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Shifts in the retinal image of a visual scene during saccades contribute to the perception of reached gaze direction in humans

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Abstract

We tested whether the perception of gaze direction is affected by the shifts in the retinal image of the visual scene during eye movements. To do so, we displaced the visual scene during saccadic eye movements and measured whether these unconsciously-detected shifts altered subjects' perception of the reached gaze direction. While facing a visual environment composed of light-emitting diodes, subjects first performed a rightward saccade of a great amplitude before producing a leftward saccade towards a target that appeared in the environment. During the primary saccade, the visual environment could be shifted by 4.5° on either side. Subjects overestimated the target by 3.69° and underestimated it by 2.45° when the shift of the retinal image of the environment was greater and smaller than the extent of eye deviation, respectively. This suggests that the perception of gaze direction is largely based on the processing of retinal excitation both before and after the eye movements.

Keywords: Gaze perception; Retinal signals; Saccades; Visual environment; Target position; Human

Evidences are cumulating suggesting that retinal signals influence the processing of other afferent signals which are also involved in constructing space representations. It has been notably shown that individuals are more accurate in determining head [1] and gaze [2,3] orientation in presence of retinal stimulation than in the dark. Interestingly, this visual stimulation does not have to convey spatial information to be contributive. Indeed, even fovea-fixed or head-fixed lights help individuals interpret extraretinal and cervical signals. These results argue for an enhanced egocentric encoding of gaze and head direction by the retinal inputs.

Retinal signals could also contribute to the coding of gaze orientation in another way. During eye-head movements, the image of the environment sweeps the retina with the same magnitude as the magnitude of the gaze shift. Processing the location of the retinal excitation before and after the eye movements could therefore provide the central nervous system with information about the reached eye position. Several studies have shown that when the target position shifts during a saccade, subjects can still produce accurate manual pointing without visual feedback of the hand (e.g. refs. [2,7,18,19]). In those studies, the mismatch between the shift in the retinal image of the environment and the magnitude of the gaze shift did not affect pointing accuracy. Such results show that the arm motor system is insensitive to the shift in the retinal excitation when determining gaze (and therefore target) direction. However, these results do not provide information about the precision with which subjects perceive their gaze direction in such circumstances.

Perceptual threshold for visual stimulus detection is increased during ocular saccades, so that shifts (usually smaller than about 8°) in the visual environment that occur near the mid-flight of the saccades are not consciously perceived (saccadic suppression phenomenon [9,17]). Therefore, if the change in retinal signals provides information about the reached gaze direction, subjects' introspective sense (perception) of where they are looking at after saccadic eye movements could be affected by displacements of the visual scene. The present study tested this hypothesis.

Seven subjects participated in the experiment (mean age: 24.5 years). They gave their informed consent after being briefed about the experiment and they all self-declared to

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have normal vision. A schematic representation of the experimental set-up is presented in Fig. 1. Subjects were seated in complete darkness in front of a horizontal semi-reflecting glass positioned at chin level. A strap immobilized their head in a *U*-shape head-rest. Several light-emitting diodes (LEDs, 3 mm in diameter) were fixed on a semicircular black, non-reflective screen positioned above the horizontal glass. A panel prevented direct vision of the LEDs. Subjects could only see their virtual images appearing 21 cm beneath the semi-reflecting glass, 70 cm from their eyes. These LEDs were used to create different visual environments. Another LED was fixed at the tip of a horizontal pointer which was mounted on the vertical axis of a motor. Subjects could activate the motor using a knob, displacing the pointer in the same arc of a circle and in the same horizontal plane as those of the LEDs forming the visual environment. Angular position of the pointer LED was measured with a potentiometer. Horizontal eye movements were recorded with the electrooculographic method using disposable Ag-AgCl electrodes and a conventional bio-isolated amplifier (Lablinc V®-Coulbourn™). Eye and pointer position signals were sampled at 400 and 100 Hz, respectively.

At the beginning of each trial, subjects were facing a visual environment composed of LEDs respectively located at 0° (straight-ahead), 12° and 36° to the right. They were instructed to gaze at the central target until they heard an auditory signal (beep), which sounded 2.5 s later. At this time, they had to produce a large rightward saccade bringing the gaze beyond the 36°-LED. Following the saccade, a target (LED) appeared either at 19.5°, 24° or 28.5°. Subjects then produced a saccade towards this target. The target remained on for 3.5 s, period during which subjects had to concentrate on the gazed target position. Then all LEDs were switched off. In complete darkness, the subjects brought their eyes back near the central target, which reappeared after the 'return saccade'. While the subjects were visually fixating the central LED, the pointer LED was switched on. Using a knob, subjects had to position the pointer LED at the 'remembered' location of the target (where they were previously gazing at). At the end of the trials, all LEDs were switched off and subjects displaced the unseen pointer LED to an unknown position, moving it back and forth several times.

For the trials where the 28.5°-target was presented, the initial visual environment (i.e. the 0°–12°–36° set of LEDs) could be shifted by 4.5° to the right when peak velocity of the primary saccade was reached (see Fig. 2 for typical raw recordings in this condition). In this case, after the visual scene displacement, the subjects were facing an environment composed of LEDs located at 4.5°, 16.5° and 40.5° to their right, respectively. The shift of the environment's image on the retina was then 4.5° smaller than the extent of eye deviation, being of 24° when subjects were gazing the 28.5°-target. If subjects processed the retinal consequence of the saccades to determine the reached gaze deviation, they should have underestimated the previously fixated target in this condition.

For the trials where the 19.5°-target was presented, the visual scene could be shifted 4.5° to the left during the primary saccade. In these trials, the fixation of the target was performed in a visual environment composed of LEDs located at 4.5° to the left, 7.5° and 31.5° to the right of the subjects, respectively. Here, the shift of the environment's image on the retina was 4.5° greater than the extent of eye deviation, being of 24° when subjects were fixating the 19.5°-target. Therefore, if the change in retinal excitation during eye movements contributed to the perception of the reached gaze deviation, subjects should have overestimated the eccentricity of the fixated peripheral target in this condition.

The experiment was therefore composed of five experimental conditions; three with stationary visual scenes (using the 19.5°-, 24°-, 28.5°-targets) and two with shifts of the visual scene (using the 19.5°-, 28.5°-targets). Subjects were not informed about the possibility that the visual scene could be displaced during the trials. They performed ten trials in each experimental conditions. The order of presentation of these conditions was randomized by the computer.

Subjects never reported having seen the shifts of the visual environment. The mean perceived positions of the three targets are represented in Fig. 3, in conditions with and without visual scene displacements for the trials in which

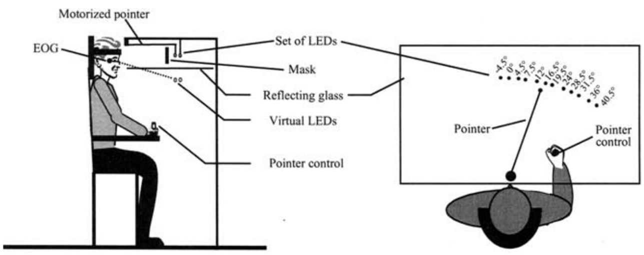

Fig. 1. Side view (left panel) and top view (right panel) of the experimental set-up.

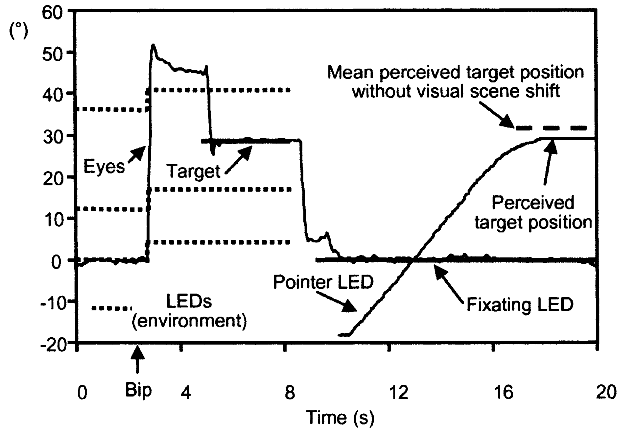

Fig. 2. Typical raw recordings when the visual environment shifted 4.5° to the right during the primary saccade.

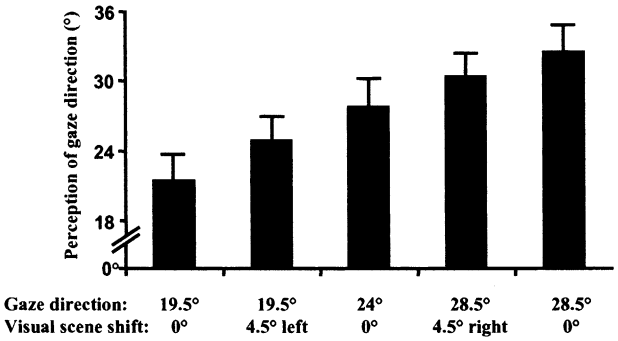

Fig. 3. Mean perceived positions of the three targets, in conditions with and without visual scene displacements in the trials using the 19.5°- and 28.5°-targets.

the 19.5°- and 28.5°-targets were presented. The eccentricity of the gazed targets was overestimated in the conditions without shift in the visual scene. The overestimation increased with target eccentricity (2.17°, 3.93° and 4.44°, for the 19.5°, 24° and 28.5° targets, respectively). This could be due to the tendency to overestimate the eccentricity of visual images (here the pointer LED) seen in peripheral vision [5,11,15]. Subjects' perception of both the 19.5°- and the 28.5°-target positions depended of whether or not a shift in the visual environment occurred during the primary saccade. Indeed, subjects perceived the 19.5°-target as being 3.69° further to the right when there was a 4.5° leftward shift of the environment compared to when the visual scene remained stationary. On the other hand, subjects perceived the 28.5°-target to be 2.45° less to their right when the visual scene shifted 4.5° rightward. An one way analysis of variance followed by a Post-hoc Tukey test ($P < 0.05$) showed that the perceived position of the targets was significantly different in each experimental condition [$F(4,24) = 131.28$, $P < 0.001$]. The variability in the perceived target position was not significantly different between the different conditions [global mean = 2.18°, $F(4,24) = 1.10$; $P > 0.05$].

It is well known that the perceived position of a gazed target can be affected by several factors. These include the type of ocular behaviour that brings the eyes to the final target position (e.g. smooth pursuit, saccade [4,16]), the presence and the location of visual cues with respect to the target [10,14] and the motion of the visual space surrounding the target [6,20]. Because the shifts in the visual scene had a marked impact on the perception of gaze direction, the results of the present study show that the retinal consequence of the saccades also affects the perceived position of gazed targets. As much as 82 and 54% of the experimentally increased and decreased shift of the visual scene respectively were taken into account when subjects estimated the direction of the fixated target after their saccades. Contrary to some of the above cited studies, misperception of target positions could no be explained by illusory target displacements resulting from motion of the visual environment. Indeed, the targets only appeared after the shifts of the visual scene and at different positions. Therefore shifting the visual environment affected primarily subjects' perception of their gaze direction, leading them to mislocalize the targets they were gazing at.

In a recent experiment, similar unconsciously detected shifts of the visual scene (also composed of three LEDs) during the saccades failed to affect the accuracy with which subjects reached with their unseen index finger for a gazed target [2]. Retinal information would therefore play different roles for perception and action, as already suggested by others [6,13]. Perception of gaze direction would be based largely on the processing of retinal excitation both before and after the eye movement, whereas motor actions, such as goal-directed arm movements, would rather be essentially guided through extra-retinal signals such as proprioception and efference-copy [8,12].

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