Influence of global motion onset on goal-directed eye movements

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Saccades are very rapid eye movements in between two phases of fixation, which offer a precise measure of behaviour for the direction of the spotlight of attention. The onset of global motion is known to attract our attention reflexively. We asked whether brief global motion stimuli are able to modify the execution of saccades. When participants performed visually guided saccades towards a target presented in front of a structured background, saccade latency was 174 ms on average and correctness of saccades was 100%. If the presentation of the target occurred at the same time as the onset of a brief global motion signal, then the saccade latency increased dramatically to 243 ms with a slight decrease in correctness to 89%. However, if the motion stimulus preceded the presentation of the target, then the latency decreased to 114 ms while the correctness dropped close to chance levels (62%). *NeuroReport* 00:000–000 © 2010 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

While we are awake, every second, we perform three to five very quick eye movements, which are called saccades. Yet despite the fact that we perform approximately 250 000 saccades each day, we are not aware of the neuronal computations necessary to execute these eye movements. Saccades are known to be executed as a reflex-like behaviour and thus represent a means to measure overt shifts of individuals' attention [1,2]. A common attention mechanism underlying saccade target selection and object recognition was reported earlier [3].

In addition to the tight relationship between movement of the eyes and of the spotlight of attention, it is well known that the onset of motion reflexively captures attention [4–6]. In case of a local motion stimulus, the attention of an individual is drawn to this location. However, attention cannot be directed towards a specific location if a global motion stimulus is presented.

In this study we asked whether it is possible to determine interactions between the execution of visually guided saccades and the presentation of global motion stimuli.

Methods

To examine details of these neuronal computations, we instructed our five participants to perform visually guided eye movements, as fast and precisely as possible, toward targets appearing unpredictably on the horizontal meridian (-15, -10, 10 and $15°$).

Experimental setup

Eye position of four healthy naive participants (female) and one author (UI) (age 25–45 years, mean 33.1 years) was precisely measured using the magnetic search coil technique (SKALAR Medical, Delft, The Netherlands; [7]). We used an i486/50-based real-time computer system to control the experimental paradigm including stimulus presentation and data acquisition. The visual stimuli were back-projected onto a translucent tangent screen (viewing distance 1 m, subtending $\pm 42°$ horizontally and $\pm 32°$ vertically, pixel size 0.2°) using an active-matrix LCD video projector (SHARP; Sharp Corporation, Osaka, Japan). The frame rate of the display system was 70 Hz. Horizontal and vertical positions of the centre-aligned right eye were sampled at 1000 Hz with a nominal spatial resolution of 30 s arc.

Experimental paradigm

Each trial started with a computer-controlled fixation period (randomized between 500 and 1000 ms, eye position window $\pm 0.5°$) of a small centre target ($0.4 \times 0.4°$) surrounded by a textured background (300 randomly distributed vertical line elements, $0.2 \times 0.8°$). After successful fixation, a salient target ($0.8 \times 0.8°$) appeared at either 10 or 15° to the left or right on the horizontal meridian. The background motion onset relative to the saccade presentation varied between -200 ms (i.e. the motion started 200 ms before the target was presented) and 200 ms (i.e. motion started 200 ms after target presentation). In accordance with our regulations for the use

of search coils, a session never lasted more than 30 min. This procedure also ensured that our data were not affected by subject fatigue.

Description of motion stimuli

We applied three different types of global motion stimuli: translational, expansion and rotational flow fields. The duration of the motion stimuli was restricted to 200 ms to prevent steady-state, closed-loop compensatory eye movements. It is important to note that flow fields were computed to maintain the local motion signal in the proximity of the saccade target constant across all three motion stimuli.

Data analysis

Eye position was first filtered using an adaptive smoothing cubic spline. Then, eye velocity was obtained by a 2-point differentiation [8]. Finally, saccades were detected automatically using combined velocity and acceleration criteria. Saccade parameters such as latency, amplitude, duration and peak velocity were determined automatically. We emphasize saccade latency and saccade correctness here. Note that the chance level was 50% as we only used leftward and rightward target presentations. Valid trials were those in which individuals performed saccades within a time window starting at 100 ms after target presentation and lasting until 600 ms. Correctness of saccades was determined by the percentage of trials in which individuals performed saccades within this time window in the direction of the presented target. All data processing was performed off-line using a commercial software package (MATLAB; The MathWorks Inc., Natick, Massachusetts, USA).

Results

The onset of the motion stimulus was in close temporal relationship to the presentation of the saccade target, that is, from 200 ms before to 200 ms after the saccade target presentation. Note that the presented motion stimuli were irrelevant for the execution of the saccade paradigm. As the target position varied randomly from trial to trial, participants were not able to predict the location of the next saccade target.

From our eye position recordings, saccade latencies and saccade correctness were extracted automatically. These data obtained from all five participants, together with the grand mean across participants, are shown in Fig. 1. As target position affected neither saccade latency nor saccade precision significantly, we pooled the data for all four target positions for a given participant. The rightmost data in Fig. 1 depict saccade latency and correctness for saccades performed across a stationary background. On average across all participants, the latency was 174 ms and correctness was 100%. When a global motion stimulus was applied, two observations concerning saccadic latencies were made. Saccade latencies were substantially increased if the global motion onset was synchronous to the saccade target presentation. Across all participants and motion types, the latency was 243 ms and correctness of saccades was 89%. If the background motion started 200 ms after the target presentation, then saccade execution was not different from control with respect to latency and error rate. In between these two times, the latency decreased exponentially (see below).

In contrast, if the motion stimulus was shown 200 ms before the target was presented, then latencies were clearly reduced to 114 ms, but saccade correctness decreased to 62% on average. The fact that correctness declined to (near) chance levels suggests that the participants did not direct their gaze towards the target. Instead, the disappearance of the fixation target triggered saccades in these trials. When we questioned participants after the experiments, they reported that in some trials there was no saccade target at all.

Although there are some individual differences in the data, the major findings are consistently present in all participants. Obviously, there are two different mechanisms of decay in latency, depending on whether the motion stimulus was presented before or after the target, respectively.

In the case where background motion onset was delayed with respect to saccade target presentation, there seemed to be an exponential decay in latency. Figure 2 shows fitted curves of pooled latency data across all participants. The three parameters A, B and C that describe the exponential decay are quite similar for all three types of motion stimuli. The time constant (variable C) describing the decay in latency across all participants varied between 30 and 38 ms, depending on the specific motion type.

In the case where background motion preceded saccade target presentation, we observed a pronounced decrease in saccade latency that could be fitted by a linear regression. At the same time, the rate of correctness dropped down to chance level. The reduction in latency seemed to be linear to the absolute value of background motion onset independent of motion type (Fig. 2).

Discussion

The increase in saccade latency with synchronous global motion onset indicates that global motion is a very powerful stimulus for attracting attention [4,9], similar to visual transients [10]. Similarly, changes in luminance elicit masking effects [11]. Even the reverse is true, if subjects had to detect the onset of coherent motion in a dual task, a change in the colour of the fixation spot was able to mask motion perception [12]. In general, the attraction of attention, even when triggered by an irrelevant stimulus, is equivalent to the allocation of computational resources. These resources are missing for the accomplishment of the actual task in our experiment,

Fig. 1
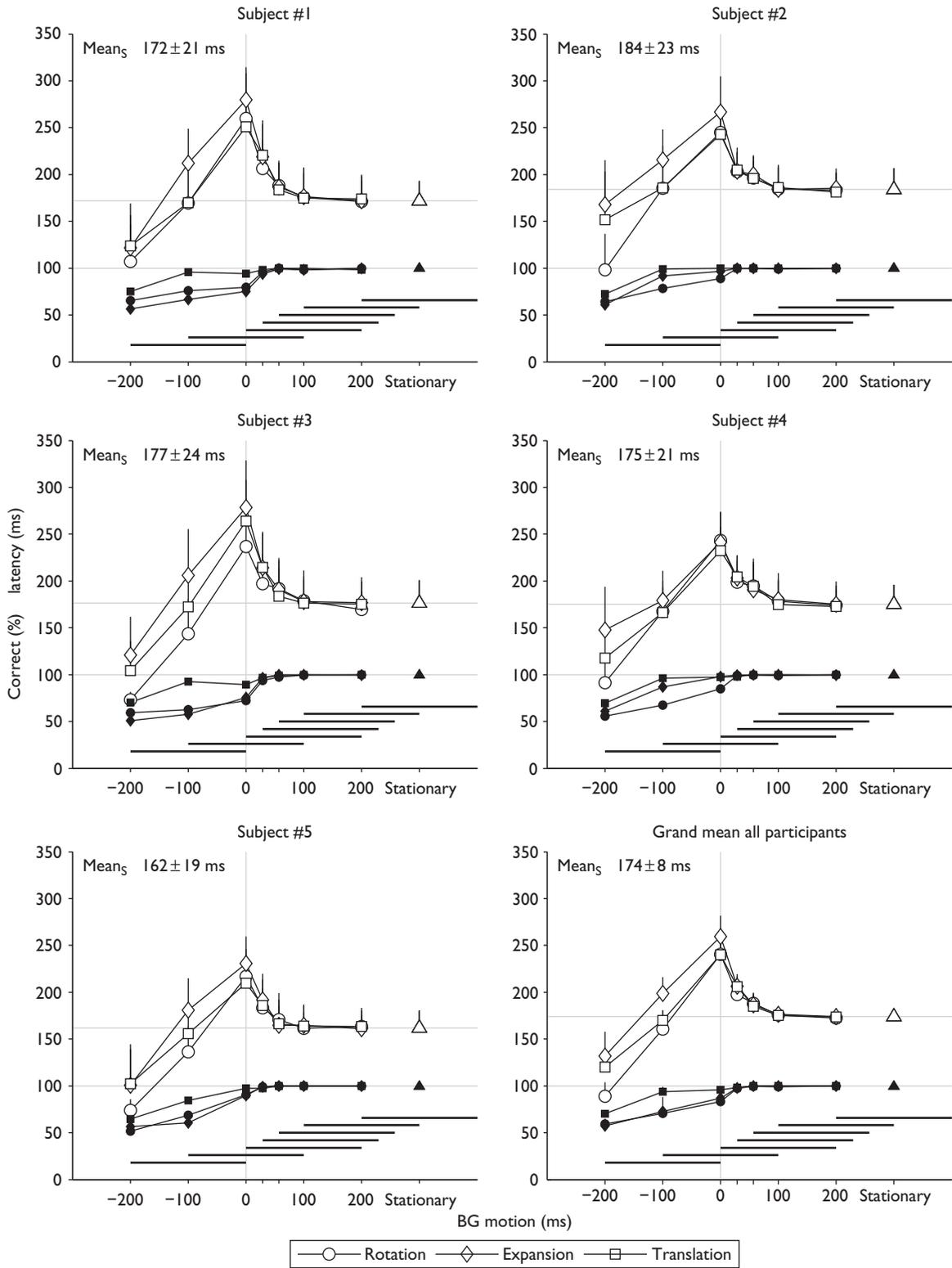
Saccade latencies and correctness. The dependency of saccade latency and saccade correctness on brief global (BG) motion is shown for all five participants and for the average across all participants. Data obtained from all possible target positions are pooled. Horizontal black lines give the time of the global motion stimuli. The rightmost data (triangle) in each figure refer to saccades performed across a stationary background whose mean and standard deviation are given in each figure.

Fig. 2
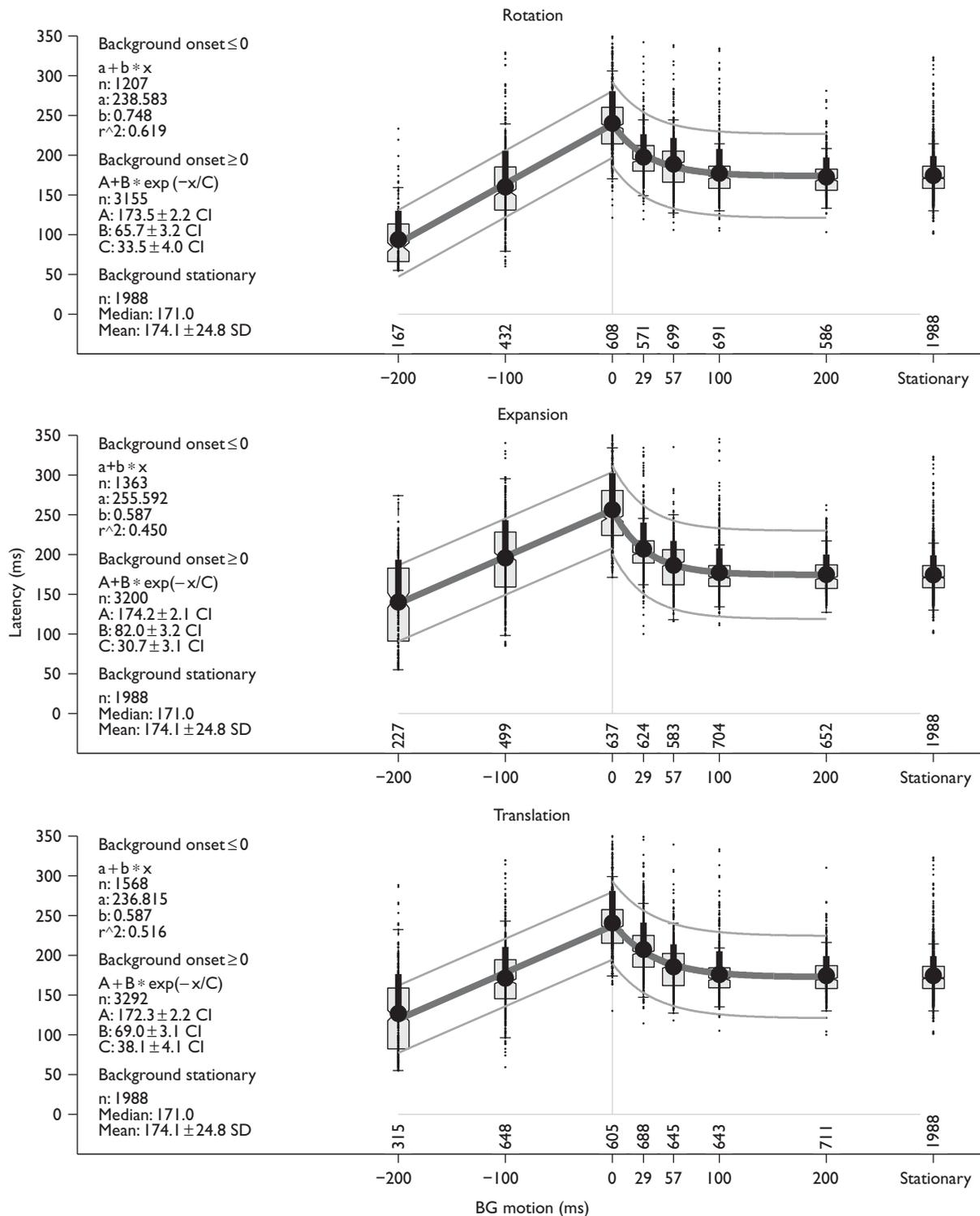
Curves fitted to saccade latency. Pooled individual saccade latencies from all five participants for three different types of background motion are shown. Latencies resulting from negative brief global (BG) motion (onset ≤ 0) are fitted by a linear regression, latencies from positive BG motion (onset ≥ 0) are fitted by an exponential function as indicated on the left. The rightmost data show the values obtained from saccades performed across a stationary background. The number of saccades in each condition is shown by the vertical numbers above the x-axis indicating the onset of BG motion (ms) relative to the onset of target displacement (0 ms). Box-plot (gray) illustration of saccade latencies: median (notch), upper and lower quartile, coverage of approximately 99.3% of data (whiskers), outliers (black dots), mean values (black circles), and standard deviations (thick black lines). The fitted curves are shown as thick lines; thin lines reveal the standard deviations (SDs). CI, confidence interval.

for the correct programming of a saccade. A much earlier but similar explanation introduced the concept of a bottleneck in dual-task processing [13]. The time constant describes the duration of this allocation of computational resources.

The time constant of the exponential decay in our data is significantly shorter than the time constant of an attention blink, which was reported on the order of some hundred milliseconds [14]. One reason for this pronounced difference in time constants might be the differing complexity of the tasks; saccades are automatically programmable, whereas the study addressing the time constant of the attention blink [14] required object recognition by the participants.

Interestingly, the marked reduction in saccade latency for negative background motion onset values was not observed if visual transients such as changes in background orientation or luminance were used [10]. It has been shown that motion stimuli are able to elicit the apparent disappearance of visual objects, a phenomenon called motion-induced blindness [15]. Similarly, if the visual object and the motion stimulus are presented dichoptically, the motion stimulus is able to block the perception of the visual object (generalized flash suppression). In fact, this perceptual suppression is closely related to the low frequency, local field potential recorded from the primary visual cortex of rhesus monkeys, not to the firing rates of individual neurons [16]. However, the generalized flash suppression does not hold for the perception of all visual objects. Surprisingly, when the sensitivity of participants for faces and global motion is tested during binocular rivalry, no effects of motion on face perception, and vice versa, were found.

More generally, humans are blind to major differences between two images if a distracter was presented between the two images (change blindness) [17,18]. Recently, it was reported that single-unit activity from the medial temporal lobe in the human brain follows the detection or the blindness of the changed stimulus [19]. These activities are in agreement with earlier functional magnetic resonance imaging studies which showed larger activation for change detection as compared with change blindness [20,21]. The common denominator of these change blindness studies is that perception of an object was severely impaired by global motion stimuli. In the present − 200 ms background motion onset condition, we showed a severe impairment of action owing to a global motion stimulus.

Earlier, it was proposed that separate mechanisms exist for action generation and for subjective perception [22]. Specifically, it was proposed that the ventral stream of cortical processing is responsible for perception, whereas the dorsal stream is responsible for action [23]. As appealing as this proposal is, especially because it is able to account for many of the deficits of neuropsychological

patients, motion-induced blindness seems to violate this concept of dual-stream processing. Action and perception suffer very similarly from the simultaneous withdrawal of computational resources. This indicates the existence of significant interactions between the ventral and dorsal processing streams, perhaps at various stages.

Finally, saccades are only one example of a rich variety of goal-directed behaviours. In addition to these fast eye movements, we also reach out for an object frequently. In a similar setting, when global motion stimuli were applied during fast pointing movements, hand trajectory shifts were induced by the motion stimulus [24]. Transcranial magnetic stimulation of area MT + in humans substantially reduced the amplitude of the manual after response [25]. Comparison of these results and ours emphasize the difference between saccades and fast hand movements; the execution of saccades is not affected by motion stimuli. Saccades are described by their ballistic nature, as opposed to the real-time controlled hand movements. The mechanisms underlying the execution of these eye movements are therefore of high relevance for fast acting technical control systems.

Conclusion
When the presentation of a saccade target coincides in time with the onset of a global motion stimulus, saccadic latency is massively increased compared with the condition with a stationary background. The execution of the saccade itself is not altered by the additional motion stimulus. We conclude that the increase in latency represents the automatic allocation of computational resources that are missing for programming the subsequent saccade. If the onset of the motion stimulus precedes the presentation of saccade target, a clear drop in saccadic latency was observed. However, saccades were not directed towards the target, because saccade precision was at chance levels in this condition. We conclude that the participants observed motion-induced blindness in this condition and generated default horizontal saccades. In summary, our results show that there are observable interactions between global motion processing and the execution of visually guided saccades; two processes that previously were seen as totally independent and separate processes.

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