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Motion Processing for Saccadic Eye Movements During the Visually Induced Sensation of Ego-motion in Humans

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During ego-motion an observer is often faced with the task of controlling his heading direction while simultaneously registering the movement of objects in order to avoid possible obstacles. Psychophysical experiments have shown that the detection of moving objects is impaired by concurrent ego-motion. We investigated the interaction between ego-motion and object-motion by examining the latencies of saccades executed to moving targets under a visually induced sensation of ego-motion. Saccadic latencies increased during this sensation, with a global or non-retinotopic effect of optic flow on motion detection. Furthermore, separating stereoscopically the moving target and the optic flow into foreground and background, respectively, still resulted in increased latencies. We propose that an inhibitory influence of the perception of self-motion exists on the perception of object-motion. These results support a model of space constancy which strives to create a stable world during locomotion. © 1997 Elsevier Science Ltd

Eye movement Saccadic latency Motion processing Ego-motion Human

INTRODUCTION

When moving through natural environments, retinal image motion induced by optic flow and object-motion in relation to the observer often occur simultaneously. The observer is faced with the complex task of controlling his heading direction, while simultaneously perceiving the movements of objects or hindrances in order to eventually assume new heading directions offroad or to avoid obstacles. The visual system thus has to distinguish between retinal motion evoked by ego-motion and object-motion in relation to the observer.

Different classes of theories concerning the perception of ego-motion and object-motion have been proposed. In the traditional theory based on the principle of reafference, perception depends on the comparison of two neuronal signals (e.g. von Holst & Mittelstaedt, 1950). For example, extraretinal signals of eye movements (efference copy) are evaluated using signals that code the retinal image slip and then generate the perception of either a stable environment, ego-motion, or object-motion. In contrast, the direct perception theory developed by Gibson (1954) does not require an extraretinal signal. In this case only the afferent visual information is necessary to perceive ego-motion and object-motion. The visual world consists of certain invariant structural features describing object-, eye-, or ego-motion. For example, a stationary world would never contain moving invariant features. Thus, a coherently moving retinal image cannot be interpreted as a moving world, but as eye- or ego-motion. However, neither model is compatible with the occurrence of perceptual phenomena during the visually induced sensation of ego-motion. As an example, an observer with a fixed body, head and eyes sitting in a rotating optokinetic drum will first perceive an external drum rotation that appears to stop after an interval of a few seconds. The observer will then experience ego-motion (circular vection) (Dichgans & Brandt, 1978; Wong & Frost, 1978). While the initial perception of the drum rotation is in line with the traditional theory of reafference, the subsequent perception of ego-motion can be explained more adequately by the theory of direct perception. Thus, Wertheim (1994) proposed a modification to the reafference principle, namely that the extraretinal signal should be combined with a visual signal. This composed reference signal occurs not only when the eyes are moving but also during ego-motion in response to the retinal image slip, thus indicating stationarity, ego-motion, or object-motion.

Recent psychophysical experiments have demonstrated that the detection of object-motion is impaired by concurrent ego-motion (Büchele *et al.*, 1980; Probst *et al.*, 1984, 1986; Brandt *et al.*, 1991). The sensation of ego-motion in these studies was induced by either

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vestibular, cervico-somatosensory, or visual stimulation or real ego-motion. They showed increased manual reaction times for detecting moving objects during the sensation of ego-motion. The influence of the visually induced sensation of ego-motion on motion detection was only investigated with a large-field horizontally moving pattern. This stimulus induced the sensation of rotation or circular vection. Thus, the aim of this examination is to investigate the interaction between the visually induced sensation of ego-motion and the detection of moving objects in more detail. For example, detecting moving objects was also investigated with moving patterns which evoked a sensation of translation or linear vection. This resulted in a comparatively impaired detection of object-motion. Moreover, we examined whether the impairment was only due to a moving background or whether it was connected to the sensation of visually induced ego-motion. Results suggest that apart from an influence of the pure motion of the background on motion detection, an additional influence occurs in the case of the sensation of ego-motion. Moreover, local and global effects of stimuli inducing the sensation of ego-motion on motion detection and the influence of disparity were subjects of this investigation. However, revealing modulations on motion detection in these experimental configurations impaired motion detection was still present during the visually induced sensation of ego-motion.

The latency of foveation saccades was used as an objective measurement of motion detection in our investigation. In natural environments the execution of foveation saccades to objects of interest, either moving or stationary, occurs naturally and continually. Impaired detection of moving objects during a visually induced sensation of ego-motion is reflected in increased saccadic latencies and may give information about the perception of ego-motion, object-motion and stationarity in the world. These results will be discussed in the context of the modified reafference principle important for a space-stabilizing mechanism during ego-motion.

METHODS

Subjects

The experiments employed seven subjects, ranging in age from 25 to 32 yr with normal or corrected vision, all of whom had prior experience of psychophysical oculomotor experiments.

Eye movement recording

The horizontal and the vertical eye movements of one eye were measured with a non-invasive infrared eye-tracker (Ober2) allowing records of eye movements with a high degree of accuracy and resolution (sensitivity of <5 minarc) to be made. The subjects wore a pair of light goggles in which the infrared monitoring components are incorporated. Their range of vision was approximately ± 40 deg horizontally and ± 20 deg vertically. The sampling rate of the 12 bit analog-to-digital converter was 500 Hz.

Experimental set-up

For a stimulus presentation, two monitors (or one monitor and a transparent screen) were positioned at right angles to each other. A semi-silvered mirror was positioned at an angle of 45 deg between both screens, thus optically superimposing the two stimuli. In the experiments using the transparent screen, a video projector (Bauer VP 2000) projected the stimulus onto the screen. The superimposed stimuli were presented either coplanar or at different depths.

In the case of the coplanar stimulation, the subject viewed the stimulus from a distance of 57 cm. In the disparate configuration the distance of the subject from one screen was also maintained at 57 cm, whereas the distance from the other monitor was increased so as to achieve disparities of 0.4 and 3 deg between the two stimuli.

The subject's head was stabilized using chin and forehead rests, and the ambient luminance of the laboratory was <0.01 cd/m^2.

Stimuli

Two types of stimuli were presented; a target and a background, both computer generated and optically superimposed.

The target-stimulus consisted of a fixation cross, which was constantly present during the trial, and four targets placed in each quadrant of the visual field. The targets had an eccentricity of 8 deg of visual angle relative to the fixation cross. The duration of the fixation lasted for 800–1200 msec. Then one of the four targets, which had been randomly selected, moved horizontally towards the vertical meridian of the visual field. This paradigm is comparable with a simple ramp paradigm (e.g. Gellman & Carl, 1991). The target had a velocity of 2.5 deg/sec and moved for 1000 msec. The size of the targets was 8×11 minarc^2 of visual angle, at a luminance of 50 cd/m^2.

The background stimulus was either homogeneous, structured but stationary, or an optic flow (resulting in a visually induced sensation of ego-motion). The optic flow consisted of either expanding black and white rings (simulating a forward speed of 6 m/sec) or horizontally moving black and white stripes [1 c/deg] (simulating a rotation of the subject at 10 deg/sec). The rings were presented on the monitor with 30 deg $\times$ 20 deg of visual angle, and the stripes were projected on the transparent screen with 60 deg $\times$ 40 deg of visual angle. The stationary background consisted of the same stimuli (rings or stripes) but was stationary. The luminance of the homogeneous and dark parts of the background was 1 cd/m^2 and that of the bright parts 4 cd/m^2.

Experimental procedure

The subject fixated the cross until, after a random delay, a peripheral motion of the target was detected. The subject's task was to catch up with the target by executing a saccade and then to pursue it across the screen. All the trials were viewed binocularly.

The following experiments were performed under coplanar and disparate conditions:

The coplanar condition.

1. Execution of foveation saccades on moving targets with a simultaneous presentation of a homogeneous [HB], or a stationary, structured [SB], or an optic flow [OF] background (translation or rotation).

2. Execution of foveation saccades with a stationary, structured [SB], a brief optic flow presentation [OF], or a continuous presentation of optic flow that evoked the sensation of ego-motion [OF-Vection]. The duration of the brief presentation was not more than 7 sec, which was too short for the sensation of ego-motion to get in (Dichgans & Brandt, 1978). After this time interval, the optic flow was stopped, the direction was reversed and re-started. A rotation pattern was used as an optic flow stimulus.

   Also latencies of foveation saccades to stationary targets were examined with these background paradigms (SB, OF and OF-Vection). The target either changed contrast (from dark to light), colour (from green to red), or orientation (from a horizontal bar to a vertical bar). The spatial position of the stationary targets and the timing of the target presentation were the same as with the moving targets. Subjects had to detect the change in contrast, colour, or orientation of the target followed by the foveation saccade to this target.

3. Execution of foveation saccades on moving targets with a covered background around the target trajectory. The covered area had a vertical width of either 0.5 or 6 deg of visual angle, with the target trajectory in the middle. This experiment was only performed with an optic flow stimulus simulating forward translation.

The disparate condition.

4. Execution of foveation saccades with a disparity between the target and background of either 0.4 or 3 deg. The target and fixation cross were always in the foreground. A translation pattern was used as an optic flow stimulus.

5. In the case of a 3 deg disparity the fixation cross was either coplanar to the target or coplanar to the background. A rotation pattern was used as an optic flow stimulus.

At least two subjects took part in each experiment. All had to perform each condition at least 150 times, over a period of 3 days.

Data analysis

The latency of the saccades was calculated off-line from the eye-position trace, by measuring the time interval between the onset of movement and the onset of the saccade. The time resolution was 2 msec.

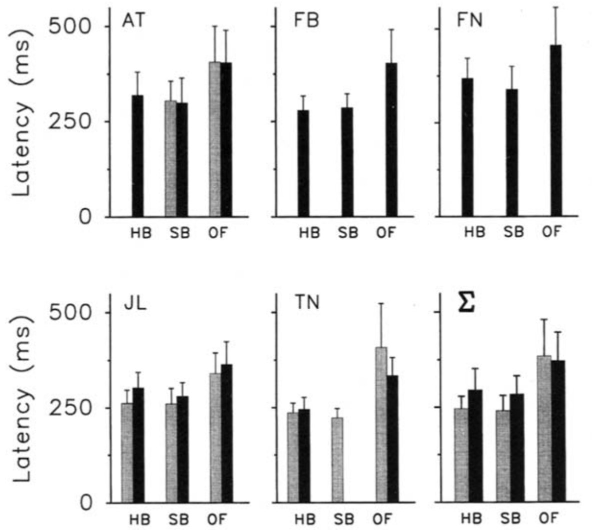

FIGURE 1. Saccadic latencies to moving targets with different backgrounds. Individual data of five subjects (AT, FB, FN, JL, TN) and accumulated data (Σ). Latencies with different backgrounds (homogeneous [HB], stationary [SB], optic flow [OF]). Black bars: experiments with an expansion optic flow stimulus. Grey bars: experiments with a horizontal, rotational optic flow stimulus. A Kruskal–Wallis ANOVA showed significant effects on latencies with different backgrounds ($P < 0.0001$). All latencies were significantly increased during the visually induced sensation of ego-motion [OF] ($P < 0.05$, Dunn's test, multiple comparison) compared with the latencies, when using a homogeneous [HB] or stationary background [SB]. Each value (except subject JL $N > 40$) comprises at least 125 trials. Accumulated data of five subjects (Σ): significant effects on latencies with different backgrounds (Kruskal–Wallis ANOVA, $P < 0.0001$). Saccadic latencies to moving targets were significantly increased by the visually induced sensation of ego-motion ($P < 0.05$, Dunn's test [black bar (OF) $N = 636$, grey bar (OF) $N = 535$]), and latencies with a stationary background were slightly but significantly decreased ($P < 0.05$, Dunn's test [black bar (SB) $N = 447$, grey bar (SB) $N = 177$]), compared with the latencies found with a homogeneous background [black bar (HB) $N = 349$, grey bar (HB) $N = 213$].

RESULTS

All the subjects experienced the sensation of ego-motion during the optic flow presentation and a strong motion after effect (MAE) after its cessation.

Coplanar condition

Experiment 1. Figure 1 shows the saccadic latencies for five subjects as the subjects' responses to movement onset of a peripheral target with a velocity of 2.5 deg/sec. Subjects' responses were tested with a homogeneous (HB), stationary structured (SB), and optic flow (OF) background, the latter resulting in visually induced sensation of ego-motion. The different backgrounds showed a significant effect on saccadic latencies to the moving targets (Kruskal–Wallis ANOVA, $P < 0.0001$, all subjects). The latencies of the saccades to the moving target were significantly increased by the visually induced sensation of ego-motion, compared with the latencies using a homogeneous background ($P < 0.05$, Dunn's test, multiple comparison, all subjects). Despite individual differences, the lengthening of the saccadic latencies during the visually induced sensation of ego-motion was independent of an optic flow simulating translation or rotation. In general, when compared with the stimulus simulating a translation the pattern simulating a rotation revealed a stronger influence on object-motion detection. In the case of the pattern simulating rotation, targets moved once in the direction and once in the opposite direction of the pattern movement. Saccadic latencies to targets moving opposite to the direction were shorter than latencies to targets moving in the direction of the pattern movement. However, even the shorter latencies were significantly longer than the latencies with the homogeneous or stationary background conditions.

Moreover, latencies with a stationary background were often slightly shorter than latencies with a homogeneous background. This coherence can be seen more clearly in the accumulated data ($P < 0.05$, Dunn's test). When comparing the latencies of the homogeneous and the stationary background in the experimental series with the ring and striped optic flow, the latencies of the latter series (optokinetic) are shorter for the homogeneous and stationary backgrounds. Subjects obtained more practice of carrying out the task in the course of experiments. Control experiments at the end of all the sessions, using the initial stimulus configuration, showed that latencies were on average 30–40 msec shorter than at the beginning. However, compared with the latencies with a homogeneous background, the observed lengthening of latencies during the visually induced sensation of ego-motion and the slight reduction of latencies during the presentation of the stationary background were significantly preserved. In Experiment 1 the sessions with expanding rings as an optic flow were performed first. Work with the optokinetic pattern then followed.

Experiment 2. In order to investigate whether the effect of increased saccadic latencies to the moving target during optic flow presentation is only due to the movement of the background or also due to the sensation of ego-motion, the following experiment was performed: in one case, the onset of optic flow movement was triggered at the beginning of the trial. No sensation of ego-motion was reported by the subjects in this set-up. In the second case, the presentation of the optic flow stimulus preceded the beginning of the trial. The target stimulus was not started until the subjects had reported the sensation of ego-motion (circular vection).

Figure 2(A) shows the saccadic latencies for three subjects and the mean data for the group. The saccadic latencies for all the subjects were significantly larger during the continuous optic flow presentation where the sensation of ego-motion was present compared with the brief optic flow presentation without the sensation of ego-motion. When compared with the stationary background condition the brief optic flow presentation still resulted in a significant increase in saccadic latencies. However, the visually induced sensation of ego-motion has an additional effect on motion detection, apart from the movement of an optic flow background itself. Again, the saccadic latencies to targets moving in the opposite direction of the pattern movement were shorter than the latencies to targets moving in the same direction as the pattern movement. However, in comparison with the brief optic flow presentation, both the latencies to targets moving in the same direction and those moving in the

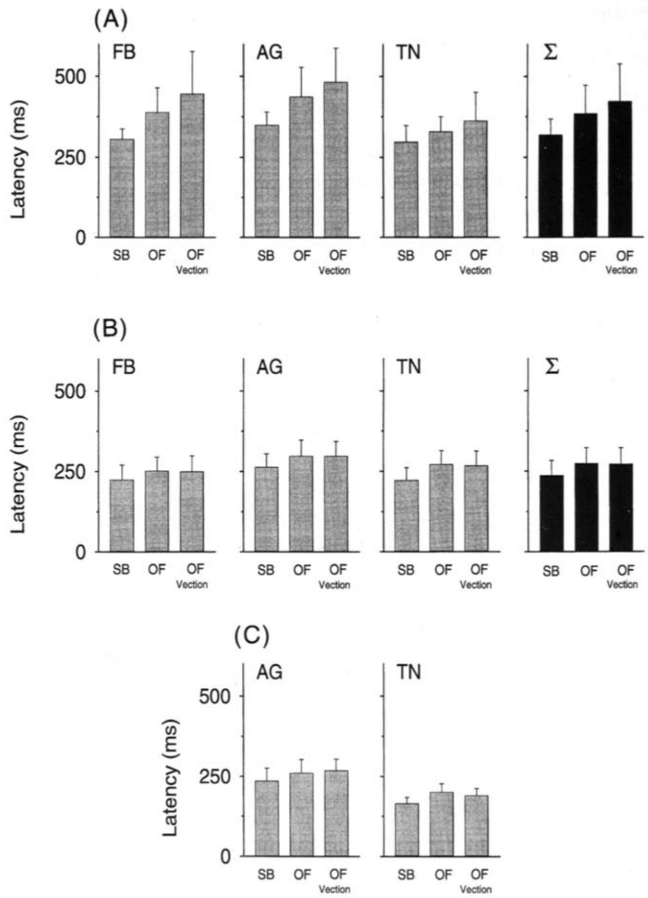

FIGURE 2. (A) Saccadic latencies to moving targets with stationary background (SB), brief presentation of optic flow (OF) and continuous presentation of optic flow (OF-Vection). Individual data of three subjects (FB, AG, TN) and accumulated data (Σ). A Kruskal–Wallis ANOVA showed significant effects on latencies with different backgrounds ($P < 0.0001$). The increase in latencies during brief presentation of optic flow (OF) was significant with $P < 0.05$ (Dunn's test, all subjects) compared with the latencies with a stationary background (SB). The increase in latencies during continuous presentation of optic flow (OF-Vection) was significant with $P < 0.05$ (Dunn's test, all subjects) compared with the latencies during the brief presentation of optic flow (OF). (B) Saccadic latencies to stationary targets changing colour. Individual data of three subjects (FB, AG, TN) and accumulated data (Σ). The different backgrounds showed significant effects on the latencies (Kruskal–Wallis ANOVA, $P < 0.0001$). The increase in latencies during the brief and continuous presentation of optic flow (OF, OF-Vection) was significant with $P < 0.05$ (Dunn's test, all subjects) compared with the latencies with a stationary background (SB). No significant difference was observed between the latencies during the continuous presentation of optic flow (OF-Vection) and the brief presentation of optic flow (OF) (all subjects). (C) Saccadic latencies to stationary targets changing contrast with different backgrounds. Individual data of two subjects (AG, TN). Significances as in (B). Each individual value comprises at least 125 trials.

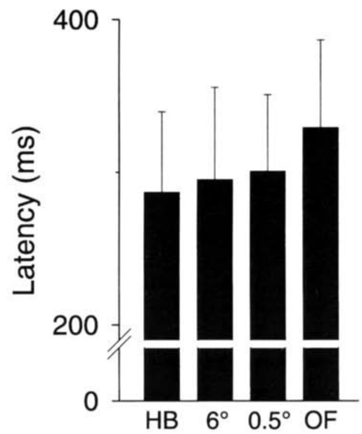

FIGURE 3. Saccadic latencies to targets moving along a trajectory with the background covered. Data from three subjects. Abbreviations under the corresponding bars: (HB) homogeneous background, (6 and 0.5 deg) vertical width of the mask around the target trajectory during optic flow presentation, (OF) optic flow presentation without mask. A Kruskal–Wallis ANOVA showed significant effects on latencies with different backgrounds and masks ($P < 0.0001$). The increase in latencies when using a 6 deg mask was not significant ($N = 386$, Dunn's test) compared with the latencies with a homogeneous background [HB] ($N = 393$). When using a 0.5 deg mask, the increased latencies were significant ($P < 0.05$, Dunn's test, $N = 391$) compared with the latencies with a homogeneous background [HB]. The increase in latencies by the visually induced sensation of ego-motion [OF] was significant ($P < 0.05$, Dunn's test, $N = 376$) compared with the latencies when using a homogeneous background [HB].

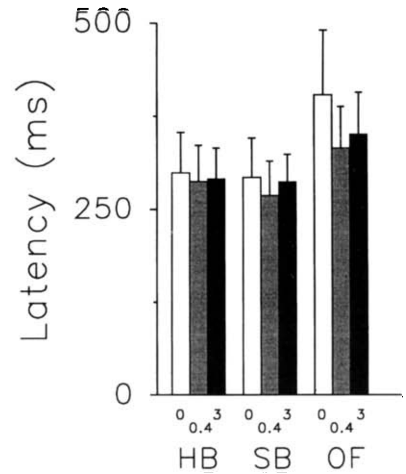

FIGURE 4. Saccadic latencies to moving targets at different depths of target and background. Data from two subjects. Abbreviations under the corresponding bars: (HB) homogeneous, (SB) stationary background, (OF) optic flow presentation, (0/0.4/3) disparity between target and background in degrees, with the target and fixation cross in the same plane [white bars: 0 deg-disparity (target and background coplanar) (accumulated data of subjects AT/FB taken from Fig. 1), grey bars: 0.4 deg-disparity, black bars: 3 deg-disparity]. The different backgrounds showed significant effects on the latencies (Kruskal–Wallis ANOVA, $P < 0.0001$). The increase in latencies by the visually induced sensation of ego-motion [OF] was significant ($P < 0.05$, Dunn's test [0.4 deg-disparity (OF) $N = 263$, 3 deg-disparity (OF) $N = 248$]) compared with the latencies using a homogeneous background [0.4 deg-disparity (HB) $N = 263$, 3 deg-disparity (HB) $N = 247$].

opposite direction as the pattern movement increased during the presentation of the optic flow, leading to the sensation of ego-motion.

The saccadic latencies were examined also for stationary targets that either change colour, contrast, or orientation while simultaneously presenting an optic flow with or without the sensation of ego-motion. This control experiment was performed in order to see whether the effect of a long-lasting optic flow presentation is also present when visual cues other than motion are given to the target. Figure 2(B) shows the saccadic latencies for three subjects and the mean data for detecting a green target changing to red. No difference in the latencies was observed during the continuous optic flow presentation leading to the sensation of ego-motion compared with the brief optic flow presentation. This was also true for the stationary targets changing contrast [Fig. 2(C)] or orientation (only one subject, not shown here). However, both optic flow presentations resulted in a significant increase in saccadic latencies compared with the stationary background condition.

In conclusion, optic flow presentations leading to a visually induced sensation of ego-motion only seem to influence the detection of moving targets and result in an additional increase in saccadic latencies when compared with the brief presentation of optic flow.

Experiment 3. In order to test whether the effect of optic flow on latencies is global or local, we covered the background of the target trajectory. Two different widths (0.5 or 6 deg) were chosen and the target trajectory was placed in the middle.

Figure 3 shows the accumulated data for the three subjects (AT/FB/FN) during the presentation of: (i) a homogeneous background; (ii) optic flow; and (iii) optic flow with covered target trajectories. Masking the background still resulted in a small increase in saccadic latencies by optic flow, compared with the latencies present for a homogeneous background. The effect of lengthening the latencies was more pronounced with the smaller mask (0.5 deg width). As the luminance of the homogeneous background and that of the masked area were the same, the local contrast between the target and background was identical in the homogeneous and masked optic flow condition. Any local interactions between the target and the homogeneous background, and the target and the masked area should also be the same. Thus, the increase in the latencies was solely due to the global motion of the optic flow in the masked optic flow condition. However, compared with a full optic flow presentation the increase in the latencies was only small during an optic flow presentation with either the large or the small mask. Local interactions between the target and the background motion possibly occur while presenting a full optic flow resulting in distinctly longer latencies. Thus, the lengthening of latencies during the visually induced sensation of ego-motion can probably be attributed mainly to local mechanisms. However, the results also indicate a global or a non-retinotopic effect of optic flow on motion detection.

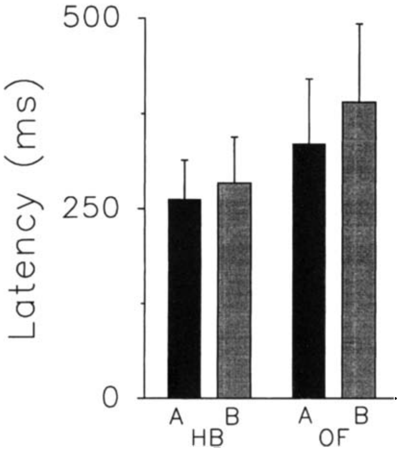

FIGURE 5. Saccadic latencies to moving targets in front of the background. Data from three subjects. Abbreviations under the corresponding bars: (HB) homogeneous background, (OF) optic flow presentation. (A) Fixation and targets in the same plane, but 3 deg in front of the optic flow background (black bars); (B) fixation in the plane of the background, and the moving targets in a plane 3 deg in front of the background (grey bars). Difference between the latencies for different fixation depths in the homogeneous background [HB (A) $N = 375$, HB (B) $N = 348$] and optic flow condition [OF (A) $N = 319$, OF (B) $N = 308$] was significant, with $P \leq 0.0001$ (U-test).

Disparate condition

We also investigated the influence of optic flow on motion detection when the target's motion occurred in front of the background. Under natural conditions, the object and background are usually at different depths. A spatial separation of the object and background may facilitate the detection of object-motion during a visually induced sensation of ego-motion. The disparate stimulus was designed to simulate such a situation.

Experiment 4. Figure 4 shows the accumulated data for two subjects (AT/FB) during the presentation of the target and background with disparities of 0.4 and 3 deg. At both disparities the latencies show behaviour similar to that found in the coplanar experiment 1; when compared with the motion detection against a homogeneous background a stationary structured background results in a slightly faster motion detection, whereas the visually induced sensation of ego-motion results in a poor motion detection. Additionally, Fig. 4 shows the accumulated data of the subjects AT and FB taken from Fig. 1, where the target and background were presented as being coplanar.

Experiment 5. Additionally, we investigated the influence of different depths of fixation on motion detection. In the experiments described above the fixation cross and the targets were always presented in the same plane. Under natural conditions moving objects often occur in a plane other than the actual planes of fixation. In this experiment a distinction was made between two conditions: (A) The initial fixation was in the same plane as the background. (B) The initial fixation and the moving target were in front of the background.

Figure 5 shows the accumulated data for three subjects (AT/FB/TN). Apart from the already observed increase in the latencies of saccades in both conditions during the visually induced sensation of ego-motion, different fixation planes also modulated the latencies when either a homogeneous background or an optic flow was presented. When the initial fixation and target were both placed in front of the background, saccadic latencies became significantly shorter than when the fixation cross was coplanar to the background ($P \leq 0.0001$, U-test).

DISCUSSION

First of all it should be noted that the optic flow stimuli used here were adequate for generating the sensation of ego-motion. Depending on the type of optic flow presented, all the subjects reported subjective linear vection, circular vection, and a strong motion after effect (MAE) (Brandt *et al.*, 1973; Berthoz *et al.*, 1975; Harris *et al.*, 1981; Andersen & Braunstein, 1985).

The results indicate that the visually induced sensation of ego-motion influences the detection of object-motion. When optic flow is presented, motion detection is impaired, as was shown by the increases in saccadic latencies. However, long exposures to the optic flow, which lead to the sensation of ego-motion, result in increased latencies, compared with brief exposures to optic flow. This fact may be ascribed to a higher saliency of the background stimulus with a longer presentation time, but not to the sensation of ego-motion. In the experiments with the stationary targets long exposures to optic flow do not have an additional effect on the latencies, compared with brief exposures to optic flow. If saliency is responsible for a further increase during a long presentation of optic flow, this should apply to both the detection of stationary and moving targets. However, as the further increase in latencies during a long presentation was only found to be the case for moving targets, the increase may be due to the sensation of ego-motion rather than to saliency. Moreover, non-visually induced ego-motion, such as vestibular stimulation, also leads to increased reaction times for the detection of moving targets (Probst *et al.*, 1986). Thus, we believe that the observed increased latencies to moving targets during the visually induced sensation of ego-motion may be a phenomenon linked to ego-motion. This phenomenon is modulated but not abolished by a disparity between an ego-motion-inducing background and a moving target, and masking around the target trajectory.

The saccadic latencies to moving targets presented against a homogeneous background are comparable with those obtained in the experiments of Gellman & Carl (1991). They measured latencies to moving targets in a simple-ramp paradigm, and postulated a model in which the predicted latencies depended on target velocity. Our measured latencies are generally slightly longer than those predicted by the model of Gellman and Carl for a given target velocity (2.5 deg/sec→250 msec). Our targets were to be found on the periphery, and reaction times to catch up with the moving targets increase with the degree of eccentricity (Tynan & Sekuler, 1982).

Therefore, the differences we observed could be attributed to this fact.

Saccades from one plane to another have longer latencies than saccades within the same plane (Honda & Findlay, 1992), which could explain the differences in the latencies of Experiment 5. Disparate stimuli were used with homogeneous and optic flow backgrounds, and the fixation cross was positioned at different depths. The increase in latency when the fixation cross is not in the same plane as the target may be caused by sensory differences (disparity, accommodative blur), by the necessity to co-program a vergence movement, or by a combination of these factors (Honda & Findlay, 1992). Nevertheless, optic flow influences the detection of object-motion. In other psychophysical experiments (Howard & Gonzales, 1987; Howard & Marton, 1992) in which smooth pursuit and optokinetic gain were investigated, there was either no, or only a negligible, influence of the background on the disparate condition.

The increased saccadic latency due to optic flow is not caused by the reduced physical salience (contrast) of the target. The stationary, structured background had the same physical characteristics as the optic flow, apart from the fact that it did not move. However, the saccadic latencies for motion detection are shorter with a stationary background than with optic flow, and even shorter with a homogeneous background. Moreover, masking the target trajectory in the optic flow condition did not prevent the increased saccadic latencies. The effect of optic flow on motion detection during the sensation of visually induced ego-motion thus appears to involve wide lateral interactions across the visual field.

The increased saccadic latencies caused by the optic flow may reflect a space constancy mechanism, which enables a stable environment to be perceived during ego-motion, and which may simultaneously impair the detection of object-motion. Wertheim (1994) proposed a model by modifying von Holst and Mittelstaedt's (1950) reafference principle, in which a reference signal, combining extraretinal (efference copy), vestibular, and visual signals, contributes to the perception of a stable environment or object-motion. The compound reference signal is compared with the retinal signal in order to determine ego-motion, object-motion, or stationarity. For example, when one begins to move, first the vestibular component in the reference signal equals the retinal signal and will therefore contribute to the perception of ego-motion. When a constant velocity is reached, the vestibular component decreases. Then the gradually growing visual component (in the reference signal) must maintain the size of the reference signal in order to equal the size of the retinal signal and thus to maintain the perception of ego-motion and a stable environment. However, the visual–vestibular interactions are probably not perfect because of, for example, the different time courses of vestibular and visual contributions (e.g. Dichgans & Brandt, 1972; Henn *et al.*, 1980). Owing to this fact, during ego-motion, an illusory motion of the environment may occur, since the reference signal may not be equivalent to the retinal image slip. Nevertheless, we generally perceive a stable environment and the sensation of ego-motion even when running and jumping, although the contribution to the reference signal coming from the visual and vestibular source may not equal the retinal signal. To avoid an illusory motion of the environment caused by differences between the reference signal and the retinal signal, the tolerance for a concious perception of this difference should be large (Wallach, 1985; Wertheim, 1994). Small differences between the reference signal and the retinal signal would then be masked, but would result in an increase in perceptual thresholds for object-motion during ego-motion, reflected in increased saccadic latencies.

An ego-motion inducing stimulus which involves only certain parts of the retina should also create reference signals required by the space-stabilizing mechanism. This mechanism would be effective for the whole visual field, and would thus impair motion detection in all areas of the visual field. This was revealed in our masking experiments where, although the background of the target trajectory was covered, the peripheral optic flow stimulus still influenced the detection of moving targets. Nevertheless, the increase in latencies during the visually induced sensation of ego-motion in the masking experiments was not as pronounced as in those without masking. Owing to the experimental configuration in the masking experiments, the spatial dimensions of the optic flow were reduced. Thus, a spatially smaller stimulus evoking ego-motion could lead to a smaller reference signal and to a less efficient space stabilization. The overall result would be reduced latencies in detecting object-motion. In contrast, a large view optic flow should lead to an efficient space stabilization and to distinctly impaired motion detection. Our experiments support such a notion, since the greatest increase in saccadic latencies was obtained using the rotation pattern, which had the largest spatial dimensions, and generally led to the strongest sensation of ego-motion.

Since ego-motion occurs in a three-dimensional environment, a mechanism of space constancy should operate in all spatial planes. Objects, both in direct proximity and further away, should be perceptually stable during ego-motion. Consequently, a spatial separation of an ego-motion-inducing optic flow, and moving targets should still result in the impaired detection of object-motion. The experiments in the disparate condition, which produced increased saccadic latencies during the visually induced sensation of ego-motion confirm this assumption.

Recent neurophysiological investigations have revealed that in non-human primates the middle temporal and the medial superior temporal areas (MT/MST) are involved in the analysis of visual motion (e.g. Zeki, 1974; Albright, 1984; Mikami *et al.*, 1986; Saito *et al.*, 1986; Tanaka *et al.*, 1986). Subspecializations in both areas suggest some parts are involved in analysing the field of motion caused by movement of the animal itself, whereas other parts are involved in analysing object movement in external space (Born & Tootell, 1992; Tanaka *et al.*, 1993). Moreover, MT and MST reveal disparity selectivity, and may thus contribute to a subdivision of the environment into large regions, such as foreground and background during ego-motion (Maunsell & Van Essen, 1983; Roy *et al.*, 1992; Bradley *et al.*, 1995). Recent studies in area MST have also revealed that vestibular signals or non-visual signals of ego-motion are integrated in this area (Duffy, 1996; Pekel *et al.*, 1996). This suggests that visual and non-visual signals of ego-motion are processed together to create a perception or sensation of ego-motion. These neuronal subpopulations would be essential for the representation of a stable environment during ego-motion and for the perception of object-motion. It should be also noted that neurons in the anterior superior temporal polysensory area (STPa) in monkeys could be identified which indicate a selectivity for visual motion originating from the movement of external objects but not monkey's self motion (Hietanen & Perrett, 1996). It would be interesting to find out how the motion processing system copes simultaneously with the external and the self-induced retinal image slip at these neuronal levels. Our experiments, however, indicate that these areas may not be completely independent.

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