Eye movements of rhesus monkeys directed towards *imaginary* targets

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Abstract

Is the presence of foveal stimulation a necessary prerequisite for rhesus monkeys to perform visually guided eye movements? To answer this question, we trained two rhesus monkeys to direct their eyes towards *imaginary* targets defined by extrafoveal cues. Independent of the type of target, real or *imaginary*, the trajectory of target movement determined the type of eye movement produced: steps in target position resulted in saccades and ramps in target position resulted in smooth pursuit eye movements. There was a tendency for the latency of saccades as well as pursuit onset latency to be delayed in the case of an *imaginary* target in comparison to the real target. The initial eye acceleration during smooth pursuit initiation elicited by an *imaginary* target decreased in comparison to the acceleration elicited by a real target. The steady-state pursuit gain was quite similar during pursuit of an *imaginary* or a real target. Our results strengthen the notion that pursuit is not exclusively a foveal function. © 1999 Elsevier Science Ltd. All rights reserved.

1. Introduction

Research on smooth pursuit eye movements (SPEM) in the last 20 years has been dominated by the view that this type of visually guided eye movement depends on the presence of retinal image motion. However, there are numerous observations which require an expansion of this view. Firstly, if the feed-back loop of the pursuit control system is cut open by retinal stabilization of the target, SPEM can still be executed, despite the total absence of retinal image motion (Morris & Lisberger, 1987; Barnes, Goodbody & Collins, 1995). The amount of position offset during retinal stabilization determines whether a sequence of saccades or SPEM is performed: large offsets yield saccades whereas small offsets yield SPEM (Kommerell & Klein, 1971; Grüsser, 1986). Secondly, human subjects are able to produce anticipatory pursuit in expectation of target movement (Kowler & Steinman, 1979; Barnes & Asselman, 1992). Thirdly, also non-visual stimuli can elicit SPEM. For instance, subjects are able to track the movement of their own

thumb in complete darkness (Gertz, 1916; Steinbach, 1969; Gauthier & Hofferer, 1976; Glenny & Heywood, 1979), suggesting usage of somatosensory and/or efference copy signals to elicit SPEM. Furthermore, moving auditory targets can be used to elicit smooth pursuit, although SPEM gain is usually small and SPEM are therefore contaminated by many saccades (Zambarbieri, Schmid, Prablanc & Magenes, 1981; Hashiba, Matsuoka, Baba & Watanabe, 1996).

If SPEM is elicited by visual stimuli, these stimuli need not to be seen foveally. When Winterson and Steinman (1978) instructed their subjects to look 6° below a moving single dot, they could generate SPEM, although the steady-state gain was clearly reduced (Winterson & Steinman, 1978). The authors' conclusion that "*pursuit is not a foveal function*" was further supported by an observation by Lisberger and Westbrook (1985), who found that, although eye acceleration during SPEM initiation declined with target eccentricity, movement in the peripheral visual field was able to initiate SPEM prior to the execution of an initial saccade (Lisberger & Westbrook, 1985).

The fact that SPEM can make use of non-foveal visual stimuli and even non-visual stimuli seems reason-

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able from an ecological point of view. In a natural environment, visual objects are often incomplete due to partial masking by foreground structures. For instance, human subjects are able to track a hidden, invisible corner of a rectangle or the invisible hub of a rolling wheel (Steinbach, 1976). Inspired by these observations, a sequence of experiments, in which human subjects were asked to track an *imaginary* target, usually the invisible center of two moving points, were performed in several laboratories (Barnes & Hill, 1984; Barnes & Crombie, 1985; Collewijn & Tamminga, 1986). As pointed out by Wyatt and colleagues (1994), all these studies used periodic target trajectories so that the subjects were able to predict and to anticipate the movement of the target, an effective non-retinal input for the pursuit system (Bahill & McDonald, 1983). To remove the influence of prediction in experiments designed to reveal the ability to pursue the movement of an *imaginary* target, Wyatt and colleagues (1994) therefore introduced non-periodic target trajectories. They were able to show that parafoveal information alone can be used to reconstruct "*imaginary foveal image motion*" guiding SPEM (Wyatt, Pola, Fortune & Posner, 1994).

Our experiments reported here demonstrate that rhesus monkeys similar to humans can be trained to use parafoveal information to reconstruct *imaginary* foveal position and/or motion guiding eye movements. Some aspects of this work were previously published in abstract form (Ilg & Thier, 1997).

2. Methods

The eye movement data presented here were obtained from two female rhesus monkeys (*Macaca mulatta*) prepared for chronic recordings of eye movements using the search coil technique (Robinson, 1963; Judge, Richmond & Chu, 1980) as described in detail in an earlier publication (Ilg & Thier, 1996). In brief, after successful initial fixation training (Wurtz, 1969), the monkeys underwent sterile surgery in which an eye coil

and a post allowing the painless restraint of the head were implanted under intubation anaesthesia. All experimental procedures were carried out in accordance with the guidelines laid down by the NIH, the German law and approved by the local ethic committee.

2.1. Visual stimulation

The monkeys faced a $86° \times 66°$ tangent screen at a viewing distance of 85.5 cm onto which the visual stimuli were back-projected (Electrohome Videoprojector ECP 4100) whose spatial resolution was 1280×1024 pixels and temporal resolution was 60 Hz. The real target was a red hourglass (size 20°, luminance 0.5 cd m^{-2}) whose narrowest point, defined by the intersection of the diagonals, the monkeys had to track (see Fig. 1A). The *imaginary* target was the same red hourglass with the central area of 12° blanked out (see also Fig. 1B). In this case, the intersection of the diagonals was invisible and had to be reconstructed mentally.

The eye position control window was smaller than the blanked region. This ensured that the monkey could not simply fixate one of the four visible line endings in the *imaginary* target. Violation of the eye control window led to the instantaneous abortion of the ongoing trial.

2.2. Experimental paradigm

The search coil signals were calibrated requiring fixation of stationary dots at known positions. During the experiments, every single trial started with the presentation of the real figure for 1 s in the center of the tangent screen. Subsequently, the target, either real or *imaginary*, was displaced into unpredictable horizontal locations (step paradigm) or moved smoothly towards the right or left from the center of the screen at 12 deg s^{-1} (ramp paradigm). To minimize the effect of anticipation (Kowler & Steinman, 1979), the sequence of trials was determined by a random process. An experimental session never exceeded 1 h to avoid fatigue.
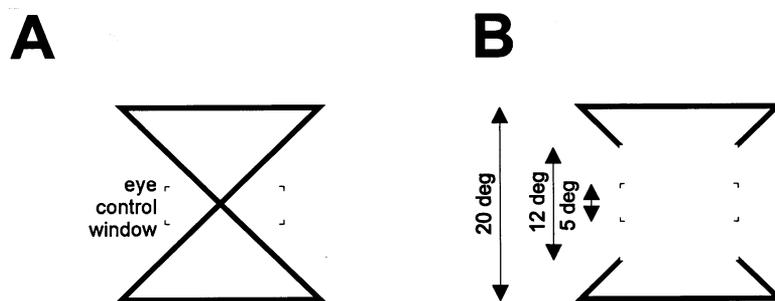

Fig. 1. The real (**A**) and *imaginary* target (**B**): the stimuli are drawn at scale together with the eye control window (invisible in the display for the monkeys). The monkeys had to fixate the intersection of diagonals in the case of the real figure and to reconstruct this location in case of the *imaginary* figure.

2.3. Data analysis

The analog horizontal and vertical eye position signals were lowpass filtered at 250 Hz before sampling at 500 Hz each. Eye velocity and acceleration were calculated off-line from the stored eye position records using digital filter techniques providing simultaneous differentiation and lowpass filtering (-3 dB at 60 Hz). Note that the subsequent data analysis as explained in detail below was based on single trials. The onset and termination of saccades were detected using an acceleration threshold criterion and saccade amplitude and saccade latency were determined automatically. In order to characterize SPEM initiation, pursuit onset latency and initial eye acceleration were determined (see Fig. 4 for details). During steady-state pursuit, catch-up saccades were detected and eliminated. The eye velocity record was then interpolated by a linear segment connecting the pre- and post-saccadic velocities. The mean smooth eye velocity was calculated based on de-saccaded eye velocity profiles for a period starting immediately after the initial saccade (or 200 ms following the onset of target movement in case no initial saccade was detected) and lasting until the end of the trial. The steady-state gain of SPEM corresponded to the ratio of this mean eye velocity and target velocity.

2.4. Statistics

To determine whether an experimental variable had an effect on the eye movement response, we calculated two-way ANOVAs with a significance level of $P \leq 0.01$ for main effects and interactions. For further analysis of significant interactions, post-hoc Scheffé tests with a significance level of $P \leq 0.01$ were carried out.

3. Results

This report is based on two rhesus monkeys (E and L) who learned to direct their eyes towards the center of an hourglass like figure (see Fig. 1), which in case of the real target was the intersection of the two diagonals. In the case of the *imaginary* target, this intersection was blanked out.

The training procedure of the monkeys consisted in three steps: firstly, we trained the monkeys to track the ramp-like movements of the real target, i.e. to direct their eyes towards the intersection of the diagonals. Next, we started to remove a central area of $12° \times 12°$ from the hourglass for some 100 ms. Although eye velocity dropped initially as a result of the removal of the intersection, the temporal gap was short enough to ensure that the eyes did not leave the eye position control window. Finally, we subsequently enlarged the time interval, the central area was blanked out until it

finally encompassed the total duration of the trial. Interestingly, although we trained the monkeys on SPEM only, the monkeys did not have any difficulties in switching to saccades as a response to a step in target position once having learned to track the *imaginary* target smoothly. Hence, the trajectory of the target determined the type of eye movement the monkeys performed. Fig. 2 shows the superimposed eye and target position traces of single trials in which monkey L was either asked to perform saccades (Fig. 2A and B) or SPEM (Fig. 2C and D) guided by the real (Fig. 2A and C) or the *imaginary* target, respectively (Fig. 2B and D).

In the following sections, we will analyze the similarities and dissimilarities in detail between the different eye movements elicited by real and *imaginary* targets, respectively.

3.1. Saccades

We used the step paradigm to elicit horizontal saccades with amplitudes of 5, 10 or 20° left or right towards the real or the *imaginary* hourglass. Every condition was repeated 90 times resulting in a total number of 540 saccades towards real and towards *imaginary* targets, respectively. All saccades were detected automatically using an eye acceleration threshold criterion.

The mean latencies of saccades elicited by sudden changes in the position of the real or the *imaginary* target are shown for both monkeys in Fig. 3. The dependence of saccade latency on target amplitude and type (*imaginary* vs. real) was determined by subjecting the data from each monkey to a two-way ANOVA with the factors target amplitude and type. For both monkeys, we found a tendency for saccade latencies to decrease with target amplitude (significant effect of factor target amplitude, $P < 10^{-6}$) and furthermore that saccades to the *imaginary* target were delayed by roughly 20 ms (significant effect of the factor target type $P < 10^{-6}$). In monkey E, the interaction between the factors target type and amplitude did not reach significance ($P = 0.09$), indicating that the longer latencies for the *imaginary* target were not specific for specific target amplitudes. In contrast, in monkey L the interaction of target type and amplitude was significant ($P < 10^{-6}$). Consecutive analysis of this interaction by post-hoc Scheffé tests ($P < 0.01$) revealed that saccades to the imaginary target were significantly delayed for all target steps except a step of 20° to the right (asterisks in Fig. 3 mark those target steps for which saccades to the *imaginary* target were significantly delayed).

We also analyzed the amplitudes of the initial saccades directed towards the real and imaginary targets. Therefore we calculated a two-way ANOVA with the factors target type and amplitude on the saccade ampli-
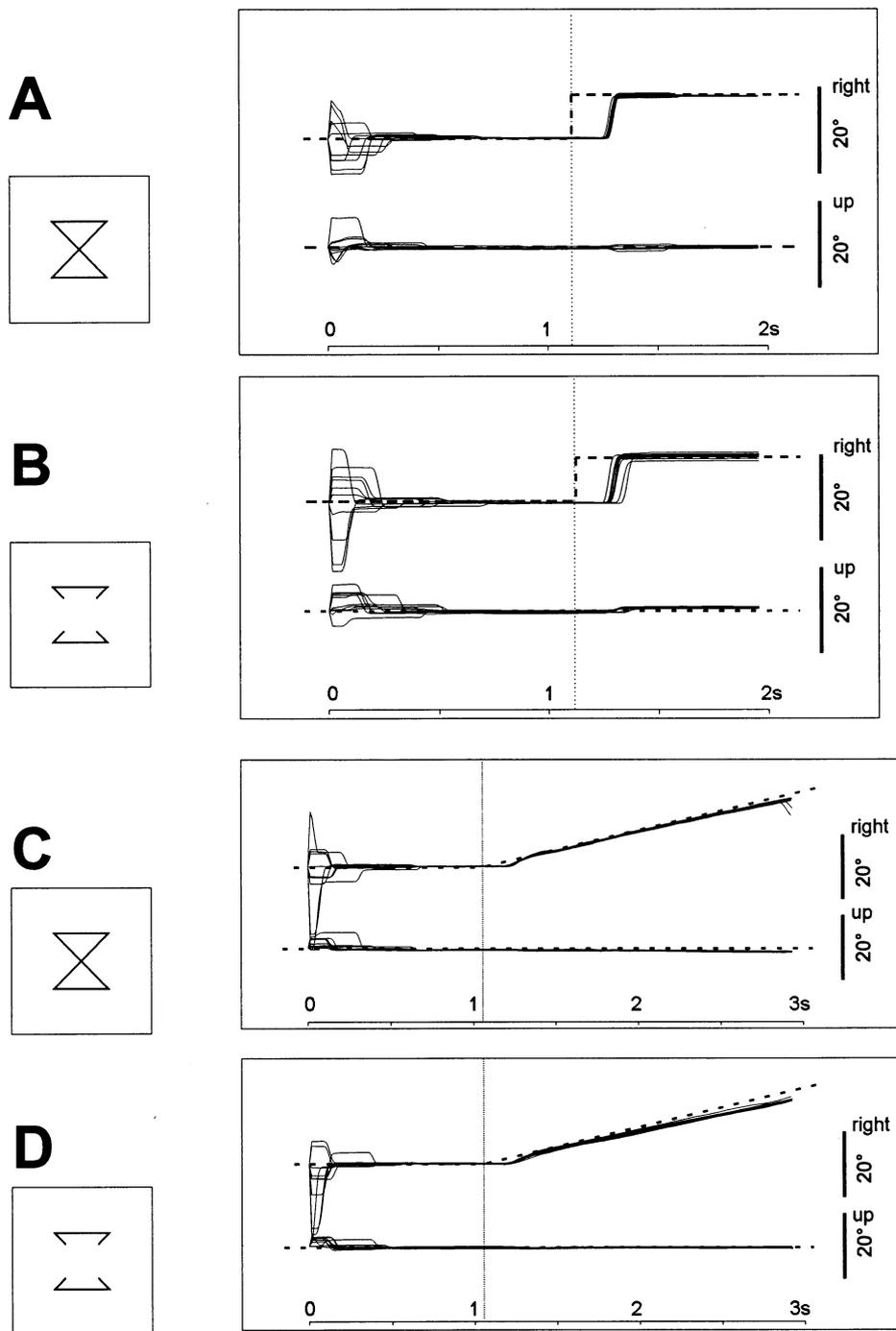
Fig. 2. Examples of horizontal and vertical eye movements (thin lines) of monkey L in register with target position (dashed lines, preceding and succeeding the eye position traces for better visualization) for step and ramp target movements. In **A** and **B** the target stepped rightward 10° ($n = 10$), (**A** real target, **B** *imaginary* target). In **C** and **D** the target moved rightward at 12 deg s^{-1} ($n = 20$) (**C** real target, **D** *imaginary* target). The vertical dotted line represents onset of target movement.

tude for each monkey separately. While we found a significant effect of target amplitudes ($P < 10^{-6}$) in both monkeys, the effect of target type was not significant in both monkeys. In monkey E, the saccade amplitudes were not affected by the factor target type ($P = 0.028$), but in monkey L this fac-

tor had an significant effect ($P < 10^{-6}$). Interestingly, the interaction between both factors was significant in both monkeys ($P < 0.003$) suggesting that differences in saccade amplitude towards a real and an *imaginary* target exist for specific target amplitudes.

3.2. Smooth pursuit eye movements

As a consequence of the finite latency of SPEM, two phases of SPEM can be distinguished. The first phase, usually referred to as SPEM initiation, consists of eye movements which are solely based on visual information prior to the onset of eye movements. The following phase, steady-state pursuit, reflects retinal motion of the object image influenced by object movement as well as the SPEM itself. In this section, we will first compare pursuit initiation for real and *imaginary* targets and then compare steady-state pursuit for real and *imaginary* targets.

Typical examples of SPEM directed towards the real and the *imaginary* target are shown in Fig. 4. As described in the method section and as illustrated in this figure, saccades were detected automatically and relevant pursuit parameters such as pursuit onset latency, initial eye acceleration and steady state pursuit gain were determined.

3.2.1. SPEM initiation

Table 1 shows that pursuit onset latency was increased for the *imaginary* target as compared to the real
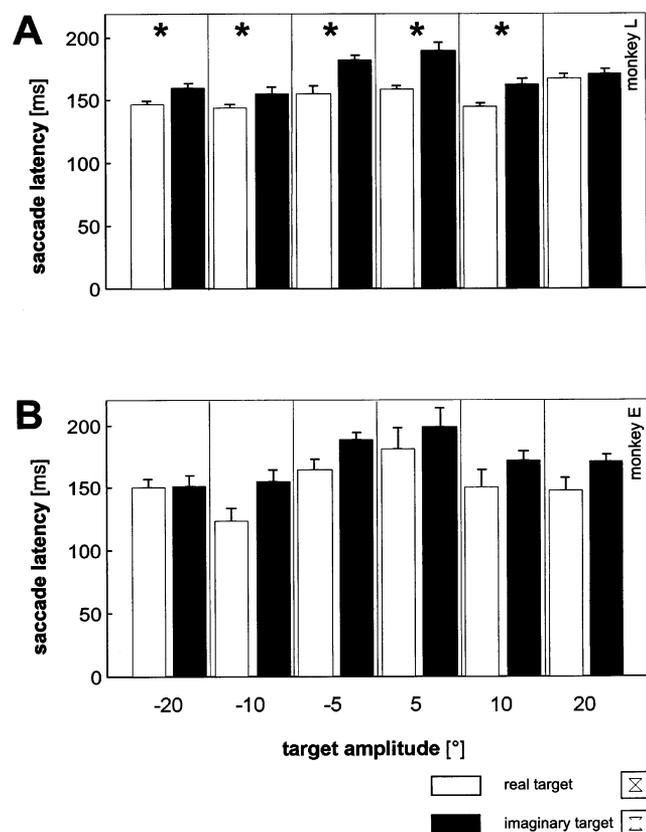

Fig. 3. In **A**, saccade latencies of monkey L are displayed for saccades directed towards real and *imaginary* targets for target amplitudes of 5, 10 and 20°. In **B**, the latencies of monkey E are shown. The asterisks mark target amplitudes for which the latencies were significantly different ($P < 0.01$, post-hoc Scheffé test).
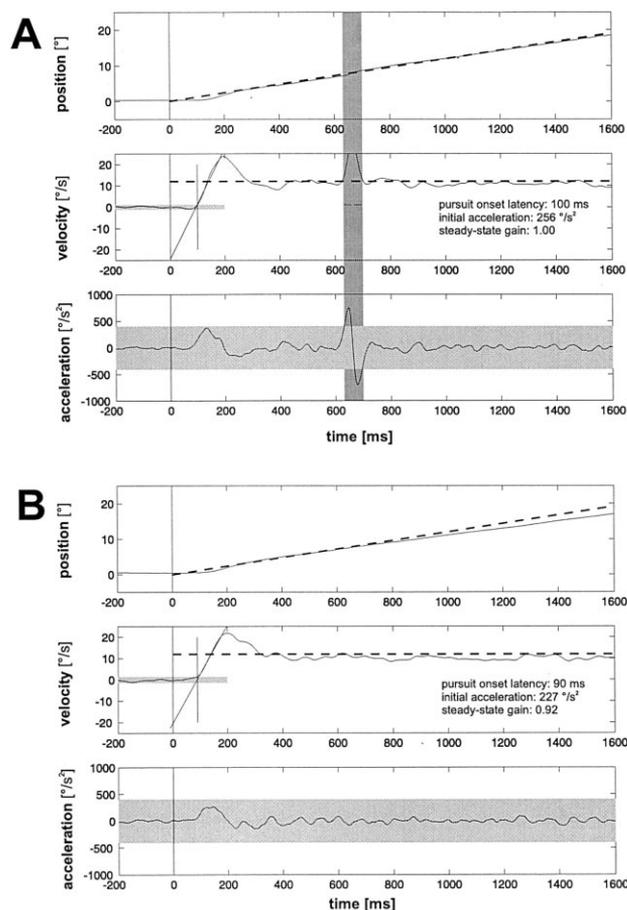

Fig. 4. Single eye position, velocity, and acceleration profiles elicited during SPEM towards a real target (**A**) and an *imaginary* target (**B**) of monkey L taken from Fig. 2 are shown. Target position and velocity are shown by dashed lines. The gray area in the velocity plot indicates the threshold (three times the standard deviation of eye velocity during fixation) to detect pursuit onset latency, indicated by the vertical line. The gray area in the acceleration plot shows the threshold for saccade detection (400 deg s^{-2}). The initial acceleration is shown by the linear regression line subsequent to the pursuit onset. The vertical gray column across all three traces indicates the occurrence of a catch-up saccade. Note that there is a velocity overshoot during SPEM initiation, clearly different to the saccade during steady-state pursuit with a symmetrical acceleration profile.

target in monkey L (two-tailed *t*-test, $P < 0.05$, marked ** in Table 1) but not in monkey E.

In contrast, the initial eye acceleration of both monkeys was significantly reduced when the *imaginary* target was pursued compared to the tracking of the real target ($P < 0.01$, two-tailed *t*-test, marked *** in Table 1).

3.2.2. Steady state pursuit of imaginary targets—what is being pursued?

The results presented so far show that monkeys are able to track the *imaginary* hourglass. However, this does not necessarily mean that they track a mental reconstruction of the invisible intersection of the two

diagonals of the *imaginary* figure. A much more parsimonious interpretation would be that our monkeys had made use of the parafoveal information available. For instance, their gaze may have been kept inside the center of the void region, because of the balanced repellent action of the four symmetrically positioned line ends defining the void. A triangle whose lower, hidden corner has to be tracked, lacks a comparable centering symmetry. We therefore measured SPEM gain (shown in Table 2) of such an *imaginary* triangle with SPEM of a real and an *imaginary* hourglass and compared these values with the gain obtained during parafoveal pursuit of a single spot. In this condition, the monkeys had to fixate 6° below a moving dot. The target velocity was kept at 12 deg s^{-1}, every condition was repeated 80 times.

Although the gains of both monkeys obtained by the real target and during the parafoveal tracking of a single spot were very similar, the values for the two monkeys obtained during tracking of the *imaginary* targets differ qualitatively. While monkey E showed a steady-state gain > 0.94 for both types of *imaginary* targets, the gain of monkey L paralleled the amount of parafoveal information showing a monotonic decrease along the sequence real to *imaginary* hourglass to *imaginary* triangle. However, parafoveal pursuit of a single spot, obviously lacking any figure-related information, yielded clearly reduced gains in both monkeys.

4. Discussion

We have shown that rhesus monkeys can use an *imaginary* figure based on extrafoveal cues as a target for rather precise visually guided eye movements. The target trajectory determined the type of eye movement executed: target steps elicited saccades, target ramps elicited smooth pursuit eye movements.

4.1. Latency of eye movements

In accordance with the literature (for instance Merrison & Carpenter, 1994), the initiation of SPEM directed towards a moving target in the ramp paradigm had shorter latencies than saccades elicited by a step in target position. This difference did not depend on the target being real or *imaginary*. In both monkeys, there was a statistically highly significant difference in saccade latency with saccades towards *imaginary* targets being executed later. However, the latency of SPEM onset revealed a comparable difference between real and *imaginary* targets only in monkey L. This monkey showed a 30 ms delay of SPEM onset towards an *imaginary* target compared to pursuit of a real target, quite similar to the delay in saccade onset. We do not have a satisfactory explanation of this inconsistent effect of target type on SPEM latency.

4.2. Smooth pursuit eye movements—what is being tracked?

One might argue that the monkeys did not track an *imaginary* figure at all, but, instead presented an optokinetic reflex (OKR), elicited by the coherent visual movement in the peripheral visual field. In the same line of evidence it must be noted that additional retinal image motion in the peripheral visual field is able to facilitate the ongoing SPEM (Yee, Daniels, Jones, Baloh & Honrubia, 1983; van den Berg & Collewijn, 1986).

However, this possibility can be discounted since, firstly, the latency of the eye movement onset was longer than the OKR latency (Robinson, 1981). Secondly, the precision with which the center of the *imaginary* target was positioned on the fovea is incompatible with an OKR, which compensates retinal image motion without compensating for retinal position errors (Robinson, 1981).

In a similar study concerning the human SPEM system, Wyatt and colleagues (1994) arrived at the conclusion that "*foveal enclosure*" was necessary to

Table 1
Mean and 95% confidence interval of latency and eye acceleration during SPEM initiation (target velocity 12 deg s^{-1})

Target	Latency		Acceleration		Number
	Mean (ms)	95% (ms)	Mean (deg s^{-2})	95% (deg s^{-2})	
Monkey L					
Real	108	2	196	3	205
Imaginary	139**	4	88***	2	208
Monkey E					
Real	104	1	154	3	220
Imaginary	103	2	123***	2	220

Table 2
Smooth pursuit gain (mean and 95% confidence intervals) elicited by four different SPEM targets (target velocity 12 deg s^{-1})

	Real hour-glass	Imaginary hour-glass	Imaginary triangle	Parafoveal pursuit
Monkey L	0.920 ± 0.002	0.838 ± 0.009	0.758 ± 0.006	0.723 ± 0.016
Monkey E	0.988 ± 0.018	0.940 ± 0.020	0.971 ± 0.015	0.720 ± 0.035

generate pursuit towards *imaginary*. However, our monkeys were able to track a target devoid of foveal enclosure shown by their ability to track the hidden corner of an *imaginary* triangle. Our findings, alternatively, suggest therefore that any extrafoveal cues sufficient to derive a complete figure may be sufficient to generate accurate goal-directed eye movements. This view is in accordance with Steinbach's conclusion (1976) that subjects pursue a perceptual rather than a retinal stimulus. When we emphasize the need for extrafoveal information sufficient to complete a figure, we do not imply that the *imaginary* figure has to stand out perceptually similar to a true illusory figure such as e.g. the Kanizsa triangle (Kanizsa, 1979). Although we, and possibly also our monkeys, did not perceive the intersection of the diagonals in the *imaginary* hourglass, the monkeys were nevertheless able to reconstruct this invisible intersection and to direct their eyes towards this *imaginary* target.

A final remark relates to the potential of *imaginary* targets for electrophysiological studies on the neuronal substrate underlying the execution of SPEM. Studies of pursuit-related single-units usually have to deal with the question if pursuit-related activity reflects foveal image motion or, alternatively, non-retinal information such as eye velocity. Imaginary targets such as the figures used in this study lacking foveal features but nevertheless being able to evoke precise SPEM, may turn out to be very useful tools in order to address this question.

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