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RESEARCH NOTE

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The saccadic component of ocular pursuit is influenced by the predictability of the target motion in humans

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Abstract Predictive control is an important aspect of the smooth pursuit eye movements: it has been shown that when the target motion is composed of a mixture of sinusoids of different frequencies it becomes unpredictable and there is a decline in gain for the lowest frequencies but not for the highest one. Using such a pseudo-random paradigm we studied the effect of predictability of the target motion on the saccadic component of pursuit. For both the saccadic and the smooth components of pursuit, we observed that the gains for the lowest frequencies were significantly lower than the gain for the highest frequency. Thus, predictability of the motion of a visual target seems to influence both the smooth pursuit component and the saccadic component of ocular pursuit in the same way.

Keywords Eye movement · Smooth pursuit · Humans · Predictability · Saccades

Introduction

Smooth pursuit eye movements (SPEM) are visual tracking movements that ideally keep the image of a moving target on the fovea. SPEM use prediction based on internal representation of the target movement: whilst the pursuit response to a target moving randomly has a delay of about 150 ms, a subject presented with a periodic target movement will, often within a single cycle, lock on the target and track with no delay (Bahill and McDonald 1983). The predictive component of smooth pursuit has been studied by comparing the gain, i.e., the ratio of eye velocity and target velocity, during predictable (pure sinusoid) and unpredictable (pseudo-random stimuli composed of a mixture of sinusoids of different frequencies) target motions (Collewijn and Tamminga 1984; Barnes et al. 1987; Barnes and Ruddock 1989). These authors showed that the mix of different frequency sinusoids is not enough to induce unpredictability in such a paradigm. To become unpredictable, a pseudo-random stimulus must include at least one frequency component higher than 0.4 Hz. When the highest frequency was less than 0.4 Hz, gains for all the different frequency components were identical to the gain observed for the pursuit of pure sinusoids at the same frequencies. When a pseudo-random stimulus includes a frequency component higher than 0.4 Hz, there is a decline in gain for the lowest frequencies but not for the highest one, as if the subjects actively pursue only the highest frequency component of the target and passively the other frequency components, with gains near a basal level (Barnes and Ruddock 1989).

When the SPEM gain is less than 1, saccades are needed to catch up with the target. The resulting composite pursuit (smooth pursuit + saccades) should track the target with greater accuracy. While the saccadic system is required during pursuit, the influence of predictability on this component has never been studied. Therefore, the aim of this study is to characterize the influence of the unpredictability on the saccadic component of the pursuit.

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Methods

Subjects

Twenty-four healthy subjects (19 males, 5 females) were recruited from the general population through newspaper advertisements. They were between 22 and 51 years old (average = 31.2 ± 7.7 years). The subjects were screened by the Diagnostic Interview Schedule (Robins et al. 1981), and had no personal history of neurological or psychiatric disorders and no family history of psychotic illness. Subjects with strabismus, nystagmus, neurological disease, mental retardation and alcohol or substance abuse were not included in the study. Visual acuity was normal or corrected if necessary.

The study was approved by the ethical committee (CCPPRB) of Basse-Normandie, it was then performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki. All subjects gave written informed consent before participating in this study.

Oculomotor measures

Eye movements were recorded by an infrared scleral reflection device (Iris, Skalar, Delft, The Netherlands) in a quiet darkened room. The targets were projected on a flat screen placed 110 cm in front of the subjects. A chin rest was used to minimize head movements. Each experimental session started and finished with a calibration accomplished by sequentially illuminating light emitting diodes (0°, ±5°, ±10°, ±15°, ±20° and ±25°). For the pseudo-random pursuit task, the subjects were asked to track a moving laser spot for 1 min. The target motion composed of five different sinusoidal waveforms, each of peak velocities ±5.5°/s: 0.1, 0.2, 0.4, 0.6 and 0.8 Hz, this mix of the five frequencies composed a cycle of 10 s duration, which was repeated six times during the recording session which lasted 1 min.

The target position (Fig. 1a) and the eye position ("composite eye position," Fig. 1b) were sampled at 200 Hz. Eye movement velocity was calculated digitally using the two-point central difference algorithm (50 ms step size). From the eye velocity signal, the saccadic eye movements were removed and replaced by a linear interpolation resulting in a smooth pursuit eye velocity. This was then integrated resulting in a smooth eye position (Fig. 1c). A saccadic eye position (Fig. 1d) was computed by subtracting smooth pursuit eye position from raw eye position.

To separate the results for each frequency component, a discrete Fourier transform was performed for each subject, on target position, eye position, smooth eye position and saccadic eye position. The composite, smooth and saccadic eye position gains were calculated for each subject at each frequency as the ratio between the amplitude of the eye position and the amplitude of the target position. The smooth eye position gains represented the eye following the target without eye saccadic movements, i.e., the capacity for the subjects to pursue a pseudo-random target without undertaking eye saccadic movements. The smooth eye position gain is mathematically equal to the smooth eye velocity gain (ratio of the slow phase eye movement to the target velocity). The saccadic pursuit gains represent the part of the pursuit due to the saccades.

Statistical analysis

The gains were described using average ± standard deviation (SD). ANOVAs were used to detect the frequency effects on the composite, smooth and saccadic gains.

The gains of the four lowest frequencies were averaged together and compared (*t*-tests) with the gain at 0.8 Hz because all the previous studies showed that breakdown of the predictive component of the smooth pursuit system was expressed by low gains for the lowest frequencies and a high gain for the highest frequency of the stimulus whatever the number and the level of different frequencies.

Results

Figure 2 summarizes the results for the 24 subjects.

Eye position

The ANOVA showed a significant frequency effect ($P < 0.0001$). The average gain of the four lowest frequencies (average = 0.948 ± 0.114) was significantly lower than the highest frequency gain (1.196 ± 0.189; $P < 0.0001$).

Smooth eye position

The ANOVA showed a significant frequency effect ($P < 0.0001$). The highest frequency gain (0.763 ± 0.155) was significantly higher ($P < 0.0001$) than the average of the four other frequencies (average = 0.617 ± 0.106).

Saccadic eye position

The ANOVA showed a significant frequency effect ($P < 0.0001$). The average gain of the four lowest frequencies (0.374 ± 0.149) was significantly lower than the highest one (0.528 ± 0.202; $P = 0.0002$).

Discussion

As in earlier studies (Barnes et al. 1987; Barnes and Ruddock 1989; Collewijn and Tamminga 1989; Xia and Barnes 1999), we observed that the smooth pursuit gains for the four lowest frequencies were significantly lower than the gain for the highest one. This means that the pseudo-random stimulus induced a breakdown in the

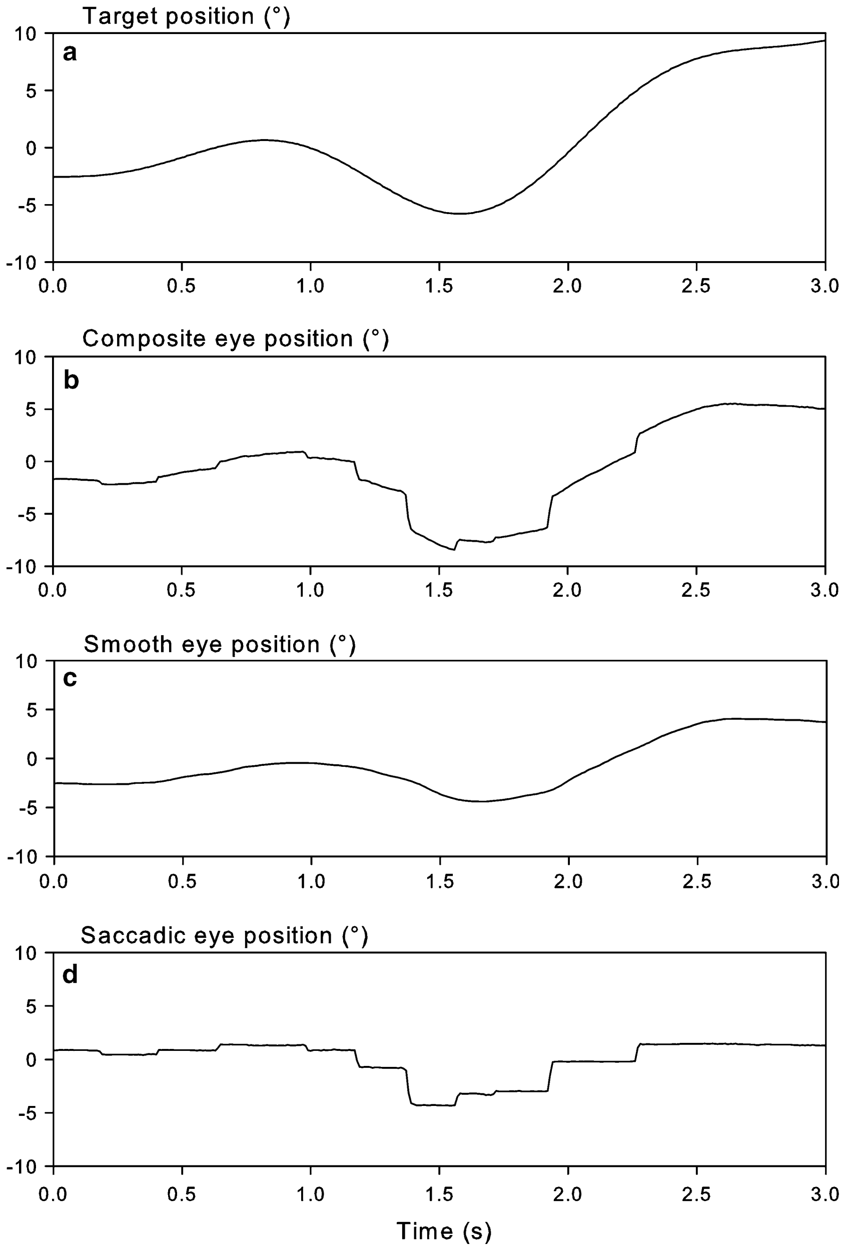

Fig. 1 Representative data during pursuit of a target moving pseudo-randomly. **a** Target position (°); **b** eye position (°); **c** smooth eye position (°); **d** saccadic eye position (°)

predictive behavior of the smooth pursuit response. To explain the breakdown, Barnes et al. (1987) suggested that two distinct and separate components could be involved in the control of the pursuit eye movements: a primary pathway provides a direct and continuous feedback of the retinal velocity error, while a secondary pathway uses prediction based on the identification of the highest frequency component. Hence, the primary pathway could be responsible for the basal gain (0.5–0.6) response, and that response could be enhanced specifically for the highest frequency component of the stimulus, by the activity of the secondary pathway.

While pursuing a target, if the saccadic system was only used to compensate a low smooth pursuit gain, the saccadic gain should be higher when the smooth pursuit gain is lower. Thus, in our pseudo-random paradigm, saccadic gain should be higher for the lowest frequencies than for the highest one. In fact, we observed that saccadic gain was lower for the four lowest frequencies than for the highest one. Therefore, as for the smooth pursuit, the saccadic response to the stimulus also seems to be at a basal level for the four lowest frequency components with significantly higher response for the highest frequency. This indicates that the saccadic system seems to have been influenced by the predictability of stimulus too. As the breakdown of the predictability seems to act in the same way both on the smooth and the saccadic components of pursuit, we suggest that during tracking behavior the "predictive" target movement estimation mechanism described above

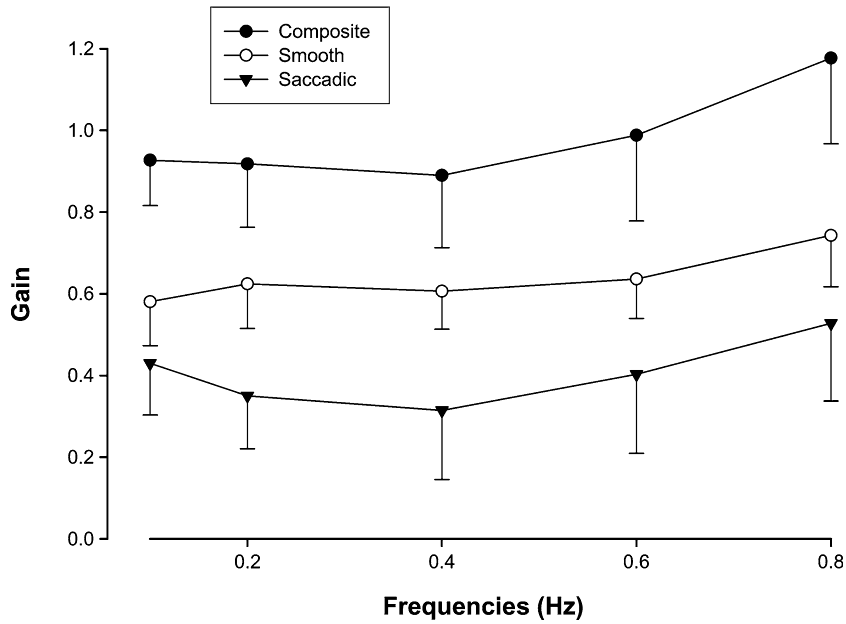

Fig. 2 Gains for the composite, smooth and saccadic pursuit at each frequency (mean ± SD)

acts on both the smooth pursuit and the saccadic components. This hypothesis is in line with recent studies showing that the functional architecture of the pursuit system is much more similar to that of the saccadic system than the preceding belief, suggesting that these two movements could be different outcomes from a shared common oculomotor system (Krauzlis 2004).

Conclusion

In this study, characterized by the use of an unpredictable pseudo-random paradigm, we observed the breakdown of the predictive component of the smooth pursuit system, and also of the predictive component of the saccadic eye movements system. So when pursuing an ocular target, three systems are used: the smooth pursuit component, the saccadic component and the predictive component that influences both of them.

Some neurological or psychiatric pathologies, such as schizophrenia, are well known to impair the pursuit eye movements of patients. It could be interesting to study the pseudo-random pursuit to determine which component of the pursuit system is impaired in such pathologies.

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