



Mislocalization of peripheral targets during fixation

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Abstract

To investigate the effect of the visual stimulus configuration on localization when oculomotor performance is excluded, we evaluated the errors made when subjects compare the horizontal location of two sequentially presented peripheral targets while looking at a visual or memorized fixation spot. Eye position was monitored by means of an infrared eye tracker. Significant localization errors were observed. As long as the fixation spot stayed on or off during the entire presentation time of both peripheral targets, the localization error did not depend on the presence or absence of the fixation spot. A significant change in the localization error was observed only if the fixation spot was presented together with the first peripheral target but disappeared before the presentation of the second one. The localization error did not depend on: (1) the visual asymmetry (unilateral versus bilateral target presentation); (2) the distribution of visual attention (cued versus non-cued test location); or (3) the time interval between the two targets. These results suggest that the mislocalization observed during fixation is partially due to a mismatch between egocentric and exocentric localization mechanisms. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

To orient the eye, the head, or the body toward a visual target appearing transiently in the periphery, it is necessary to evaluate the location of the target with respect to an egocentric reference frame, such as the eye, the head, or the body. Systematic undershooting of orienting movements is known to occur in pointing movements without visual feedback (Osaka, 1977; Medendorp, Van-Asselt, & Gielen, 1999) and saccadic eye movements (Becker, 1989). Mateeff and Gourevich (1983) investigated the perceptual localization of a peripheral flash with respect to a scale that was permanently visible. The subjects fixated at the center of the scale when the flash appeared and then made a saccade in the direction of the flash and reported verbally the scale division where they had seen the flash. Under these conditions the reported scale divisions were closer to the center than the actual positions of the flash.

Localization errors increased with flash-eccentricity. Using the same type of paradigm (subsequently referred to as the 'scale paradigm'), Mitrani and Dimitrov (1982) obtained similar results. When the structure of the visual background was more clearly visible, the localization error decreased (Mateeff & Gourevich, 1984). On the basis of these results, the authors suggested that in these experiments, perceptual localization was affected by the evaluation of absolute (egocentric) direction even though the instructions required the relative (exocentric) location of the flash on the scale. It seems likely that perceptual localization involves both egocentric and exocentric mechanisms. Such a combination has also been suggested for saccade-contingent localization (Dassonville, Schlag, & Schlag, 1995; Honda, 1999).

It has not yet been clarified whether the perceptual localization errors observed in the scale paradigm were due to the occurrence of a saccade. Later studies clearly demonstrated that the localization of a target that is flashed before, during, or after a saccade depends on the timing of the flash with respect to the saccade (Honda, 1989; Jordan & Hershberger, 1994; Schlag & Schlag, 1995).

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The first aim of the present study was to answer the question of whether the systematic localization errors reported by Mateeff and Gourevich (1983, 1984) can be reproduced under experimental conditions, in which fixation is controlled to exclude saccade-contingent mislocalizations. By using eye movement recordings for the control of fixation, we focused on the perceptual aspects of visual localization. We used an experimental paradigm in which subjects had to compare the locations of two sequentially presented spots in a two-alternative, forced-choice procedure during fixation.

The second aim of this study was to investigate potential factors that modify the properties and/or the use of egocentric and exocentric spatial representations, and possibly affect the mislocalization of peripheral targets. We determined whether the localization of brief flashes depends: (1) on the asymmetry of the visual stimulation around the point of fixation; (2) on the center of spatial attention, which can be shifted even without a subsequent saccade (Posner, 1980); (3) on the presentation time of the first spot; or (4) on the presence of a central fixation spot, which can be used as a visual reference, and therefore may modify the localization mode (egocentric/exocentric). Additionally, we tested the influence of the time gap between the two peripheral spots.

2. Methods

2.1. 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. All target spots had a diameter of 0.1° of visual angle. A green helium-neon laser was used to project the central fixation spot, which could be turned on and off by means of a piezo-controlled optical device. To change the color of the fixation spot from green to red, a red laser beam was projected onto the same central location on the screen. A second red laser diode (which could be modulated up to 1 MHz) was used to project the peripheral spots onto the screen. Their positions were controlled by a mirror galvanometer (General Scanning G120D, USA), which can execute a step of 20° amplitude in less than 2 ms with an absolute position error of less than 1 mm (0.04° of visual angle). By stepping the mirror from one position to another every 10 ms two spots 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 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 ($0, \pm 4, \pm 8, \pm 12^\circ$), 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.

3. Subjects

Six volunteers, all employees of the university, participated in the experiments. Four were naive with respect to the purpose of the experiment. All subjects performed all eight experiments, each on a different day. Different sequences of the experimental sessions were used for different subjects in order to compensate for long-term learning effects.

4. Paradigms

4.1. Stimulus configurations

In a series of eight experiments the visual configuration of the two targets and the attentional bias of the subjects were systematically varied.

4.1.1. Experiment 1

Unilateral reference: The timing of this basic paradigm is illustrated in Fig. 1A. Subjects sitting in the dark were instructed to permanently fixate the center where the green fixation spot appeared. The first peripheral spot (subsequently referred to as ‘the target’) was switched on for 800 ms at a lateral position that was chosen randomly between 8° and 11° right or left of the fixation spot (mean: 9.5° , std: 0.9°). In addition to the eccentricity, the side of the target presentation was also randomized. The central green fixation spot was switched off 450 ms after blanking the target. The task of the subjects was to maintain fixation. The second peripheral spot (subsequently referred to as ‘the test flash’) was briefly (50 ms) flashed 100 ms later in the neighborhood of the previously shown target. In a two-alternative, forced-choice task the subjects then had to indicate by joystick response whether the test flash had appeared to the right or to the left of the location of the target. The central fixation spot was switched on again 100 ms after the joystick response. In

trials in which the subjects did not pay attention to the location of either the target or the test flash, they were instructed not to respond with the joystick, and the central fixation spot was switched on 3 s after the test flash. A new trial began with the presentation of the next target 1 s after the fixation spot was turned on.

4.1.2. Experiment 2

Non-cued, symmetrical target: The timing and the distribution of the visual stimuli were identical to that in Exp. 1 but for the following: in addition to the target being on one side, a second target with the same lateral eccentricity as the first was shown simultaneously on the other side. Hence, the visual configuration of the target in this experiment was symmetric with respect to the fixation spot. The subjects had to memorize the location of both targets and to indicate whether the test flash appeared on the right or left of the target that had been on the same side as the flash. As in Exp. 1, the side on which the localization task had to be solved was chosen at random for each trial. Consequently, when the two targets were presented, the subjects could not anticipate which was important to memorize in order to solve the localization task.

4.1.3. Experiment 3

Cued, symmetrical target: Exp. 3 was identical to Exp. 2 except for a cue made about the side where the test flash would appear. The color of the fixation spot was used to indicate which target had to be compared with the test flash. A green fixation spot indicated that the test flash would appear on the right side, and a red fixation spot was used as a cue for the left side. Subjects were instructed to concentrate on the cued target.

4.1.4. Experiment 4

Symmetrical test flash: Exp. 4 was identical to Exp. 1 except that in addition to the unilateral test flash target, a contralateral second flash appeared simultaneously at the same lateral eccentricity as the test flash. This second flash was a visual distracter that had to be disregarded.

4.1.5. Experiment 5

Short target presentation: This experiment was identical to Exp. 2 except for the duration of the target. In contrast to all previous experiments, the targets were shown for only 50 ms.

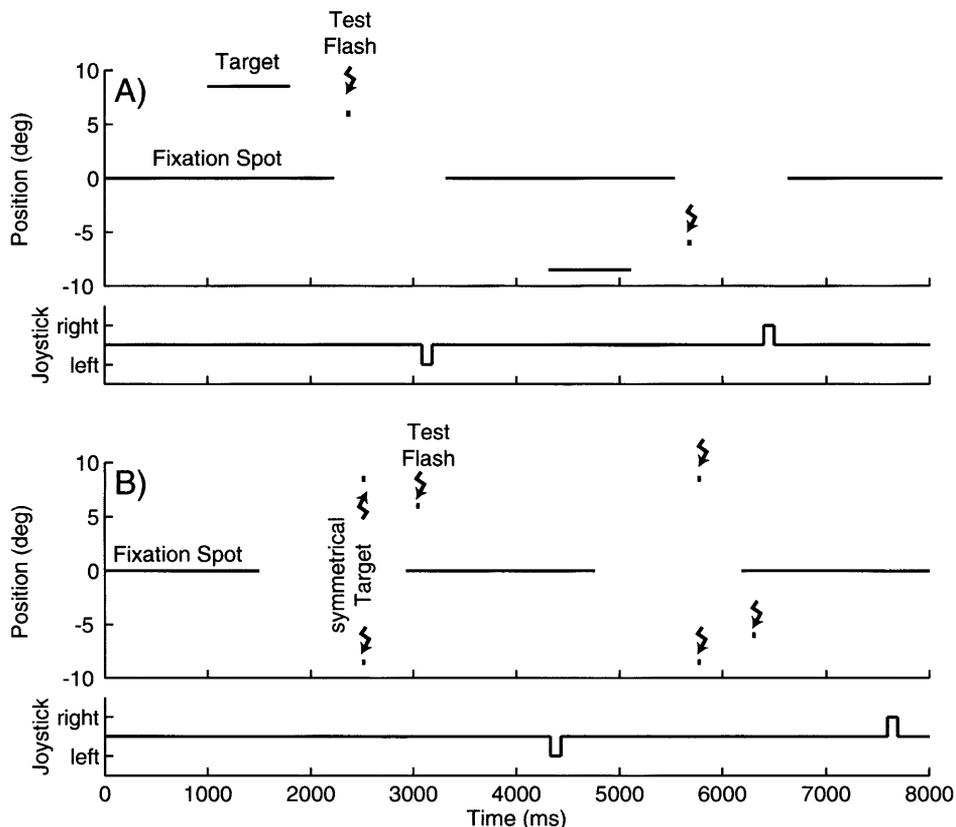


Fig. 1. Timing of the stimuli used in Exp. 1 (A, fixation spot during target presentation) and Exp. 6 (B, fixation spot during test flash).

4.1.6. Experiment 6

Inverse fixation spot: As in Exp. 5 a pair of symmetrical targets was flashed for 50 ms, and a unilateral 50 ms test flash was presented after a memorization gap of 550 ms. In contrast to all other experiments, the targets were presented here in total darkness, that is, the fixation spot was absent. The fixation spot turned off 1 s before the target appeared. It turned on 450 ms after the targets were extinguished and 100 ms before the test flash appeared (Fig. 1B).

4.1.7. Experiment 7

Continuous fixation spot: This experiment was identical to Exp. 6 except that the fixation spot was continuously visible.

4.1.8. Experiment 8

No fixation spot: This experiment was identical to Exp. 6 but the fixation spot was turned on just 100 ms after the joystick response. Thus, both peripheral spots, the target and the flash, were presented in darkness.

4.2. Variation of memorization time

4.2.1. Experiment 9

The memorization time was defined as the time between the extinction of the target and the onset of the test flash. To test for the effect of the memorization time, which was 550 ms in all eight experiments, Exp. 2 and Exp. 3 were repeated with a shorter (250 ms) and a longer (1100 ms) memorization time. This variation in memorization time was achieved by modifying the time between the extinction of the target and the extinction of the fixation spot to 150 and 1000 ms, respectively. The time between the extinction of the fixation spot and the test flash was always 100 ms. Only three of the six subjects who participated in the first series of experiments were available for these control experiments.

A total of 200 joystick responses were recorded for each subject under each experimental condition. One hundred responses were collected from trials in which the localization had to be performed on the right side and 100 responses were collected from trials with stimulation on the left side.

5. Online control of test flash position

The computer determined the position of the test flash for each trial on the basis of a random distribution centered on an adaptive estimate of the subject's mean error in the localization task. The random distribution was also scaled with an adaptive estimate of the standard deviation of this subject-specific error. At the beginning of the session (when no responses of the subject were available) the distribution had a range of

$\pm 5^\circ$ and was centered on the location of the target. After each joystick response these two estimates were updated separately for the trials with the test flash on the left and on the right side and were based on all prior responses on the same side. This method has the advantage of combining non-predictability with a maximum number of test flashes in the region where the subject believed the target was.

6. Offline data analysis

The fixation error (FE) was calculated for each trial by the difference between the horizontal eye position at the time of extinction of the target and at the time of appearance of the test flash. Positive values indicate an eye-movement toward the test flash. To ensure stability of fixation, all trials in which FE exceeded $\pm 1^\circ$ were excluded from the analysis. The median of the number of excluded trials was nine out of 200 (lower/upper quartile: 1/41). Within this selection no systematic eye movement occurred (median of the absolute values of the mean FE per session: 0.015°).

The relative frequency of trials in which the subject perceived the test flash at a more eccentric location than the target was computed as a function of the actual distance between test flash and target. A Gaussian cumulative distribution was fitted to this histogram by maximizing its likelihood. In these histograms, the likelihood computation was based on the exact binomial distribution of the absolute frequency (see Fig. 2). The perceptual misalignment (M) of the subjective judgement was defined by the mean of the fitted Gaussian distribution. Positive values of M indicated that the test flash had to be presented more peripherally than the target in order to appear at the same location. The precision (P) of the judgement was defined by the standard deviation of the fitted Gaussian distribution. To evaluate side asymmetries of the perceptual misalignment in the first step of the analysis, separate histograms were computed for trials in which targets were localized in the right or the left hemifield. The side asymmetry, quantified by the difference of the perceptual misalignment (M) between the right and left the field, was not affected by the experimental condition (repeated measures ANOVA: $F(7, 35) = 0.49$; $P < 0.84$). The individual mean of the side asymmetry, averaged over experimental conditions, did not differ from zero (mean: $-0.23 \pm 0.50^\circ$; $N = 6$; $P < 0.3$). The histograms collected from the two hemifields were pooled together for further analysis, and for each subject and experiment a single Gaussian distribution was fitted to compute M and P.

Statistical analysis of the perceptual misalignment evaluated in this way was performed using commercial software (Statistica, Statsoft, Tulsa, OK, USA)

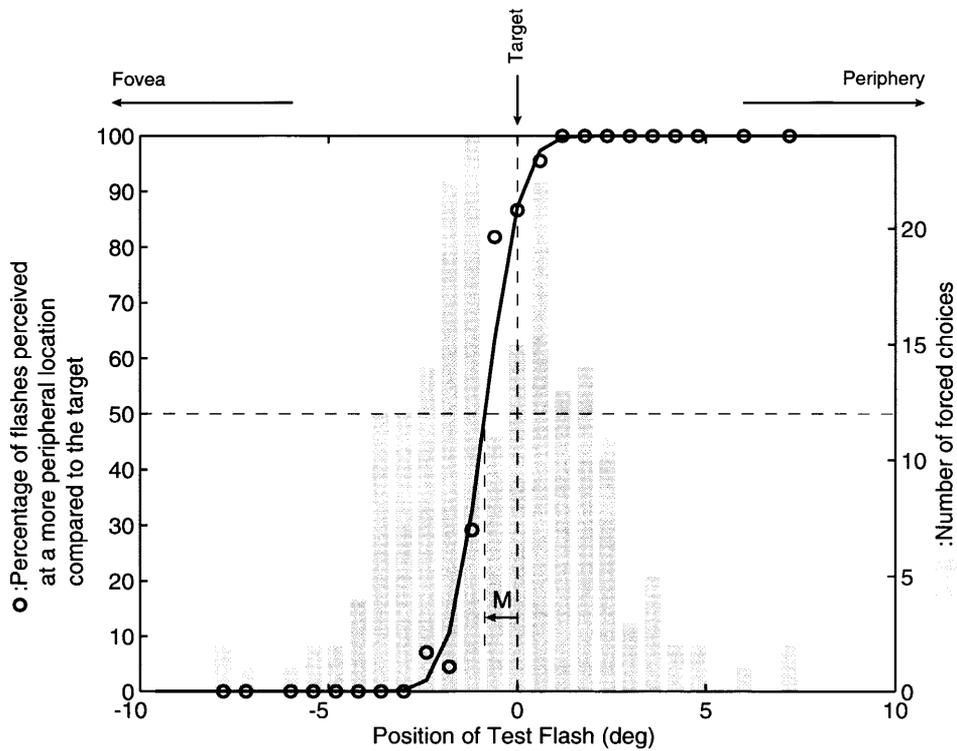


Fig. 2. Psychometric curve (solid) fitted to the relative frequency (circles) of the test flash being perceived at a more peripheral location than the memorized target. The position of the test flash is shown on the abscissa with respect to the horizontal position of the target with which the test flash had to be compared. Typical example of the data acquired in an experiment in one subject. In all, 100 two-alternative, forced-choice responses were collected, on each side which were pooled together. The 50% value of the fitted Gaussian cumulative distribution (solid line) defines the perceptual misalignment M . The negative value of M (-0.86°) indicates that the test flash has to be presented closer to the fovea than the target in order to appear at the same location. The precision (P) of the subjective localization is quantified by the standard deviation of the fitted Gaussian (0.76°).

7. Results

7.1. Dependence on stimulus configuration

The precision (P) of the subjective judgements did not differ between the eight experimental conditions (Friedman Anova: $P < 0.79$). The median precision was 1.1° .

The perceptual misalignment (M) for the six subjects under the eight conditions are shown in Fig. 3. In contrast to the precision of the subjective judgements there was a highly significant overall effect of the experimental condition on the perceptual misalignment (M) as confirmed by a repeated measures ANOVA with one factor with eight levels (experimental conditions) and with six cases (subjects) ($F(7, 35) = 6.01$; $P < 0.001$). The small negative mean of the perceptual misalignments found under conditions of Exps. 1–5 in contrast to the positive mean misalignments in Exps. 6–8 (Table 1) suggests that this overall effect is mainly caused by a difference between these two groups. The post-hoc planned comparison confirmed that the perceptual misalignment in Exps. 1–5 differed significantly from all other experiments ($F(1, 5) = 22.7$; $P < 0.006$).

The perceptual misalignment did not differ under the conditions of Exps. 1–5 since the overall effect of the repeated measures factor (experimental condition) became insignificant when Exps. 6–8 were excluded from the ANOVA ($F(4, 20) = 0.16$; $P < 0.96$). A repeated measures ANOVA computed on Exps. 6–8 revealed only a non-significant tendency of an effect of these three experimental condition on the perceptual misalignment ($F(2, 10) = 3.6$; $P < 0.07$).

The perceptual misalignment of the six subjects averaged over Exps. 1–5 was negative. The test flash had to be presented more centrally than the target in order to be perceived at the same location (mean: $-0.49 \pm 0.39^\circ$; $N = 6$; $P < 0.03$). In contrast, the perceptual misalignment found in Exps. 6–8 was positive ($+0.89 \pm 0.55^\circ$; $N = 6$; $P < 0.01$).

7.2. Dependency on memorization time

Fig. 4 shows the mean perceptual misalignment (M) in each of the subjects who participated in both experiments. M is plotted as a function of the memorization time. Each symbol shows the individual mean of the localization error E for the stimulus configura-

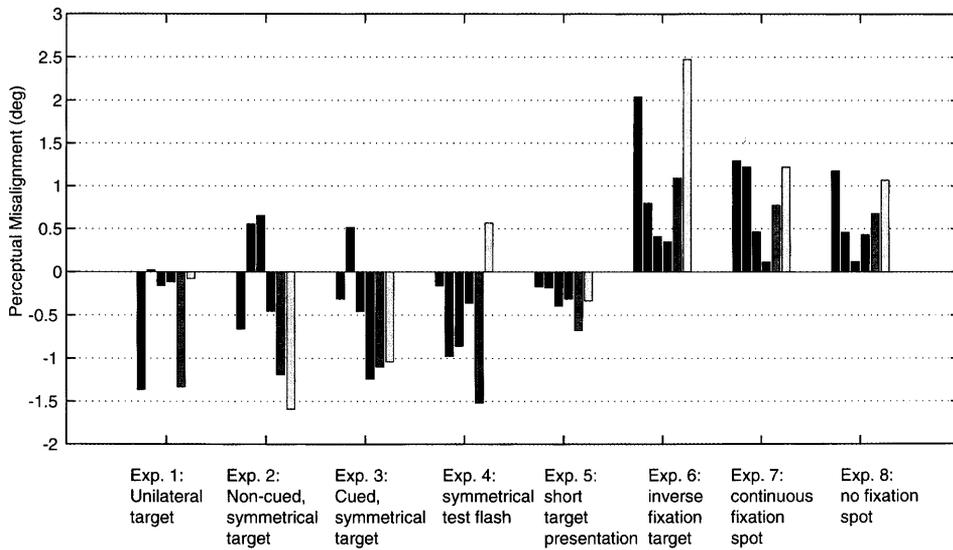


Fig. 3. The perceptual misalignment M (bars) as defined in Fig. 2 is shown for all six subjects and under all eight experimental conditions. In Exps. 6–8 the test flash had to be presented more peripherally than the target in order to be perceived at the same location. This perceptual misalignment changed its sign in Exps. 1–5, in which the target was presented together with the central fixation and disappeared before the test flash occurred.

Table 1
The mean and the standard deviation of the perceptual misalignment (M) for the six subjects under the eight experimental conditions

	Exp. 1	Exp. 2	Exp. 3	Exp. 4	Exp. 5	Exp. 6	Exp. 7	Exp. 8
Mean (deg)	-0.50	-0.45	-0.60	-0.55	-0.35	+1.19	+0.85	+0.65
Std (deg)	0.66	0.91	0.66	0.73	0.18	0.88	0.48	0.40
$P <^a$	0.13	0.29	0.08	0.13	0.01	0.02	0.01	0.01

^a P : significance for the mean being different from zero (t -test).

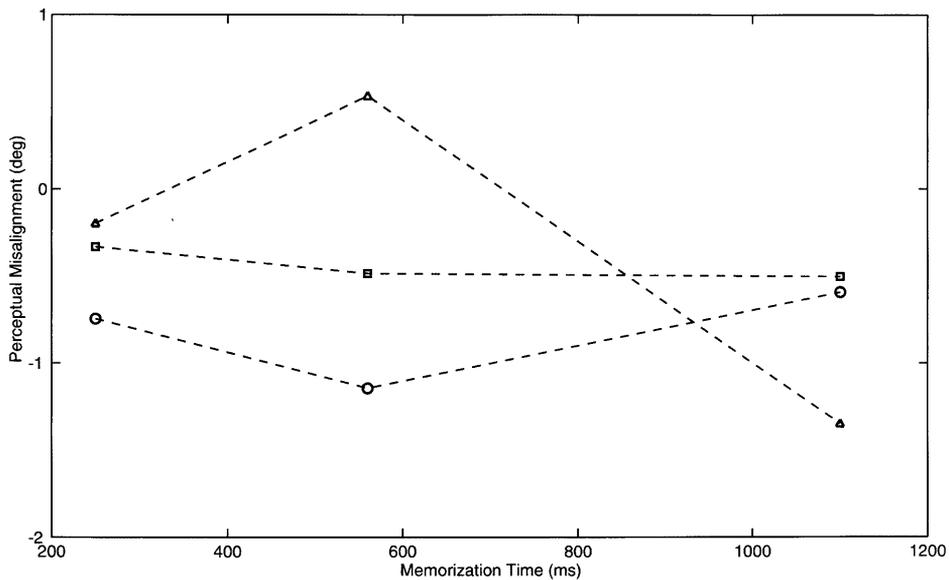


Fig. 4. Symbols: Individual mean of the perceptual misalignment (M) observed in Exp. 2 and Exp. 3 for three subjects (squares, triangles, circles). Both experiments were performed with three different memorization times: 250 ms, 550 ms, and 1100 ms. No systematic dependency on memorization time was observed.

tion Exp. 2 and Exp. 3. The memorization time had no effect on the localization error (repeated measures ANOVA: $F(2, 4) = 0.44$; $P < 0.68$).

8. Discussion

The main results of this study are as follows: (1) When the perceived locations of two sequentially presented peripheral targets are compared during fixation, systematic perceptual misalignment is observed; (2) The perceptual misalignment did not depend on the time interval between the two targets, the visual asymmetry, or the distribution of visual attention; (3) The sign of the perceptual misalignment changed when the central fixation spot was extinguished between the presentation of the first and the second peripheral target.

8.1. Other localization studies

Before interpreting these results in the context of the literature, it is important to emphasize that our experiment addresses a particular aspect of the large variety of localization tasks. Human performance in visual localization can be measured by comparing the direction of a visual target with the direction of a behavior oriented to the target, e.g. saccadic eye movements, manual pointing to a target, or positioning of a test stimulus at the perceived location of a target stimulus. Since in these types of tasks mislocalization is defined as the difference between the target direction and the direction of a motor output, it is difficult to attribute errors to a specific part of the sensorimotor loop and to differentiate errors that occur during visual perception, memorization, or motor execution. The advantage of the paradigm presented here is that by controlling eye movements, it allows to focus on the perceptual and memory processes involved in localization. However, it is important to note that even for experiments in which the locations of two visual objects have to be compared perceptually, it is impossible to attribute a perceptual misalignment to a mislocalization of one of the two objects.

A particular feature of our experiments is that the target and the test flash were presented sequentially. In this case the process of comparing the location of two sequentially presented retinal stimuli can be divided into (at least) three subprocesses: (1) mapping of the retinal position of the target on an internal representation that is the basis for spatial perception; (2) storing this internal representation during the memorization time; and (3) mapping the retinal test flash position on the memorized internal representation of the target position. In our experiment systematic perceptual misalignments may be related to any of these three subprocesses. The total task involved in our paradigm, which asked for the relative location of the second stimulus with respect to the first

one, can be characterized as a relative exocentric task (Howard, 1991). This does not refer to the mechanisms involved in the two localization subprocesses (1) and (3). In this paper we use the terms ‘egocentric-’ and ‘exocentric localization’ to characterize the subprocesses (1) and (3), they do not refer to the type of task. An internal representation of the target location with respect to a coordinate system attached to the body is called ‘egocentric localization’. If the coordinate system is attached to an external visual object, we speak of ‘exocentric localization’.

The perceptual misalignment of two peripheral targets presented during fixation was also studied by means of a forced-choice procedure by Mateeff and Hohnsbein (1988) and Rose and Halpern (1992). Although the sign of the perceptual misalignment reported by Mateeff and Hohnsbein (1988) is consistent with the one in our Exps. 1–5, we believe that a direct comparison is not possible because of the different mechanisms involved. Whereas they presented the test flash simultaneously with a continuously visible target, we presented the two peripheral stimuli one after the other. While our task requires all three subprocesses mentioned earlier, tasks with simultaneous presentation of target and test flash can be solved without subprocesses (2) and (3), namely by only one single exocentric localization.

In the scale paradigm of Mateeff and Gourevich (1983) subjects perceived a scale division that was closer to the center than the flash at the same location. The authors suggested that, due to impaired vision in the visual periphery in this paradigm, the subjects could not directly identify the relative location of the flash on the scale and therefore they were “... forced to estimate the direction of the stimulus and then to identify and report the number or letter which corresponds to the perceived direction.” This hypothesis suggests that in the scale paradigm, as in our paradigm, two visual stimuli were localized sequentially: the test flash after the target in our paradigm and the reported scale division after the peripheral flash in the scale paradigm. In our Exps. 1–5 in which the fixation spot was present with the target and absent with the flash, on the average, a negative perceptual misalignment (M) occurred, i.e. the test flash had to be presented closer to the center than the target in order to appear at the same location. This result is similar to the result of Mateeff and Gourevich (1983) in the sense that the second stimulus had to be closer to the center than the first one in order to be perceived at the same location.

Nevertheless, the question arises whether the conditions of Exps 1–5 really match the conditions of the scale paradigm. On the one hand, our Exp. 7 seems more similar to the situation of the scale paradigm, since the scale was continuously visible as was the fixation spot in Exp. 7. On the other hand, in the scale paradigm it may have been difficult for the subjects to reidentify the

divisions of the scale seen before the saccade with the ones seen afterward due to the low visual acuity in the periphery. This reidentification would have been necessary to use the scale as an exocentric reference for the localization of both stimuli, i.e. the flash and the scale division. Hence, the situation may be considered similar to our Exps. 1–5, where the fixation spot disappeared between target and flash. Quantitatively, the localization errors reported by Mateeff and Gourevich (1983) were larger than the perceptual mislocalizations we observed in Exps. 1–5. This difference may be related to the saccade that was executed in the scale paradigm while in our experiments the localizations of both stimuli, were performed during fixation.

Thus, despite some qualitative similarities between both paradigms a direct quantitative comparison of the results seems difficult, especially since different results have been reported in the literature for experiments using the scale paradigm (e.g. Mapp, Barbeito, Bedell, & Ono, 1989).

8.2. Possible factors for perceptual misalignment of sequentially presented stimuli

This subsection discusses the factors that proved not to be critical for the perceptual misalignment as shown by the results of Exps. 1–5.

One simple explanation for perceptual misalignments between two sequentially localized stimuli is a process taking place during memorization. To explain systematic perceptual misalignments, one would have to hypothesize a drift of the memorized target position. The result of Exp. 9 shows that varying the memorization time between 250 and 1100 ms was not critical for the perceptual misalignment observed. Apparently no drift of the memorized target position occurred.

An internal representation of a target location may depend on the spatial distribution of stimuli in the visual field and the distribution of the spatial attention. Two aspects of spatial distributions were considered by our paradigms: (1) Spatial asymmetries might shift the internal representation toward the side of the asymmetric target or to the center of spatial attention; (2) The size of the image or the size of the attention focus might affect the scaling of the internal spatial representation of the target location.

The finding that no difference in the perceptual misalignment occurred for experiments with a unilateral (Exp. 1) or symmetrical (Exps. 2 and 3) target shows that the perceptual misalignment did not depend on the size or the asymmetry of the targets in the visual field. The localization of the target was also not affected by an attention shift toward the target, since there was no systematic difference between the non-cued (Exp. 2) and the cued experiment (Exp. 3), in which the subjects directed their attention asymmetrically to one side.

It has been shown that the size of the attention focus (in contrast to its location) cannot be changed in a short time interval of 40 ms (Castiello & Umiltà, 1990). Thus, in contrast to Exps. 1–4, during the short (50 ms) target presentation in Exp. 5 the size of the attention focus did not have sufficient time to change. Nevertheless, there was no difference in perceptual misalignment between Exp. 5 and Exps. 1–4. Therefore, it seems unlikely that the size of the attention focus is important for the scaling of the internal representation of the visual space.

A perceptual misalignment could be caused by a modification of the internal representation of the target or of the test flash. However, the asymmetry of the test flash seems also irrelevant for the observed perceptual misalignments, since there was no difference between Exp. 4 (symmetrical test flash) and Exp. 2 (symmetrical target).

8.3. Interaction of egocentric and exocentric localization

The difference between the perceptual misalignment between Exps. 1–5 and Exps. 6–8 may be due to the particular property of the Exps. 1–5, i.e. the target was presented together with the fixation spot, which disappeared before the test flash. It is possible that in these paradigms two peripheral locations had to be compared which were represented within different visual reference frames. If the target location were primarily evaluated exocentrically (with respect to the fixation spot) then a specific problem would arise when the fixation spot unexpectedly disappeared. The test flash, presented in darkness, could not be localized exocentrically and thus the egocentric location of the test flash had to be compared with the exocentric location of the target. Even if there is not direct evidence that the subjects evaluated the distance between the target and the fixation spot instead of the egocentric location of the target, this strategy might be useful if the system relies implicitly on the assumption that the time to evaluate the egocentric location of the fixation spot is unlimited.

Hence, the simplest hypothesis accounting for the sign change of the perceptual misalignment between Exps. 1–5 and Exps. 6–8 is that a mismatch occurs when an exocentric representation of a location has to be perceptually compared with an egocentric representation of the same location. It seems that a peripheral target, which is localized exocentrically with respect to a foveal fixation spot, is perceived more centrally than the same target when localized egocentrically. Two problems linked to this hypothesis have to be discussed.

The first results from the consideration that, as long as direct visual feedback is excluded, exocentric metrical information cannot be used for goal-directed movements without being transformed into egocentric coordinates, which are needed to execute the movement. Therefore,

one would expect exocentric and egocentric spatial representations to match, at least under static circumstances when the relation between the egocentric and exocentric reference frames are well established. A persistent mismatch between egocentric and exocentric localization mechanisms would mean that subjects were unable to integrate both localizations in a common, consistent space percept. The conditions of our Exps. 1–5 were not static, since the fixation spot, which served as the center of the exocentric space, was switched off 100 ms before the test flash. Since the disappearance of a visual reference requires a reorganization of the exocentrically stored spatial information, matching errors between egocentric and exocentric locations could occur during this transient phase.

The second problem is why there was no clear difference between the perceptual misalignment in Exp. 6 and Exps. 7, 8. In Exp. 6 the target was presented in darkness and the fixation spot appeared only 100 ms before the test flash. Thus, the relations of presence and absence of the fixation spot during the presentation of the target and the test flash were simply reversed in Exp. 6 compared to Exps. 1–5. One possible explanation is that in Exp. 6, the role of the fixation spot as the center of the visual reference frame might not have been fully established after 100 ms. Moreover, when sequential peripheral stimuli have to be compared, there might be a preference for localizing the second stimulus in the same reference frame as the first one. Both of these ideas would predict that the preference of the system for localizing the test flash exocentrically is smaller in Exp. 6 than the preference for localizing the target exocentrically in Exps. 1–5. This would explain why the results of Exp. 6 resemble those of Exp. 8, in which all peripheral targets had to be localized egocentrically.

In Exp. 7 and in Exp. 8 there was no change in the external visual reference frame, and in Exp. 6, there was no need to compare two locations represented within different reference frames. Thus, the conditions of these three experiments can be considered static. The positive perceptual misalignment observed in all three experiments does not seem to be related to the reference frames involved, especially since there was no difference in the results between Exp. 7 and Exp. 8. The mechanism responsible for the absolute perceptual misalignment observed in Exps. 6–8 remains unclear.

In summary, the difference in the perceptual misalignment between Exps. 1–5 and Exps. 6–8 could be due to a dynamic mismatch between egocentric and exocentric localization mechanisms.

8.4. Transsaccadic perceptual misalignments

It is difficult to interpret the results of this study in the context of transsaccadic mislocalization, which can be much larger than the perceptual misalignments we ob-

served during fixation. Nevertheless, it seems interesting to mention two qualitative similarities. Ross and co-workers (Ross, Morrone, & Burr, 1997) found a transient scaling of the relation between retinal and perceived locations during saccades, centered around the final position of the saccade target. As in our Exp. 6, a flash presented shortly after appearance of the new visual reference was perceived as being closer to this new center of the exocentric visual space than a comparison spot presented under static conditions. The finding that this transient space compression is weaker in the absence of a post-saccadic visual reference (Lappe, Awater, & Krekelberg, 2000) resembles our finding that the perceptual misalignment became smaller or even changed its sign when the second peripheral target was presented in darkness (Exps. 1–5). This raises the question of whether the scaling effects observed during saccades and during fixation share a common mechanism that could be related to the reorganization of memorized exocentric spatial information with respect to a new visual reference.

In conclusion, neither the overall size and distribution of the retinal stimulation nor the distribution of visual attention is a critical factor for the perceptual misalignment of peripheral targets presented sequentially during fixation. A transient mismatch of egocentric and exocentric localization mechanisms seems to be the cause for the change in the perceptual misalignment, which we observed when the fixation spot was presented together with the first peripheral target but was extinguished before the presentation of the second one.

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