception and saccades could be explained by separate target acquisition processes that are specific for egocentric and exocentric coordinates. Consequently, such an effect does not necessarily indicate a dissociation of target acquisition for saccades and for perception.

To test whether the global effect is specific for localization tasks involving egocentric or exocentric coordinates, we used two perceptual localization tasks. One required the use of egocentric coordinates, while the other was expected to be solved on the basis of exocentric coordinates. In the position comparison task, the second target could be localized only egocentrically, because it was presented in complete darkness. In the second task (distance comparison task) we measured the distance between two simultaneously presented spots which was perceived as equivalent to the distance between two previously presented spots. Simultaneously with and within the second pair of spots, a pair of distractors was presented. Since the distance between two simultaneously presented spots does not depend on the egocentric location of the spots, it should be evaluated on the basis of exocentric coordinates. A global effect in the distance comparison task would be indicated by the distance of the second target pair being perceived as smaller with the pair of distractors than without them. Identical distractor effects in these two perceptual localization tasks would indicate a common target acquisition process for egocentric and exocentric coordinate systems. Differences between the global effect for saccades and for perception would then suggest separate target acquisition processes for saccades and for perception. In other words, the target that guides our eyes would not be identical to the target we perceive.

Differential effects of the distractor on saccadic and perceptual localization may also be attributed to the longer response latency of perception. Thus, when a stimulus is presented during the entire latency period, the perceptual system has much more time available for processing the visual inflow than does the oculomotor

system. If the acuity of the target acquisition process improves during this additional processing time, the perceptual system can access a target representation that is less sensitive to the distractor than the oculomotor system. To control the duration of the visual inflow, we flashed target and distractor for only 50 ms. However, if the target acquisition process is able to continue working on the basis of a short term visual memory in the absence of visual inflow, the processing time may still be much longer for the perceptual system than for the saccadic system. Thus, differential effects of distractors on saccadic and perceptual localization could be explained by the dynamics of a common internal spatial processing. To check for this possibility, we performed an additional experiment in which target and distractor were immediately followed by a visual mask. This procedure is believed to reduce the available visual processing time for both the saccadic and the perceptual systems (Aitsebaomo & Bedell, 1992, 2000). If the global effect occurred in a common pathway whose processing time is restricted by the mask, then the effects of the distractor on saccades and on perception would be expected to become more similar under masking conditions.

2. Methods

2.1. Subjects

Six volunteers (age between 26 and 42 years), all employees of the university and experienced in eye movement studies, participated in the experiments. Four were naive with respect to the purpose of the experiment. Two of these naive subjects who participated in the saccade task and the “position comparison task” (see below) were not available for the “distance comparison task” and the masking experiments. They were replaced by two other subjects who were also naive with respect to the purpose of the experiment. For each subject the different experiments were performed on different days.

2.2. Apparatus

All visual targets were projected on the horizontal meridian at eye level onto a fronto-parallel screen at a viewing distance of 140 cm in a dark room. The subjects could not see other objects than the target spots, which had a diameter of 0.1 deg of visual angle. A green helium–neon laser was used to project the fixation spot, which could be turned on and off by means of a piezo-controlled optical device. A red laser diode (which could be modulated up to 1 MHz) was used to project the targets onto the screen. Its position was controlled by a mirror galvanometer (General Scanning G120D, USA) that could execute a step of 20 deg amplitude in less than 2 ms with an absolute position error of less than 1 mm

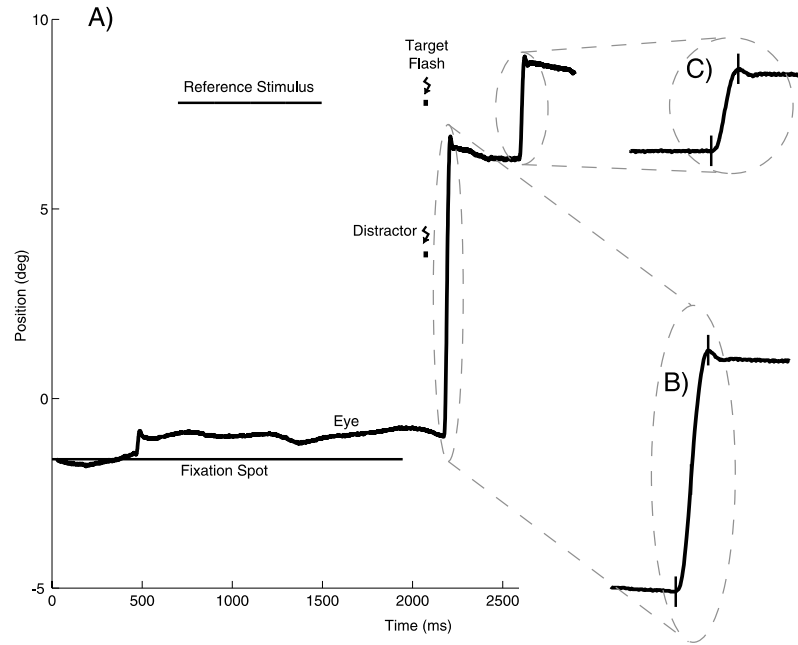


Fig. 1. Saccade task: example of a target-distractor trial. (A) The eye position trace shows the spatial averaging that is typical for the global effect. The primary saccade, which is executed in complete darkness, lands between the target flash and the distractor. The two enlarged sections of the primary saccade (B) and the secondary saccade (C) show the marks for the onset and the offset of the saccade used to compute the saccade amplitudes and the primary and final amplitude errors.

(0.04 deg of visual angle). By stepping the mirror from one position to another every 10 ms, two targets could be presented quasi-simultaneously.

The position error signal of the servo drive amplifier (General Scanning Edb2, USA), which controlled the mirror galvanometer in an analog feedback loop, was used to blank the laser diode during the transition of the mirror from one position to the other. This additional hardware circuit allowed us to present two target spots simultaneously without an interconnecting line between them. Horizontal eye movement signals were recorded with an infrared eye tracker (IRIS, Skalar, Netherlands). They were sampled and stored at 1 kHz on a computer hard disk. The software running on this system (REX Hays, Richmond, & Optican, 1982) controlled the analog and digital output for the galvanometer and laser devices. The eye movement signal was calibrated on the basis of 50 fixations on seven positions on the horizontal meridian (0, ± 4 , ± 8 , ± 12 deg), which were collected from each subject immediately before each experimental session. A third order polynomial was fitted to the horizontal position signal of the IRIS device and used to calibrate the raw data.

2.3. Paradigms

2.3.1. Saccade task

In the saccade task, a green fixation spot was presented for 2.2 s. A peripheral red target spot, flashed for

50 ms, was presented 100 ms after extinction of the fixation spot (see Fig. 1). The position of this saccade target was chosen randomly between 8 and 11 deg right or left of the fixation spot (mean: 9.5 deg, std: 0.9 deg). In addition to the eccentricity, the side of the saccade target was also randomized. In 50% of all trials a distractor flash (also red like the target), randomly intermixed, was presented simultaneously with the target flash but always 4 deg closer to the fovea. Subjects were instructed to ignore this distractor and to make a saccade directly to the more eccentric target as quickly and as precisely as possible. In order to provide a visual stimulation comparable to the one used in the task for perceptual localization (see section *Position Comparison Task*) an additional red laser spot was presented for 800 ms during the presence of the fixation spot at the location of the saccade target. This so-called reference stimulus was switched off 450 ms before the fixation spot disappeared. The fixation spot reappeared 2.8 s after the target flash at the location of the saccade target.

To test for possible effects of the reference stimulus on the saccade we performed a control experiment that was identical to the saccade task except that there was no reference.

2.3.2. Position comparison task

The sequence and the timing of the visual stimuli was identical to those in the saccade task. Also the position of the reference relative to the fixation spot was

randomly distributed as it was in the saccade task (eccentricity: 9.5 ± 0.9 deg). The only differences concerned the position of the fixation spot and the position of the target. The fixation spot always reappeared at the center of the screen (Fig. 2). The target flash did not occur exactly at the location of the randomly chosen reference, but at a location randomly selected (see below for details) in the near vicinity of the reference. The subjects then had to indicate by joystick response in a two-alternative, forced-choice task whether the target flash had appeared to the right or to the left of the reference. Again, subjects were instructed to ignore the distractor, which, as in the saccade paradigm, appeared randomly intermixed in 50% of the trials at an eccentricity 4 deg smaller than the target flash. The central fixation spot reappeared 200 ms after the joystick response.

To determine the position of the target flash for each trial we used an adaptive maximum-likelihood procedure (Hall, 1981). This method was slightly modified in order to present more of the “easy” trials than the original method provided. Briefly, the position of the target flash was randomly selected from a distribution centered on an adaptive maximum-likelihood estimate of the location where the target flash appeared to be aligned with the reference. The random distribution was bimodal and was adaptively scaled such that the distance between the two maxima was 2.6 times the standard deviation of the perceived target location. At the beginning of the session (when responses of the subject were not available) the distribution was centered on the

location of the previous reference. The initial width of the distribution was ± 5 deg. After each joystick response these two estimates (mean and standard deviation) were updated separately for the trials with the target flash on the left and on the right side. The estimates were based on all prior responses on the same side. This method has the advantage of combining non-predictability of the position of each target flash with maximization of the number of target flashes presented in the region in which the subject perceives the flash to coincide with the memorized reference position.

2.3.3. Distance comparison task

The timing and the location of the visual stimuli were identical to those used for the position comparison except that a second red laser spot was presented at the opposite side of the fixation spot simultaneously with, and at the same eccentricity as the reference. In this way the unilateral reference stimulus of the position comparison task was now replaced by a pair of reference stimuli that were symmetrically arranged around the fixation spot. In the same way the target flash and the distractor were also replaced by symmetrical pairs of spots. In a two-alternative, forced-choice task the subjects then had to indicate by joystick response whether the distance between the two target flashes was larger or smaller than the distance between the two reference stimuli. Again, the random distribution used to select the distance between the target flashes was adaptively adjusted during the experiment.

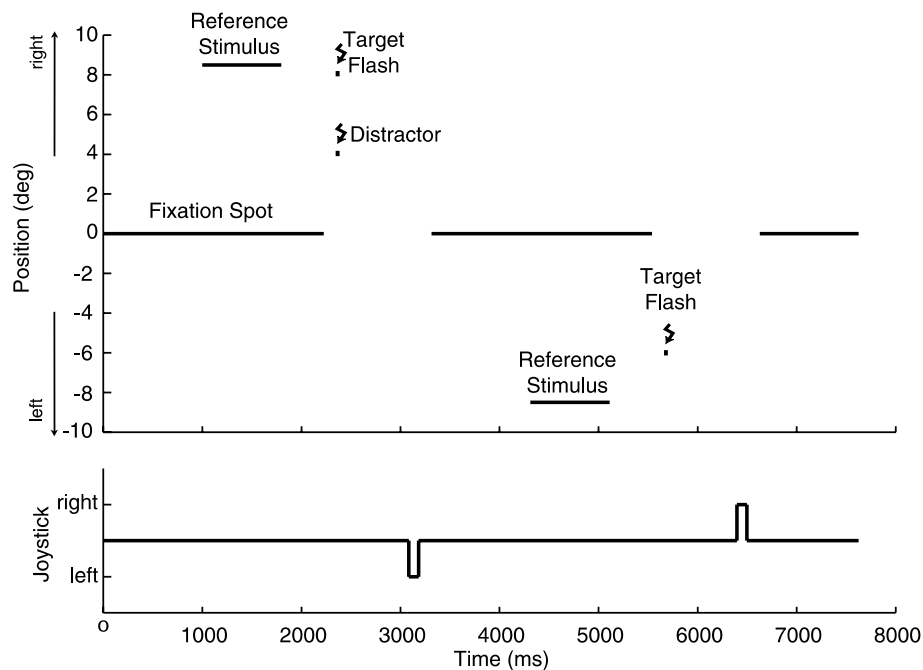


Fig. 2. Position comparison task: timing of the visual stimuli (fixation spot, reference stimulus, target flash, distractor) and an example of a joystick response by which the subject indicated the perceived misalignment between reference and target flash. In each session trials with distractor (left) were randomly intermixed with trials in which a single target flash was presented in darkness.

2.3.4. Masking experiments

The saccade task (with reference) and the localization task based on position comparison were repeated with a mask. This was presented immediately after the extinction of the saccade target or of the target flash. The mask consisted of an array of 30 red laser spots equidistantly spaced and shown on the horizontal meridian. The length of this array was 30 deg. The horizontal position of the array was randomized such that the center of the array was equally distributed between ± 2.5 deg around the actual target or target flash. The duration of the saccade target and the target flash was increased to 100 ms. The mask was switched off immediately before the new fixation spot appeared.

2.4. Off-line data analysis

In the saccade paradigm, the calibrated eye position was marked on the basis of velocity criteria. The eye velocity was computed using a symmetrical two-point differentiator after low-pass filtering with a Gaussian FIR filter with a cut-off frequency of 33 Hz (transmission gain of 0.1 at 85 Hz). Fast eye movements occurring between 100 and 600 ms after the target flash were marked as a saccade if the peak velocity was higher than 50 deg/s, the duration shorter than 200 ms, and the

amplitude of the movement larger than 0.5 deg. (Fig. 1). Beginning and end of the saccade were defined as the point where eye velocity raised above or dropped below 10% of peak velocity. The primary amplitude error was defined as the difference between the eye position at the end of the primary saccade and the flash position. If a secondary saccade occurred after the primary saccade but not later than 600 ms after the target flash, the final amplitude error was defined as the difference between the eye position at the end of the secondary saccade and the flash position. Otherwise, if no secondary saccade occurred, the final amplitude error was identical to the primary amplitude error. The sign of the amplitude error was adjusted depending on saccade direction. Thus, a negative sign indicates that the eye undershot the target location, and a positive sign, that it overshot. Trials in which the subjects did not maintain fixation for at least 200 ms before the target flash were not included in the analysis. The latency of the primary and secondary saccades was defined as the time between the onset of the target flash and the onset of the saccade.

For the position comparison task, the cumulative proportion of trials in which the target flash was judged more peripheral than the reference was measured at each misalignment of the target and the reference (see Fig. 3). A cumulative normal distribution was fitted to this

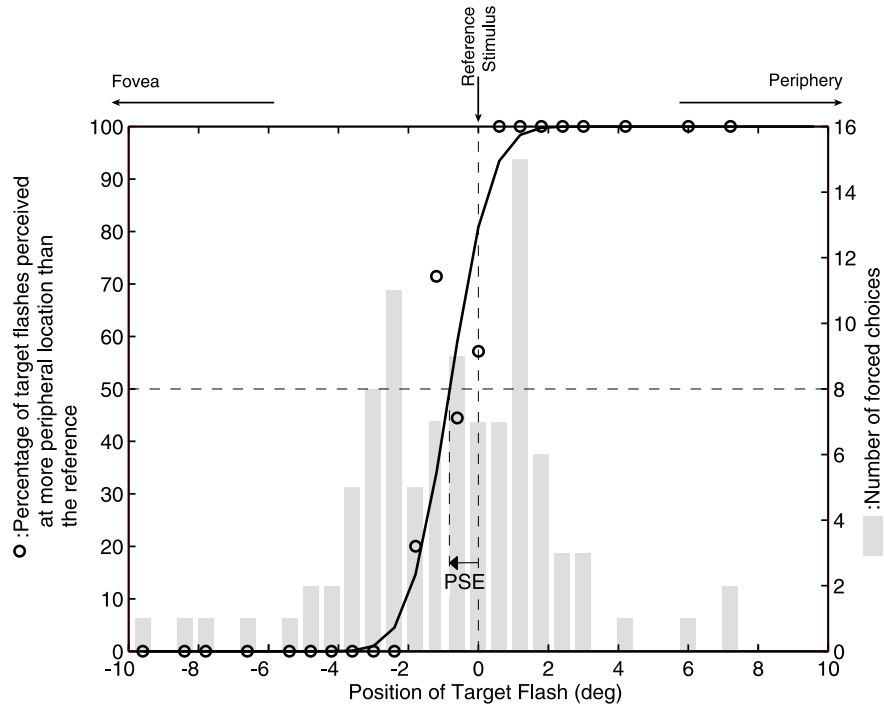


Fig. 3. Psychometric curve (solid) fitted to the relative frequency (circles) of the response that the target flashed more peripheral than the reference. The position of the target flash is shown on the abscissa with respect to the horizontal position of the reference, with which the target flash had to be compared. Typical example of the data acquired in an experiment with one subject performing the position comparison task. The graph summarizes the 100 two-alternative, forced-choice responses collected in trials with a distractor. The 50% value of the fitted cumulative normal distribution (solid line) defines the perceptual misalignment M . The negative value of M (-0.82 deg) indicates that the target flash has to be presented closer to the fovea than the reference in order to appear to be at the same location. The precision of the subjective localization is quantified by the standard deviation of the fitted normal distribution (0.94 deg).

histogram whose mean gave the point of subjective equivalence (PSE). A negative sign of the PSE indicates that the target flash had to be presented more foveally than the reference in order to appear at the same location. Equivalently, a negative PSE implies that a target, presented at the same location as the reference, was perceived more peripherally than the reference. To compare the perceptual localization error directly with the amplitude error of the saccade, a measure of the localization error should be positive when the target flash was perceived more peripherally from the reference than it actually was. Hence, because a negative PSE corresponds to a positive localization error, and a positive PSE to a negative localization error, the localization error was defined by the negative PSE. It is important to note that both the saccade amplitude error and the perceptual localization error are defined as signed errors indicating not only the absolute size of the error but also its direction. The advantage of this definition is that a similar distractor effect on saccades and on perception will manifest in a similar shift of the signed amplitude error and of the signed localization error independent of the initial error direction without distractor. The precision of the subjective judgement was defined by the standard deviation of the fitted normal distribution (Fig. 3).

The same analysis was performed for the distance comparison as for position comparison. It was based on the relative frequency of trials in which the distances between the two symmetrical target flashes appeared to be larger than the distance between the two symmetrical reference stimuli. This frequency was computed as a function of half the difference between the actual distance of two target flashes and the actual distance of two reference stimuli. Again the localization error was quantified by the negative PSE. The factor 0.5 was applied to the difference between the two distances because this allows direct comparison with the localization error as defined in the position comparison task. Trials in which the subject moved the eye by more than 0.5 deg during the time interval between the extinction of the reference and the target flash were excluded from the analysis.

The effects of the distractor on the primary amplitude error, the final amplitude error, and the localization error were evaluated for each subject by determining the difference of the corresponding means between trials with and without distractor. The significance of this effect was tested by means of a paired *t*-test based on the individual mean values. For the statistical analysis of differences between experiments, the data of only those subjects who performed both experiments were used.

For the localization paradigms (position and distance comparison) the response latency was defined as the time interval between the onset of the target flash and the joystick response. To investigate the role of response latency for the perceptual localization error the data of each subject and of each experiment were split along the median of the response latencies into two equally large categories (short/long latencies).

3. Results

The results will be presented separately for the saccade task, the position comparison task, and the distance comparison task.

3.1. Saccade task

Of the 200 trials per subject, minimally 139 and maximally 178 saccades were included in the analysis. The amplitude errors of the primary saccades are shown in the left part of Table 1. When the distractor was flashed, the primary saccade showed increased undershoot (-1.84 ± 0.49 deg; $N = 6$) compared with single target flashes (-0.42 ± 1.06 deg; $N = 6$). The paired *t*-test showed that this increase was significant ($t(5) = 4.61$; $p < 0.006$). In trials with the distractor, the average landing position of the saccade was very close to the center between the target and the distractor, which appeared at a distance of 4 deg from the target. Thus, a distinct global effect was observed. The undershoot with single target flashes corresponded to about 5% of the target amplitude.

Table 1
Primary amplitude errors in saccade task (with reference) (deg)

No mask			With mask		
Subject	Single target flash	With distractor	Subject	Single target flash	With distractor
TE	1.14 ± 1.62 ($N = 77$)	-1.17 ± 1.91 ($N = 76$)	TE	-0.27 ± 1.75 ($N = 89$)	-2.42 ± 1.46 ($N = 93$)
AS	-0.77 ± 1.87 ($N = 94$)	-1.87 ± 1.87 ($N = 76$)	AS	-1.31 ± 2.73 ($N = 53$)	-1.85 ± 3.04 ($N = 53$)
US	0.01 ± 2.53 ($N = 73$)	-2.28 ± 2.12 ($N = 78$)	US	-0.75 ± 1.70 ($N = 61$)	-2.68 ± 1.51 ($N = 71$)
JD	0.18 ± 1.56 ($N = 85$)	-1.35 ± 1.73 ($N = 93$)	ES	-1.64 ± 1.38 ($N = 65$)	-2.64 ± 1.74 ($N = 69$)
OK	-1.37 ± 2.38 ($N = 62$)	-1.99 ± 2.23 ($N = 77$)	MK	-1.65 ± 1.90 ($N = 89$)	-2.53 ± 1.44 ($N = 97$)
SG	-1.69 ± 1.73 ($N = 73$)	-2.36 ± 2.01 ($N = 74$)	SG	-1.55 ± 1.98 ($N = 79$)	-2.87 ± 2.19 ($N = 85$)
Group mean	-0.42 ± 1.06 ($N = 6$)	-1.84 ± 0.49 ($N = 6$)	Group mean	-1.20 ± 0.57 ($N = 6$)	-2.50 ± 0.35 ($N = 6$)

The subjects initiated a primary saccade at a mean latency of 184 ± 50 ms after the onset of the target flash. The latency did not depend on whether the target was flashed alone or simultaneously with the distractor ($t(5) = 0.02$; $p < 0.98$). To evaluate the effect of the primary saccade latency on the global effect, the primary amplitude errors of each subject were averaged within four equidistant groups of latencies between 50 and 350 ms. Separate means were computed for trials with and without distractor. These means were submitted to a repeated measures ANOVA with the two factors *Latency* (four levels) and *Distractor* (four levels: with/without). This analysis revealed not only that the distractor had a main effect ($F(1, 5) = 13.6$; $p < 0.05$) that corresponded to the global effect, but also that there was a significant interaction between both factors ($F(3, 15) = 3.79$; $p < 0.05$), indicating that the global effect was dependent on the latency of the primary saccade. Fig. 4A shows that the global effect was stronger for short latency saccades and weaker for latencies above 200 ms. The post-hoc planned comparison (Scheffé test) showed that the primary amplitude error for latencies between 125 and 200 ms in the trials with distractor differed significantly from the errors observed in the two groups at higher latencies (200–275 ms: $p < 0.04$; 275–350 ms: $p < 0.004$). The difference of the primary amplitude error between the two short latency groups (50–125 ms versus 125–200 ms) was not significant ($p < 0.4$). This effect of the latency on the primary saccade was not observed in the trials without distractor. The post-hoc analysis of these trials did not show any significant differences between the latency groups.

Small secondary saccades in darkness occurred in only 20% of the trials without a distractor. These secondary saccades did not have a preferred direction. In contrast, the systematic undershoot of the primary saccade after trials with distractor was compensated for by an onward secondary saccade in 43% of the cases. The mean latency of these secondary saccades, executed in complete darkness, was 467 ± 100 ms after the target flash. The distractor had no significant effect ($t(5) = 1.66$; $p < 0.15$) on the final amplitude error (Table 2, left part).

Fig. 5A shows all responses of one subject separately for the targets flashed alone (Fig. 5A, left) and together with the distractor (Fig. 5A, right). We selected the subject whose primary and final amplitude errors were closest to the overall mean. All eye position traces were shifted to coincide with their starting point and scaled by the actual target amplitude. In the trials with distractor, the continuous increase of the mean normalized eye position after the beginning of the saccade is due to frequent onward secondary saccades in darkness. These secondary saccades compensated completely for the effect of the distractor, since after 600 ms there was no difference in the mean eye position between the left and right parts of Fig. 5A.

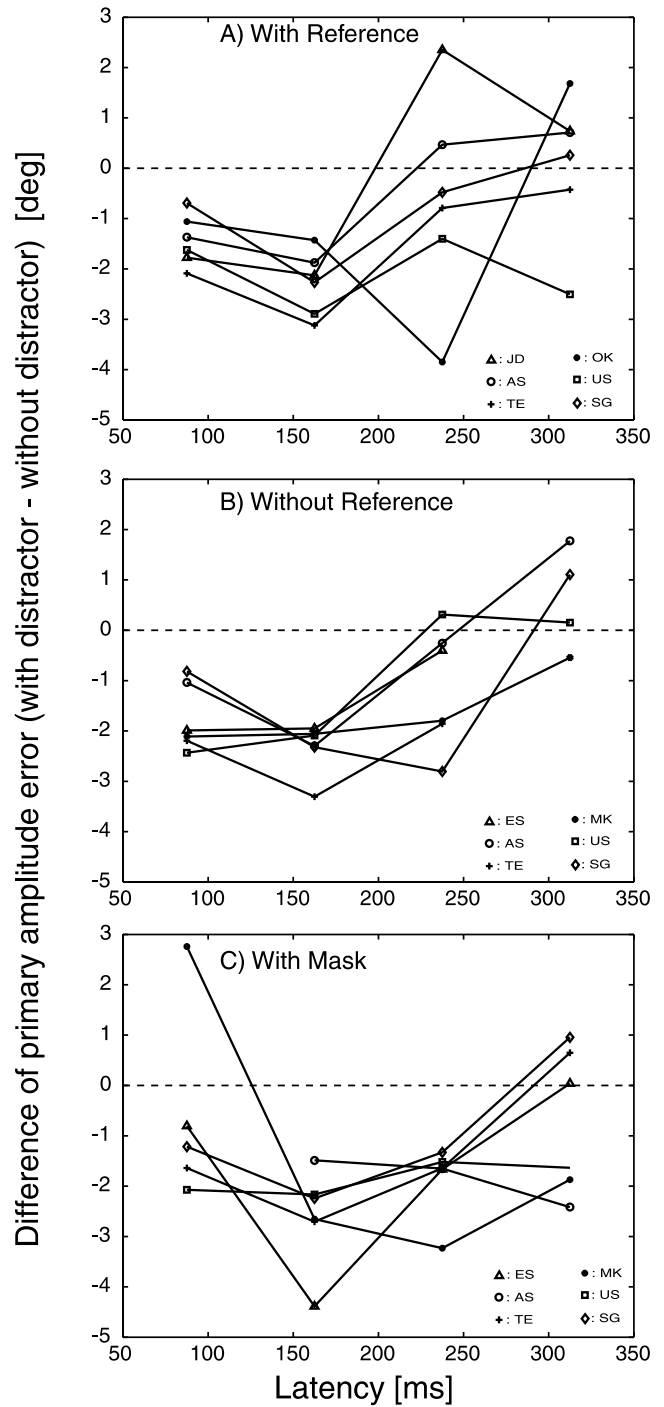


Fig. 4. Each symbol shows the difference of the mean amplitude error of the primary saccade between trials with and trials without distractor for one subject. This variable quantifies the global effect, because negative values on the ordinate indicate that the end point of the saccade deviated centrally (toward the distractor). Data are pooled within latency groups of 75 ms duration, centered around 88, 163, 238, and 313 ms. The three subfigures show data from the different saccade experiments: A: without mask and with reference; B: without mask and without reference; C: with mask and with reference. The dependence of the global effect on the latency of the primary saccade was clearly reduced or even abolished under the masking condition.

Table 2
Final amplitude errors in saccade task (with reference) (deg)

No mask			With mask		
Subject	Single target flash	With distractor	Subject	Single target flash	With distractor
TE	0.58 ± 2.67 (<i>N</i> = 77)	-0.51 ± 2.26 (<i>N</i> = 76)	TE	-0.20 ± 2.01 (<i>N</i> = 89)	-0.61 ± 1.90 (<i>N</i> = 93)
AS	0.14 ± 2.40 (<i>N</i> = 94)	0.17 ± 2.76 (<i>N</i> = 76)	AS	-0.44 ± 2.79 (<i>N</i> = 53)	-0.53 ± 3.24 (<i>N</i> = 53)
US	-0.32 ± 3.09 (<i>N</i> = 73)	-2.26 ± 2.63 (<i>N</i> = 78)	US	-0.65 ± 1.65 (<i>N</i> = 61)	-2.63 ± 1.51 (<i>N</i> = 71)
JD	0.44 ± 1.69 (<i>N</i> = 85)	0.35 ± 1.94 (<i>N</i> = 93)	ES	-2.24 ± 1.91 (<i>N</i> = 65)	-1.59 ± 1.85 (<i>N</i> = 69)
OK	-1.23 ± 2.61 (<i>N</i> = 62)	-1.25 ± 2.44 (<i>N</i> = 77)	MK	-1.61 ± 1.96 (<i>N</i> = 89)	-2.28 ± 1.50 (<i>N</i> = 97)
SG	-1.84 ± 1.55 (<i>N</i> = 73)	-2.01 ± 2.02 (<i>N</i> = 74)	SG	-1.68 ± 1.88 (<i>N</i> = 79)	-2.46 ± 2.22 (<i>N</i> = 85)
Group mean	-0.37 ± 0.97 (<i>N</i> = 6)	-0.92 ± 1.10 (<i>N</i> = 6)	Group mean	-1.14 ± 0.82 (<i>N</i> = 6)	-1.68 ± 0.93 (<i>N</i> = 6)

3.1.1. Saccade task without reference

When the saccade task was repeated without the reference being presented during the fixation period, the primary and final amplitude errors (Table 3) were similar to the condition with the reference (Tables 1 and 2, left part). This was confirmed by submitting the individual means of the four subjects who performed the saccade task with and without the reference to a repeated measures ANOVA with the factors *Reference* (with/without) and *Distractor* (with/without). For the primary amplitude error the global effect was reflected in the significant main effect of the factor *Distractor* ($F(1, 3) = 20.85$; $p < 0.02$). The final amplitude error did not depend on the presence or absence of the distractor. No significant main effect of the factor *Reference* was found. There was also no interaction between the two factors, indicating that the global effect did not depend on the presence of the reference. Fig. 4B illustrates that the dependency of the global effect on the latency of the primary saccade does not differ from that observed with the reference (Fig. 4A). Secondary saccades occurred in 19% of trials without distractor and in 40% of trials with distractor. Again, as in the saccade task with reference, the secondary saccade compensated completely for the undershoot of the primary saccade induced by the distractor (Fig. 5B).

3.1.2. Saccade task with mask

The final amplitude error in the masking experiment, when the target flash was immediately replaced by the horizontal array of dots (Table 2, right part), was more negative compared to the experimental condition without the mask (Table 2, left part). A repeated measures ANOVA (four subjects) with the two factors *Mask* (with/without) and *Distractor* (with/without) showed that this main effect of the factor *Mask* was significant ($F(1, 3) = 14.56$; $p < 0.03$). Under the masking condition (Table 1, right) the primary amplitude error showed a similar (0.6 deg) but nonsignificant tendency to shift in the negative direction. However, neither the primary nor the final amplitude error showed any interaction between the two factors *Mask* and *Distractor* (primary: $F(1, 3) = 0.1744$; $p < 0.8$, final: $F(1, 3) = 0.01$; $p < 0.9$),

indicating that the overall size of the global effect did not depend on the presence of the mask. As in the saccade task without the mask (Fig. 4A), the dependence of the global effect on the latency of the primary saccade was evaluated by means of a repeated measures ANOVA with the two factors *Latency* (four levels) and *Distractor* (two levels: with/without). This analysis again showed that the distractor had a (not surprising) main effect ($F(1, 4) = 78.48$; $p < 0.001$) on the primary amplitude error indicating the global effect. But in contrast to the experiment without the mask, the latency also had a main effect ($F(3, 12) = 9.66$; $p < 0.002$). For trials with and without distractor, the saccade with longer latency landed closer to the target. This improvement of saccade accuracy cannot be interpreted as a dependence of the global effect on latency, since, in contrast to the experiment without the mask, the interaction between the factors *Latency* and *Distractor* in the masking experiment did not reach significance ($F(3, 12) = 3.1$; $p < 0.07$). Thus, the mask weakened the effect of latency on the global effect (see Fig. 4C). Nevertheless, the mask did not prevent the occurrence of secondary saccades in the direction of the target location as shown in Fig. 5C. The average latency of these secondary saccades in the trials with distractor was 588 ± 174 ms after the onset of the target flash. A paired *t*-test for the four subjects who performed both the experiment with and without mask showed only a nonsignificant tendency ($t(3) = 1.31$; $p < 0.3$) for the latency of the secondary saccade to increase under the masking condition. A similar tendency was also observed for the primary saccade (245 ± 77 ms). On average the frequency of secondary saccades was 27% for the trials without distractor and 36% for the trials with distractor.

3.2. Position comparison task

The minimum and the maximum number of joystick responses included in the analysis of a subject was 166 and 200, respectively. On the average, the latency of the joystick response after the target flash was shorter in trials without distractor (1148 ± 187 ms, $N = 6$) than in trials with distractor (1333 ± 131 ms, $N = 6$). The mean

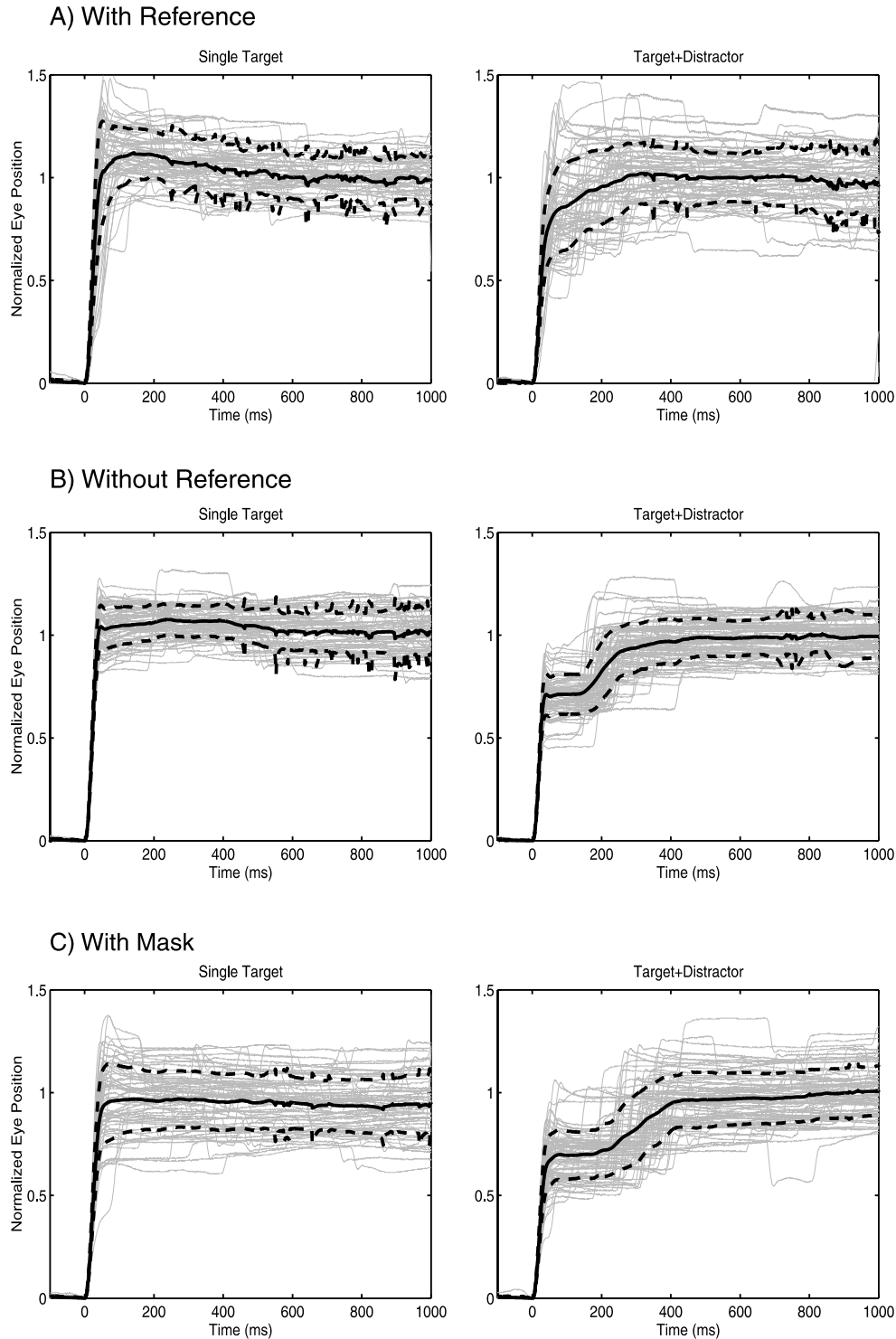


Fig. 5. All eye position traces of one subject are shown for saccades in trials without (left side) and with (right side) distractor flash. All traces were aligned such that time and position are shown with respect to the saccade onset. The shifted trace was normalized by dividing the shifted eye position by the target amplitude (the distance between fixation spot and target flash). The solid lines show the average normalized eye positions for all trials (solid) and the standard deviation (dashed). The three subfigures show data from the different saccade experiments: (A) without mask and with reference; (B) without mask and without reference; (C) with mask and with reference. Whereas the final normalized eye position is reached immediately after the primary saccade in trials without distractor, the average normalized eye position increases in the post-saccadic period in trials with distractor due to frequent secondary saccades in darkness.

paired latency difference between the two trial types (-185 ± 108 ms) was significant (paired t -test: $t(5) =$

4.2 ; $p < 0.01$). The localization errors of all subjects are shown in the left part of Table 4. For trials with a single

Table 3
Amplitude errors in saccade task (without reference) (deg)

Subject	Primary amplitude error		Final amplitude error	
	Single target flash	With distractor	Single target flash	With distractor
TE	0.36 ± 1.09 (N = 95)	-2.28 ± 0.98 (N = 95)	0.45 ± 1.02 (N = 95)	-1.01 ± 1.42 (N = 95)
AS	0.86 ± 2.46 (N = 72)	0.35 ± 2.49 (N = 56)	0.77 ± 3.36 (N = 72)	1.45 ± 3.35 (N = 56)
US	0.36 ± 1.28 (N = 86)	-1.35 ± 1.64 (N = 101)	0.28 ± 1.22 (N = 86)	-0.67 ± 1.48 (N = 101)
ES	-0.31 ± 0.70 (N = 88)	-2.09 ± 0.94 (N = 101)	-0.77 ± 1.20 (N = 88)	-1.08 ± 1.10 (N = 101)
MK	-0.56 ± 1.48 (N = 92)	-2.04 ± 1.13 (N = 100)	-0.77 ± 1.87 (N = 92)	-2.03 ± 1.15 (N = 100)
SG	-0.69 ± 1.20 (N = 90)	-2.75 ± 1.71 (N = 89)	-0.97 ± 1.38 (N = 90)	-1.48 ± 2.02 (N = 89)
Group mean	0.00 ± 0.62 (N = 6)	-1.69 ± 1.10 (N = 6)	-0.17 ± 0.75 (N = 6)	-0.80 ± 1.20 (N = 6)

Table 4
Localization error for position comparison (deg)

No mask			With mask		
Subject	Single target flash	With distractor	Subject	Single target flash	With distractor
TE	0.68 ± 0.91 (N = 100)	0.82 ± 0.94 (N = 100)	TE	0.59 ± 1.01 (N = 93)	2.17 ± 1.01 (N = 96)
AS	1.22 ± 0.90 (N = 81)	1.65 ± 1.53 (N = 85)	AS	-1.50 ± 0.76 (N = 74)	-2.27 ± 2.86 (N = 61)
US	0.64 ± 1.07 (N = 94)	0.37 ± 1.67 (N = 96)	US	-0.00 ± 1.76 (N = 98)	-0.06 ± 1.90 (N = 98)
JD	0.88 ± 0.63 (N = 97)	1.81 ± 0.65 (N = 97)	ES	-0.12 ± 2.36 (N = 96)	0.08 ± 1.41 (N = 96)
OK	0.80 ± 1.13 (N = 75)	1.00 ± 1.28 (N = 81)	MK	0.20 ± 1.29 (N = 99)	-0.19 ± 1.78 (N = 99)
SG	1.17 ± 1.19 (N = 98)	1.93 ± 0.85 (N = 96)	SG	-0.09 ± 1.26 (N = 100)	-0.35 ± 1.00 (N = 100)
Group mean	0.90 ± 0.25 (N = 6)	1.26 ± 0.62 (N = 6)	Group mean	-0.15 ± 0.71 (N = 6)	-0.10 ± 1.41 (N = 6)

target flash, the mean localization error was 0.90 deg with an inter-subject standard deviation of 0.25 deg, indicating that the eccentricity of target flash was overestimated compared to the eccentricity of the reference. The precision (as defined under “Off-line Data Analysis”) of the subjective estimates ranged between 0.6 and 1.7 deg. In the trials with the distractor, the relative overestimation of the eccentricity of the target flash (1.26 ± 0.62 deg, $N = 6$) tended to be even larger than in trials without distractor, but this tendency did not reach significance (paired t -test: $t(5) = -2.05$; $p < 0.1$). To analyze the dependence of the perceptual localization error on the response latency the data of each subject were split along the median response latency. The average response latency across subjects was 931 ± 138 ms ($N = 6$) in the “short” and 1562 ± 178 ms ($N = 6$) in the “long” category. The mean localization errors were again computed separately for these latency categories and for trials with and without distractor. The results were submitted to a repeated measures ANOVA with the two factors Latency (short/long) and Distractor (with/without). No main effects or interactions were observed, indicating that the localization error did not differ between trials with and without distractor or between trials with short and long response latencies (Fig. 6A).

3.2.1. Position comparison task with mask

When the target flash was followed immediately by the mask, the distractor had an even smaller effect on the localization errors (Table 4, right part) than without the

mask. With the mask, the paired difference between distractor trials and non-distractor trials was only 0.05 ± 0.82 deg ($t(5) = 0.15$; $p < 0.9$). The repeated measures ANOVA with the two factors Mask (with/without) and Distractor (with/without) did not show significant main effects of the factor Mask ($F(1, 3) = 2.17$; $p < 0.24$) or of the factor Distractor ($F(1, 3) = 0.65$; $p < 0.48$). For this analysis only four subjects were used (TE, AS, US, SG). There was also no interaction ($F(1, 3) = 0.05$; $p < 0.84$) between the two factors, indicating that the effect of the distractor on the localization error was not affected by the mask.

The separate analysis of the localization error for the different categories of response latencies in the masking experiment could be performed with the data of only three subjects, since the remaining three exhibited much longer latencies (about 2.7 s) with very small intertrial variability (<100 ms). The average response latency across subjects was 890 ± 262 ms ($N = 3$) in the short and 1480 ± 374 ms ($N = 3$) in the long category (Fig. 6B). The repeated measures ANOVA of the localization error with the two factors Latency (short/long) and Distractor (with/without) did not show significant main effects or interactions that would indicate a dependence of a distractor effect on the response latency.

3.3. Distance comparison task

The average localization error in the distance comparison task was very similar to the one in the position comparison task. This holds for trials without (distance:

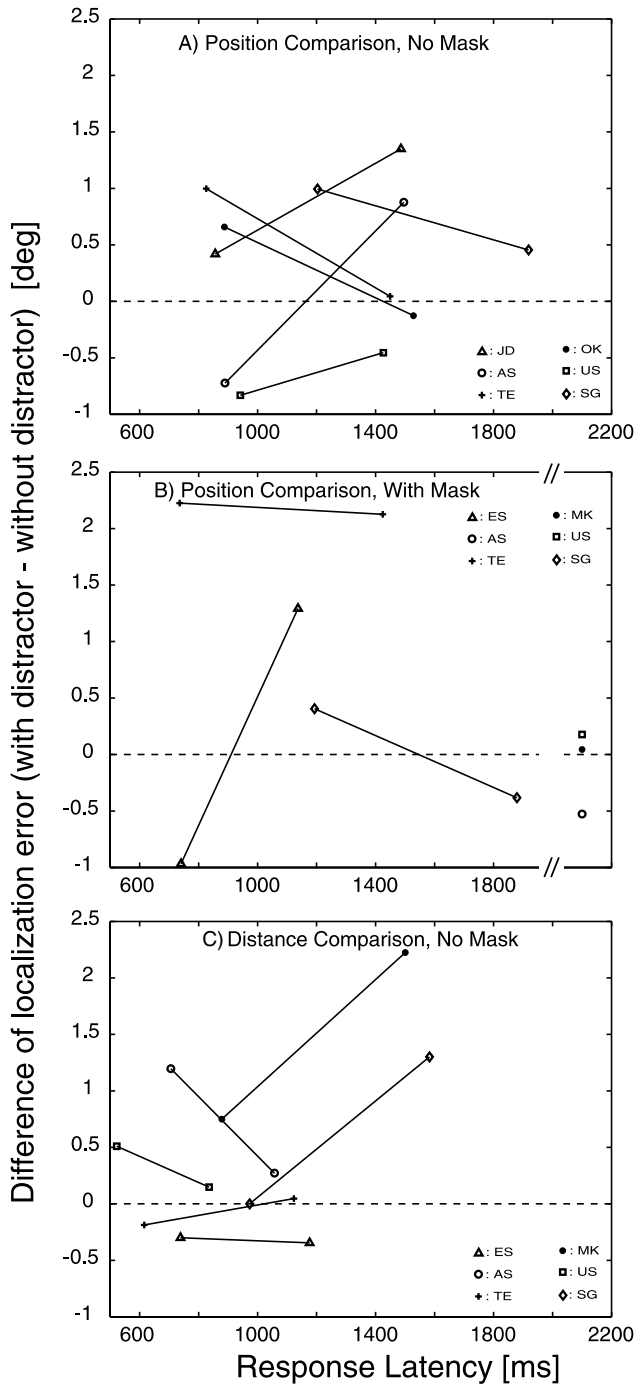


Fig. 6. Each symbol shows the difference of the perceptual localization error between trials with and trials without distractor for one subject. Positive values on the ordinate indicate that the target was perceived more peripherally in trials with distractor than in trials without distractor. For each subject and for each condition, the data were split into two groups along the median response latency, and the localization error was determined separately within each group. The median response latency of each of the two subgroups is shown on the abscissa. The three subfigures show data from the different localization experiments: A: position comparison without mask; B: position comparison with mask. In this experiment three subjects exhibited very long latencies (about 2.7 s) and were excluded from the analysis. C: distance comparison without mask. In all three experiments the localization error did not depend systematically on the response latency.

Table 5

Localization error for distance comparison (deg)

Subject	Single target flash	With distractor
TE	0.84 ± 1.13 (N = 99)	0.69 ± 0.84 (N = 100)
AS	0.75 ± 0.42 (N = 84)	1.42 ± 0.85 (N = 68)
US	1.07 ± 0.47 (N = 98)	1.12 ± 1.33 (N = 96)
ES	1.17 ± 0.46 (N = 99)	0.86 ± 0.48 (N = 99)
MK	0.49 ± 1.02 (N = 83)	2.43 ± 0.87 (N = 85)
SG	0.96 ± 0.99 (N = 98)	2.05 ± 1.05 (N = 92)
Group mean	0.88 ± 0.24 (N = 6)	1.43 ± 0.69 (N = 6)

0.88 ± 0.24 deg; position: 0.90 ± 0.25 deg) and with distractor (distance 1.43 ± 0.69 deg; position: 1.26 ± 0.62 deg). As in the position comparison task, the localization error tended to be higher in trials with distractor. The mean of the paired difference of the localization error between trials with and without distractor was positive (0.55 ± 0.86 deg; $t(5) = 1.55$; $p < 0.19$). Table 5 shows the individual localization errors in the distance comparison task. When the data of the four subjects who performed both the position comparison task and the distance comparison task were submitted to an ANOVA with the two factors *Task* (Position/Distance) and *Distractor* (with/without), there was no main effect of the factor *Task* ($F(1, 3) = 0.08$; $p < 0.8$) or an interaction between the two factors ($F(1, 3) = 1.01$; $p < 0.4$), indicating that the localization errors occurring in both task were identical.

The effect of the response latency on the localization error showed smaller errors at higher response latencies. The average response latency across subjects was 738 ± 166 ms (N = 6) in the short category and 1213 ± 280 ms (N = 6) in the long category. The repeated measures ANOVA of the localization error with the two factors *Latency* (short/long) and *Distractor* (with/without) revealed a main effect of the factor *Latency* which was significant at a level of $p < 0.03$ ($F(1, 5) = 9.27$). The mean paired difference of the localization error between the short and the long latency categories was 0.33 ± 0.26 deg (N = 6). No other main effect or interaction was observed.

4. Discussion

The saccade task yielded the following results:

- (1) In the presence of a near distractor the primary saccade landed between the target and the distractor. The effect of the distractor decreased with increasing latency of the primary saccade, even though the target and the distractor were presented for only 50 ms.
- (2) The effect of the distractor on the amplitude error of the primary saccade was not present for the final amplitude error, i.e., after completion of the secondary saccades occurring in the dark (see Fig. 7).

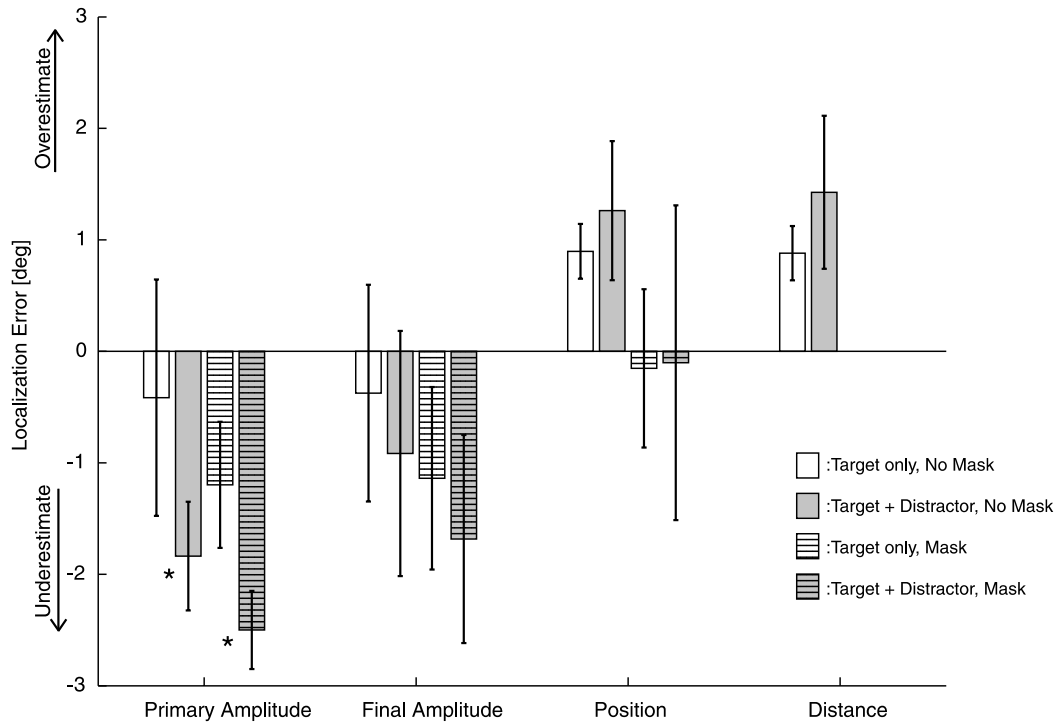


Fig. 7. The mean localization errors of all subjects are shown for trials with and without distractor. Whiskers indicate the standard deviation between subjects. The primary and the final saccade amplitude errors (left two groups of bars) show the two evaluated types of motor errors. Perceptual localization errors (right two groups of bars) are shown from the position comparison task and from the distance comparison task. The effect of the distractor on the primary amplitude error (reflecting the global effect) was consistent for all subjects and reached significance (indicated by asterisks). In contrast, the effects of the distractor on the final amplitude error and on perceptual localization errors did not reach significance.

- (3) Under masking conditions, the saccade amplitude errors shifted towards the negative direction (corresponding to smaller saccade amplitudes) for both distractor trials and non-distractor trials (see Fig. 7). Moreover, the dependence of the global effect on latency was found to be weaker than without the mask. Late secondary saccades compensating for the primary amplitude error frequently occurred even under masking conditions.
- (4) The presence and the disappearance of the peripheral reference presented shortly (550 ms) before the saccade target did not affect the amplitude error of the saccade or the dependence of this error on the presence of a nearby distractor.

The perceptual localization tasks gave the following findings:

- (1) The eccentricity of the target flash was overestimated with respect to the reference (see Fig. 7).
- (2) Compared to its effect on the primary saccade amplitude, the effect of the distractor on the perceived location of the target flash was much smaller and tended to have the opposite direction (see Fig. 7). The perceived location did not depend on the latency of the response.

- (3) No significant effect of the distractor was observed under masking conditions (see Fig. 7).
- (4) The localization error observed in the distance comparison task was very similar to the ones found in the position comparison task (see Fig. 7).

4.1. The global effect for flashed targets

The effect of distractors on the primary saccade amplitude was first described by Coren and Hoenig (1972). The finding that this effect decreases with increasing latency (Coëffé & O'Regan, 1987; Findlay, 1982; Findlay & Gilchrist, 1997; Ottes, van-Gisbergen, & Eggermont, 1985) was interpreted to indicate that the timing (When) and the metrics (Where) of visually guided saccades are processed separately. Many models of saccade generation incorporate such a separate processing (Becker & Jürgens, 1979; Findlay & Walker, 1999). This independence permits the saccade to be triggered before the process of target acquisition is completed. When a target and a distractor are presented simultaneously, the metrics of the saccade goal will be affected more strongly by the distractor shortly after the onset of the stimuli than later. Findlay and Gilchrist (1997) proposed a fragmentation of the target acquisition process in two pro-

cesses, one of which involves processing of information already represented within the system and another depending on continuous visual inflow. They called the first one target selection.

So far it has not been determined which of the two mechanisms is responsible for the global effect, because in the above-mentioned study as well as in the previous ones (Coëffé & O'Regan, 1987; Findlay, 1982; Ottes et al., 1985) the target and the distractor were presented during the entire latency period. In contrast, target and distractor were flashed for only 50 ms in our study, thus preventing continuous visual inflow. Nevertheless, primary saccades with latencies of more than 200 ms were less affected by the distractor than saccades with shorter latency (see Fig. 4). This dependence of the global effect on latency seems to be quantitatively similar to that reported in the literature with non-flashed distractors. Our result shows that the dependence of the global effect on latency is not sensitive to the presence or absence of continuous visual inflow. This suggests that the processing time of the target acquisition process is mainly determined by the processing time of target selection rather than by accumulation of visual information over time.

4.1.1. *Secondary saccades in the dark*

We did not expect to find that secondary saccades occurred in the trials with distractor and approached the location of the blanked target in darkness. Our experimental conditions did not show the typical features known to encourage corrective saccades in darkness, e.g., large target steps of more than 30 deg (Becker & Fuchs, 1969). With large target steps corrective saccades are typically executed with a mean latency of about 130 ms after the end of the primary saccade. Corrective saccades in the dark are also believed to be driven by non-retinal feedback that can be used to evaluate the motor error of the primary saccade in the absence of visual input (Becker, 1976). The probability that this type of corrective saccade will occur depends on the size of the remaining motor error. Errors larger than 3–4 deg are corrected in more than 50% of the cases (Becker, 1989). Our primary amplitude errors were only -1.8 deg on the average. However, if the distractor is assumed to lead to a smaller motor command for the primary saccade, one cannot expect a post-saccadic motor error, since the undershoot of the primary saccade in the presence of the distractor corresponds to the smaller command. The secondary saccades we observed are therefore not ordinary corrective saccades. Since the latencies of these secondary saccades (250 ms) were in the range of internally guided saccades (Mokler & Fischer, 1999), it seems likely that our subjects performed a memory-guided saccade in the dark. These saccades may have been guided by a memorized representation of the flashed target. The alternative explanation is that the

secondary saccade was not guided by the target but was a saccade to the memorized location of the previously shown reference. This is ruled out by the result of our control experiment, which showed that secondary saccades towards the target location frequently also occurred when no reference was presented. That the final eye position after these secondary saccades was not affected by the presence or absence of the distractor shows that, in contrast to the primary saccade, this secondary saccade is not influenced by the global effect. The hypothesis that the secondary saccade we observed is a memory-guided saccade toward the flashed target rather than toward the previously shown reference implies that memory-guided saccades can distinguish between target and distractor.

4.2. *Perceptual localization*

In the position comparison task, the eccentricity of the target flash was overestimated with respect to the eccentricity of the reference. This type of localization error is a characteristic of so-called gap paradigms in which the central fixation spot is extinguished shortly before the appearance of the target, as in the position comparison task of this study. In contrast, in overlap paradigms, in which the fixation spot is continuously visible, a relative underestimate of the target was observed (Eggert, Ditterich, & Straube, 2001). This difference between the “gap” and the “overlap” paradigm is characteristic for the perceptual localization errors in the position comparison task. It is not observed in visually guided saccades, which are known to undershoot the target in gap tasks as well as in overlap tasks. This motor error is the opposite of the perceptual localization error we observed. Thus, it seems obvious that there are different mechanisms involved in perceptual localization and motor execution. However, since the main interest of this study is to determine whether perceptual localization and saccades are based on the same target acquisition process, we will concentrate on the different effects of the distractor on localization and saccades.

Like the final eye position in the saccade task, the distractor also had no significant effect on the perceptual localization of a target evaluated in the position comparison task, showing that no spatial averaging was involved in perceptual localization. This result implies that perceptual averaging is not ubiquitous, even though it has been used to explain the Müller-Lyer illusion (Morgan, Hole, & Glennerster, 1990). In that same study, the authors also measured the perceptual errors in a simultaneous distance comparison task; however, in contrast to our distance comparison task, they presented the reference and the target stimuli simultaneously. The total size of their arrangement (100 min arc) was much smaller than ours (19 deg). The authors showed that the errors can be systematically affected by clusters of

texture elements in the surround of the two targets. Subjects tend to judge the distance between the cluster centers rather than the distance between the targets. This result suggests that spatial averaging occurs between the target and the surrounding texture elements. One explanation for the absence of a distractor effect in our position comparison task is that the position comparison task requires an egocentric reference frame, whereas the exocentric reference frame is much more important for the distance comparison task. Therefore, separate target acquisition processes specific for ego- and exocentric coordinates could explain the apparent discrepancies between our results and the results of Morgan et al. (1990). To test this hypothesis, we examined perceptual localization in a distance comparison task using stimuli much simpler than those of Morgan and coworkers. Our results do not support the hypothesis, since we did not observe systematic differences between the localization errors in the position comparison task and the distance comparison task. The effect of the distractor was very small in both tasks and there was only a non-significant tendency to localize the target at larger eccentricities with the distractor than without the distractor. The direction of this tendency is even the opposite of what is expected with spatial averaging, since the distractor was always presented more centrally than the target. Thus, the perceived location of the target tended to be repelled by the distractor, whereas it should deviate toward the distractor with spatial averaging.

Other differences in the experimental procedures may explain the apparent differences between our findings and that reported by Morgan et al. (1990): (i) size of the stimulus, (ii) successive versus simultaneous comparison, and (iii) differences in the gestalt of the stimulus configuration. More experiments are necessary to determine the crucial factors of this difference.

The answer to the first question of our study, i.e. is global effect shared for saccades and perceptual localization, is clearly no. As the primary saccade to the target was much more affected by the distractor than the perceived location of the target, the target acquisition process used by perception seems to be much more accurate than the one used by short latency primary saccades.

It is necessary to further elaborate on the cause for this difference, which does not seem to reflect the difference between egocentric and exocentric reference systems involved in saccade programming and perception. Both position and distance task were insensitive to the presence of the distractor. The distractor effect is also not specific for saccades, in contrast to perception, since the landing position of secondary saccades was insensitive to the presence of the distractor, even if the primary saccade was not. The results indicate that both perceived location and the programming of memory-

guided secondary saccades are based on a target acquisition process that is more accurate than the one accessed by the reflexive primary saccade. The global effect seems to be specific for only the reflexive primary saccade.

The next question is whether there are two different target acquisition processes (one for reflexive primary saccades and another for memory saccades and perception) or whether there is only one single process that is accessed at different times (first by the reflexive primary saccade and later by memory saccades and perception).

4.2.1. *Common or parallel processes of target acquisition?*

Since both the secondary saccades and the joystick responses occurred later than the primary saccades, it is possible that the differences in the distractor effect are due to the longer processing times available for the secondary saccade and for perception. A single target acquisition process that improves continuously after the onset of the target could explain our results. Secondary saccades and spatial perception may access the same process at a later time when it has already improved and is less dependent on the distractor. The processing time necessary to improve the target acquisition can be estimated from the decrease of the global effect with increasing latency of the saccade. Because the global effect disappeared for latencies of more than 250 ms (see Fig. 4A and B), one would expect the processing time of the target acquisition process to take about the same time or less. The continuous improvement of the target acquisition process could be implemented by means of a recursive “winner-take-all” mechanism in the underlying salience map as proposed by Koch and Ulmann (1985). It is still a matter of debate which brain areas are involved in the computation of salience maps that are closely linked to saccade execution (see Edelman, Gottlieb, & Goldberg, 1999; Findlay & Walker, 1999; He & Kowler, 1989; Van-Opstal & Van-Gisbergen, 1990). A processing time of about 200 ms seems to be compatible with the dynamics of neurons in the lateral intraparietal area (LIP) which are believed to form such a saccade-related salience map. When the behavioral significance of the stimulus in the receptive field is changed, the activity of these neurons change with a decay time or a buildup time in the range of 100–200 ms (Gottlieb, Kusunoki, & Goldberg, 1998; Platt & Glimcher, 1997). Thus, the dynamics of neurons in this area could account for the latency dependence of the global effect.

To test this explanation of a single target acquisition process that improves over time, we tried to limit the processing time of localization process by masking. The underlying idea is that the mask overwrites retinal afterimages or other types of short-term iconic memory that could preserve the visual input even after blanking

of the target. This effect is supported by previous findings that the global effect increases with decreasing target duration when the target was replaced by a mask (Aitsebaomo & Bedell, 2000). If masking can stop a common target acquisition in a crude state, one would expect a similar global effect for primary saccades and perceptual localization with the mask. Secondary saccades toward the target should not occur with the mask. We found that under masking conditions, primary saccades showed clearly a global effect, but in contrast to our other experiments, the distractor effect on the primary saccade did not decrease with longer latencies (up to 300 ms). These findings suggest that the processing time available for the primary saccade was indeed limited by the mask. Nevertheless, the masking in the perceptual localization experiments did not cause the perceived location to be deviated toward the distractor. Also the mask did not prevent the occurrence of secondary saccades toward the target. These results are not compatible with the hypothesis that the mask stopped a common target acquisition process in a crude state. Since no primary saccades with latencies longer than 300 ms occurred, it is possible that the mask did not stop but only delayed the common target acquisition process after 300 ms. The fact that the final amplitude error did not depend on the presence of the distractor (either with or without the mask) suggests that the target acquisition was completed at the time the secondary saccade occurred. Therefore, if the target acquisition was indeed delayed under the masking condition, then secondary saccades should have an increased latency. However, there was no significant increase of the latency of secondary saccades with the mask. The hypothesis of delayed improvement of a common target acquisition process was therefore not confirmed.

Another explanation for why the effect of a distractor is much larger for the primary saccade than for secondary saccades and for perception is based on parallel feed-forward processing rather than continuous improvement of a single target acquisition process. It is generally believed that the difference between short and long latency saccades is related to the difference between reflexive and intentional pathways. In many models of saccade generation spatial information is processed differently in parallel pathways that are specific for the control of short and long latency saccades (Findlay & Walker, 1999; Gancarz & Grossberg, 1999; Grossberg, Roberts, Aguilar, & Bullock, 1997; Pierrot, 1991). Reflexive and intentional saccades involve different brain circuits that compete at the level of the superior colliculus. This parallel structure can explain the specificity of reflexive and intentional or memory-driven saccades for latency and precision (Lemij & Collewijn, 1989), peak velocity (Smit, van-Gisbergen, & Cools, 1987), amplitude adaptation (Deubel, 1995), and gain (Eggert, Mezger, Robinson, & Straube, 1999). Thus, the

global effect may be absent for secondary saccades and perception, because it is specific for reactive, externally guided saccades that rely on a different target acquisition process than perception.

This hypothesis can most easily explain why we did not find any similarities between the distractor effect on spatial perception and primary saccades in any of our different perceptual localization tasks. It also explains why masking did not induce a distractor effect for perceptual localization, even though masking sustained the global effect for primary saccades of longer latencies.

In conclusion, our results indicate that there is a fundamental difference between the spatial processing used for the programming of reflexive primary saccades and the spatial processing used in perception and for the execution of secondary saccades. Whereas short-latency primary saccades show a global effect, perceptual localization does not. This is in line with the qualitative observation that none of our subjects reported having difficulties in discriminating trials with and without distractor. Subjects perceived the target and the distractor as clearly separate, i.e., the target of the averaging primary saccade is not consciously perceived. Apparently, perceptual localization does not access the early spatial information used to program the reflexive primary saccade. Moreover, the dissociation between the error of the primary saccade and that of perceptual localization does not seem to be sufficiently explained by a delayed access of the perceptual system to a common process of target acquisition. A separate target acquisition process that is specific for short latency primary saccades may be involved.

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