

# Anticipatory smooth-pursuit eye movements in man and monkey

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**Abstract** A fundamental problem in the generation of goal-directed behaviour is caused by the inevitable latency of biological sensory systems. Behaviour which is fully synchronised with the triggering sensory event can only be executed if the occurrence of this event can be predicted based on prior information. Smooth-pursuit eye movements are a classical and well-established example of goal-directed behaviour. The execution of these eye movements is thought to be very closely linked to the processing of visual motion signals. Here, we show that healthy human subjects as well as trained rhesus monkeys are able to initiate smooth-pursuit eye movements in anticipation of a moving target. These anticipatory pursuit eye movements are scaled to the velocity of the expected target. Furthermore, we can exclude the possibility that anticipatory pursuit is simply an after-pursuit of the previous trial. Visually-guided pursuit is only marginally affected by the presence of a structured background. However, the presence of a structured background severely impedes the ability to perform anticipatory pursuit. More generally, our data provide additional evidence that the cognitive oculomotor repertoires of human and monkeys are similar, at least with respect of smooth-pursuit in the prediction of an appearing target.

**Keywords** Pursuit initiation · Saccades · Prediction · Stationary structured background · Sensorimotor integration

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## Introduction

Eye movements are an excellent example of sensorimotor processing. However, focusing only on the motor output does not afford a complete understanding of the mechanisms of oculomotor control. Likewise, it is impossible to understand the sensory processing in vision without taking eye movements into account. Smooth-pursuit eye movements, conceptualised as a negative feedback system which minimises retinal image motion of the target (Robinson et al. 1986; Lisberger et al. 1987), provide an ideal context for studying sensorimotor processing. If the target moves in front of a dark background, retinal image motion is only caused by the target itself. In contrast, if the target moves across a structured background, a much more natural condition, self-induced retinal image motion is caused by the eye movement itself. This self-induced motion has only a minor impact on the execution of ongoing smooth-pursuit (Schwarz and Ilg 1999; Lindner et al. 2001). However, the presence of a structured background reduces considerably the saliency of the pursuit target. This reduction appears clearly before the onset of the eye movement and is able to explain the previously reported prolonged pursuit onset latency (Mohrmann and Thier 1995) and decrease of initial eye acceleration (Kimmig et al. 1992; Masson et al. 1995) due to a structured background.

A fundamental problem of sensorimotor processing is the fact that sensory processing takes time. As a consequence, goal-directed behaviour is always delayed relative to its triggering stimulus. This delay is usually referred to as reaction time. However, if a subject is asked to track a sinusoidally moving target, no phase shift between target and eye movement is seen (Westheimer 1954; Bahill and McDonald 1983b; Kettner et al. 1996). This absence of phase shift suggests that, in this situation, pursuit is driven

by predictive mechanisms, as suggested by an early tracking model (Bahill and McDonald 1983a). It is important to note that in the absence of any moving stimulus, i.e. if the subjects only imagined a moving target, no smooth-pursuit can be elicited (Hashiba et al. 1996; Berryhill et al. 2006).

In order to examine predictive mechanisms, it is beneficial to distinguish two types of predictive mechanisms: short-term and long-term prediction (Deno et al. 1995). The long-term mechanism is thought to be active for periodic target movements, while the short-term mechanism is enabled during a single ramp of a target moving at constant velocity. The first attempts to study anticipatory pursuit used periodic target movements, i.e. they addressed the mechanisms of long-term prediction. It was shown that human subjects produced very slow eye velocities (below 1°/s) in response to periodic target steps (Kowler and Steinman 1979a). Subsequently, the work of Graham Barnes and colleagues revealed many important details of anticipatory pursuit. Instead of presenting the moving target for the entire period, the target was only tachistoscopically presented for a brief moment. Usually, the target moved at constant speed to the left and right and was only presented for a short time when it was crossing the straight-ahead position. Despite this brief presentation, human subjects were consistently able to produce anticipatory pursuit before target appearance (Barnes and Asselman 1991; Barnes et al. 2002). It was shown that these anticipatory pursuit eye movements were scaled to the previously-presented target velocity (Barnes and Donelan 1999). More recently, we demonstrated that this paradigm could also be used to demonstrate the extra-retinal, eye movement related responses of neurons recorded from the medial superior temporal area in the rhesus monkey (Ilg 2003).

In order to address details of short-term prediction, mid-flight manipulations of ramp-like target movements have frequently been used. It is important to note that these manipulations are only possible after-pursuit has been initiated by retinal image motion signals. The fact that the initial saccade during pursuit initiation ends at the actual target position indicates that short-term prediction is already fully enabled early on and used to correctly compute saccade amplitude (Gellman and Carl 1991). If the target was unexpectedly switched off during maintained pursuit, eye velocity decreased 190 ms after the target disappeared (Becker and Fuchs 1985). This drop in eye speed was much smaller if the subjects received a feedback signal related to the ongoing eye velocity (Madelain and Krauzlis 2003). In this study, subjects were informed about their eye velocity by the pitch of an auditory stimulus. If, on the other hand, the subjects knew that the target would reappear, this initial drop in eye velocity was followed by a scaled recovery of eye velocity prior to target reappearance (Bennett and Barnes 2003, 2004).

Given these results, one might ask whether subjects can initiate pursuit solely based on prediction, without any retinal image motion signals. It is important to note that, in this condition, differently from mid-flight modulations or in the case of periodic target movements, a simple velocity storage mechanism can not explain the predictive pursuit. This shows that more complex memory functions are also available to use prior motion information for the generation of predictive pursuit. In fact, it was shown that human subjects are able to generate anticipatory pursuit at very low eye velocities for predictable single target displacements (Kowler and Steinman 1979b; Kowler and McKee 1987). More recently, several studies reported anticipatory pursuit at higher eye velocities. One possibility is to use an auditory cue to start the eye movements and a constant sequence of ramps (Barnes and Schmid 2002) or graphical cues for direction and velocity of target movement (Jarrett and Barnes 2002). If the direction of target movement was constant, a temporal gap before the onset of target movement (“occluded onset pursuit paradigm”) also triggered anticipatory pursuit scaled to expected target velocity (Collins and Barnes 2006). Even without a temporal gap, eye velocity scaled to the expected target velocity prior to the onset of target motion if the direction of target movement was constant (Heinen et al. 2005). Similar results have recently been reported from rhesus monkeys (Badler and Heinen 2006). Furthermore, it was shown that monkeys can use the colour of the fixation target as a cue for predicting the direction of subsequent target movement. They produced anticipatory pursuit eye movements during a 400-ms gap (de Hemptinne et al. 2006). The constancy of target movement direction together with the duration of initial fixation had a large positive effect on the anticipatory pursuit initiation of rhesus monkeys (de Hemptinne et al. 2007).

We used simple horizontal ramp-like target movements with a transient absence of the target just after the fixation. Therefore, the offset of the fixation target acted as a “go-signal”. With this simple paradigm, we tried to replicate earlier studies of anticipatory pursuit, added a control situation without prediction and carefully compared the abilities of human subjects and rhesus monkeys. In addition, we addressed the question whether a structured background, providing a rich sample of possible fixation targets, does alter the ability to perform anticipatory pursuit. Finally, we tried to exclude the possibility that anticipatory pursuit is simply a pursuit afternystagmus following prolonged execution of pursuit in a given direction (Chaudhuri 1991).

## Methods

We recorded the eye movements of five *human subjects* including one author (range 24–30 years, mean 27 years),

two male (M and D, ~10 kg) and one female rhesus monkey (*Macaca mulatta*, C, ~5 kg). All human subjects had normal or corrected-to-normal visual acuity. They performed one session (maximal duration 10 min) per day; each subject participated in three sessions. We used the first session of each subject to familiarise the subject with the set-up. We did not use data from this session for further analysis. After an appropriate training procedure, monkeys were tested for five sessions (maximal duration 15 min) on five consecutive days. The monkeys were rewarded for every correct trial (i.e. gaze deviation from target was smaller than 3° throughout the entire trial) by a small amount of water or juice (approximately 0.1 ml/trial). Animals were trained for approximately 8 weeks on this paradigm. During this training period, we gradually reduced the size of the fixation control window to the final size of 3°. All animal procedures were carried out in accordance with the guidelines laid down by the National Institutes of Health and German laws and were approved by the local ethics committee.

### Experimental paradigms

We strove to keep the paradigms for the human and the monkey experiments as similar as possible. Each trial started with fixation of a stationary target in the centre of the screen. The length of the initial fixation period was randomised between 500 and 1,000 ms. The target (diameter 0.5°, luminance 0.5 cd/m<sup>2</sup>) moved horizontally at a constant velocity. In order to elicit anticipatory smooth-pursuit eye movements, the target moved exclusively to the right at a fixed velocity (5°, 10° or 15°/s) in a block of trials (human  $n = 10$ , monkey  $n = 20$  in each condition). In 50% of the trials, the moving target was initially invisible for 500 ms. In these trials, the offset of the fixation target signalled the onset of the invisible target movement (*prediction*). The target appeared after the 500 ms at a position determined by its velocity, as if the target moved behind an occluder. In the remaining 50% of the trials, the moving target was continuously visible. We instructed our subjects to imagine the moving target and to direct their gaze as precisely as possible.

We paid particular attention to the design of control conditions. In order to report convincingly about anticipatory pursuit, it is also necessary to document its absence in unpredictable conditions. In a first control condition, we randomised the direction of target movement (leftward and rightward). The target was invisible for the first 500 ms following the offset of the fixation target (*control*). As a result, a specific and valid prediction of the direction of target movement was only possible at chance level in this condition. So even if there was a guessing in a given trial, this effect would average out across many trials. We used a second condition in which we also randomised the direction of

target movement, but kept the target visible (*visual*). In this condition, pursuit was completely guided by vision. Figure 1a–c shows these three different paradigms.

Finally, we ran all conditions with a structured background. The background consisted of 150 bars (width: 3 min, height: 14 min, luminance: 83 cd/m<sup>2</sup>) distributed randomly (no overlap and no rotation of the bars) in two dimensions across the entire monitor for our human subjects and to the central  $\pm 30^\circ$  in horizontal and vertical direction of visual field for our monkeys (see Fig. 2a). We tried to keep the paradigms and set-ups of human and monkey experiments as similar as possible. However, there were some inevitable minor differences which are summarised in Table 1. There is no reason to believe that these differences cause any difference in the oculomotor behaviour of both species.

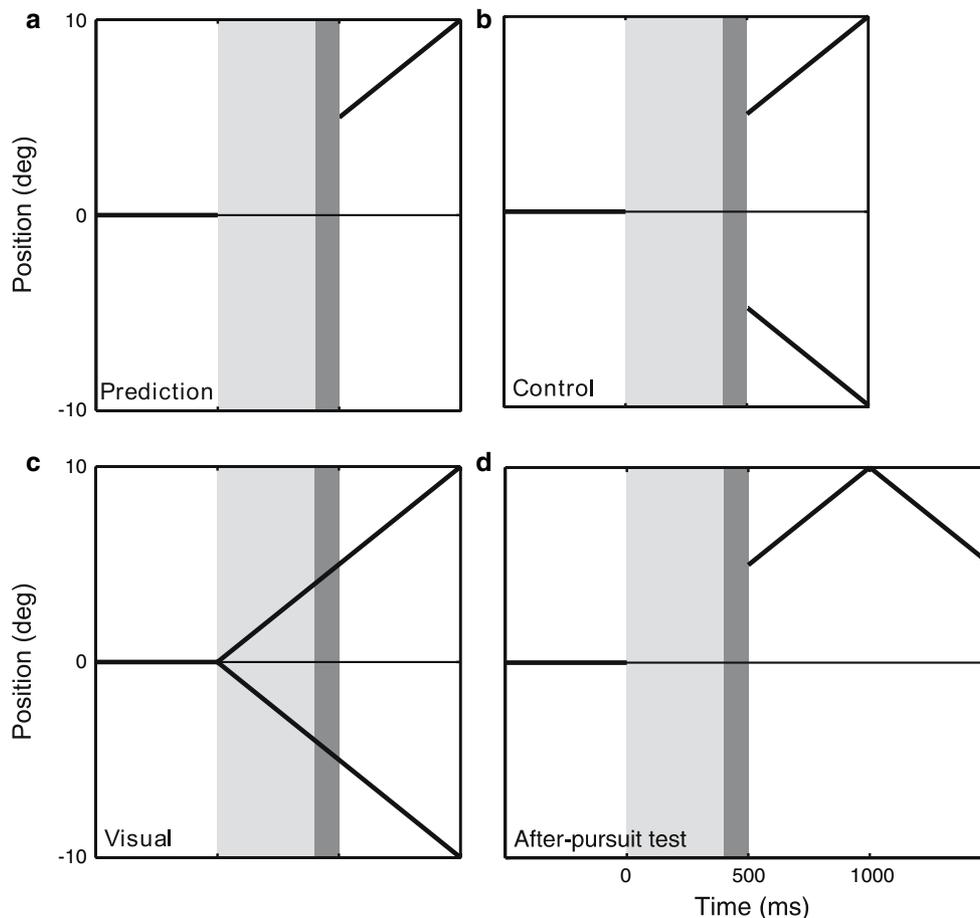
### Data analysis

All data analysis was performed using Matlab. Horizontal eye velocity was obtained by differentiating horizontal eye position signal, which was sampled at 1 kHz prior. Smoothing was performed by applying a Butterworth low-pass filter (position: 50 Hz, velocity 5 Hz). Trials obtained from the human subjects with artefacts such as eye blinks (approximately 10% of the total number), were excluded from further analysis based on a threshold ( $>20^\circ$ ) criterion. As we described above, gaze deviation from target led to the instantaneous abortion of the trial in the monkey experiments.

### Initiation of visually-guided pursuit

First, we analysed the parameters of visually-guided pursuit initiation: pursuit onset latency, initial saccade latency and initial eye acceleration. To determine pursuit onset latency, we calculated a threshold defined by the mean + 3 standard deviations of the eye velocity during the last 100 ms of the fixation period. The intersection of eye velocity and threshold was taken as pursuit onset latency. To determine initial acceleration, we performed a linear regression of eye velocity within a 100-ms time slice placed on pursuit onset (–20 ms before until 80 ms after-pursuit onset). The linear regression was only accepted if  $r^2 > 0.5$ . Saccades were detected automatically whenever eye acceleration exceeded a threshold set at 1,000°/s<sup>2</sup>. The velocity profile during the saccade was filled by a linear segment connecting pre- and post-saccadic velocity. The first saccade detected following target movement onset was labelled as the “initial saccade”. Trials in which a saccade occurred during pursuit initiation were excluded from further analysis. Figure 2b, c shows the analysis for a typical example (single trial recorded from subject SF).

We determined pursuit onset latency, saccade latency and initial acceleration independently in every trial. Subsequently,



**Fig. 1** Target positions in the three different paradigms [*prediction (a)*, *control (b)*, *visual (c)*] and the pursuit afternystagmus test (**d**) used in the present study. The *entire grey shaded areas* indicate the 500 ms time interval after fixation offset, during which the target was absent in the *prediction*, *control* and *after-pursuit test* condition. The *dark grey*

*bars* indicate the time window used to determine the median smooth-pursuit eye velocity ( $V_{500}$ ). Note that the duration of initial fixation varied randomly between 500 and 1,000 ms. A detailed description is given in the text

we calculated the median and mean deviation from the median of each parameter across all trials for all subjects in a given condition. In addition, we used repeated Kruskal–Wallis tests (KW) to verify significant influences of specific factors such as the presence of a structured background and target velocity on the presented median values. In order to mark significant effects we used  $\alpha = 0.01$ .

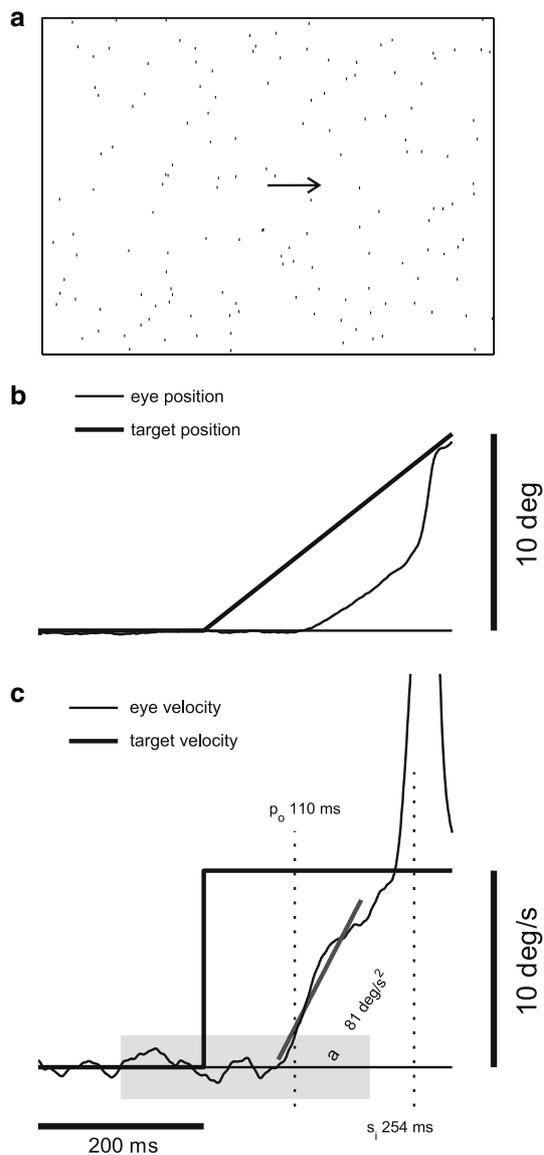
#### Anticipatory pursuit

Second, we quantified the ability to perform anticipatory pursuit by determining median eye velocity within a time window of 100 ms before the appearance of the moving target ( $V_{500}$ ). Again, this analysis was based exclusively on single trials. Trials with  $V_{500} > 20^\circ/s$  were excluded from further analysis since they contained either saccades or blinks. In the visually-guided control condition (*visual*), we calculated  $V_{500}$  over the same time interval. We averaged  $V_{500}$  across all trials performed in a specific condition. In order to test whether

specific factors such as presence of background and target velocity significantly affected the median values, we also calculated repeated KW tests. We also compared whether  $V_{500}$  in the predictive condition is significant different from the control condition using a KW tests. In addition, we tested values obtained in the control condition against 0 with a simple *t*-test. Finally, the similarity of  $V_{500}$  values of human and monkey in all experimental conditions across all subjects is documented by a two-factorial ANOVA with the factors experimental condition and species.

#### Results

In order to demonstrate the robustness of our data, we first present the parameters of visually-guided pursuit initiation by human subjects and monkeys. Next, we introduce the average eye velocities during anticipatory smooth-pursuit eye movements.



**Fig. 2** Display of the stationary structured background extending  $36.5^\circ \times 27.5^\circ$  for the human subjects. The fixation target is always presented at the centre of the screen; the arrow indicates target movement to the right. For ease of reproduction, black and white is inverted (a). The analysis of pursuit initiation is demonstrated with a typical trial recorded from subject SF. Eye position (thin line) and target position (bold line), the horizontal line represents straight-ahead (b). Eye velocity (thin line) and target velocity (bold line) are shown in c, horizontal line represents 0 velocity. The linear regression is indicated by the oblique dark grey line, whose slope represents initial acceleration (a). The light grey rectangle shows the threshold for pursuit onset latency, defined as the mean  $\pm 3$  standard deviations of the eye velocity during the last 100 ms of fixation. The pursuit onset latency ( $p_o$ ) and the onset of the initial saccade ( $s_i$ ) are marked by dotted lines

### Visually-guided pursuit initiation

As described above, pursuit initiation can be quantified by the following parameters: pursuit onset latency, initial saccade latency and initial acceleration. Figure 3 shows these

parameters and  $P$ -values resulting from KW tests of factor *background* for the three different target velocities used by human subjects.

For the human data, pursuit onset latency is not significantly influenced by target velocity (dark background:  $P = 0.839$ , structured background:  $P = 0.329$ ). In contrast, the influence of target velocity on acceleration is significantly ( $P < 0.01$ , both background types); the acceleration increases with increasing target velocity. Similarly, initial saccade latency depends significantly on target velocity ( $P < 0.0006$ , both background types); saccadic latency decreases with target velocity. The influence of the structured background during the presentation of three target velocities is not uniform. There is a tendency that pursuit onset latency increases in the presence of a structured background whereas acceleration and initial saccade latency is not affected by the background. However, most of the differences are not significant as indicated by the given  $P$ -values.

Figure 4 shows the pursuit initiation parameters and the  $P$ -values from the KW tests of the factor *background* for the three different target velocities obtained from the monkeys.

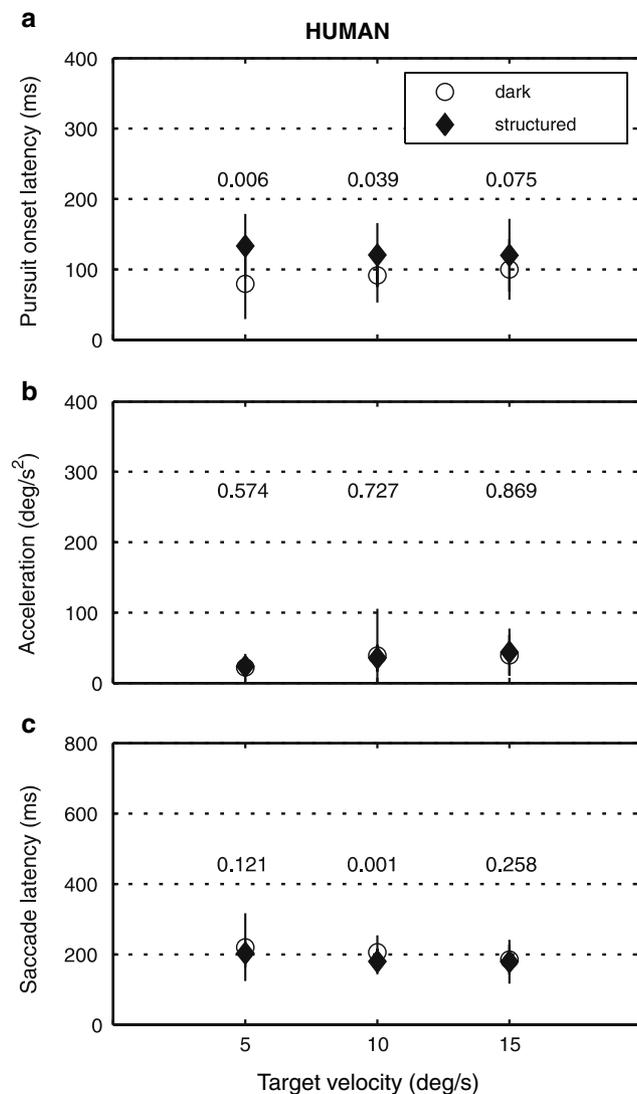
For the monkeys, target velocity influences significantly pursuit onset latency (dark background  $P < 0.0004$ , structured background  $P < 0.004$ ), initial acceleration ( $P < 0.0005$ , both background types) and initial saccade latency (dark background  $P = 0.009$ , structured background  $P = 0.0014$ ). While saccade and pursuit latencies decrease with increasing target velocity, initial acceleration increases with target velocity. In contrast to the human data, there is no effect of the structured background on pursuit onset latency. However, acceleration and saccade latency are smaller in the presence of a structured background which is not observed in the human data. These effects of the background on acceleration and saccade latency are significant for all target velocities.

### Anticipatory pursuit

The single trial eye position traces across a dark homogeneous background from a typical human subject (see Fig. 5) show the stereotypical, visually-guided high-gain smooth-pursuit eye movement (*visual*, see Fig. 5c). The median eye velocity in the interval from 400 to 500 ms ( $V_{500}$ ) after target motion onset is  $9.6^\circ/s$  which is very close to the target velocity ( $10^\circ/s$ ) in this condition. If the subject is able to predict target movement (*prediction*, see Fig. 5a), the eyes move to the right, resulting in  $V_{500} = 3.8^\circ/s$ . In contrast, if the subject is not able to predict target movement (*control*, see Fig. 5b), gaze is maintained close to the centre of the screen, resulting in a lower velocity of  $V_{500} = 0.7^\circ/s$ . Interestingly, as soon as the target becomes visible in this condi-

**Table 1** Differences in the experimental set-ups used with human subjects and rhesus monkeys

	Human set-up	Monkey set-up
Head stabilisation	Chin rest and bite bar made of dental material	Head fixed with an implanted head post
Eye movement recording	Infrared eye tracker (IRIS by scalar)	Search coil system (Robinson 1963; Judge et al. 1980)
Spatial and temporal resolution	1,600 pixel $\times$ 1,200 pixel at 104 Hz	1,024 pixel $\times$ 768 pixel at 123 Hz
Stimulus presentation	19" CRT monitor; 36.5° $\times$ 27.5°	Video projector on screen; 106° $\times$ 90°
Viewing distance	57 cm	44 cm
Trials per block	Ten trials per condition	20 trials per condition

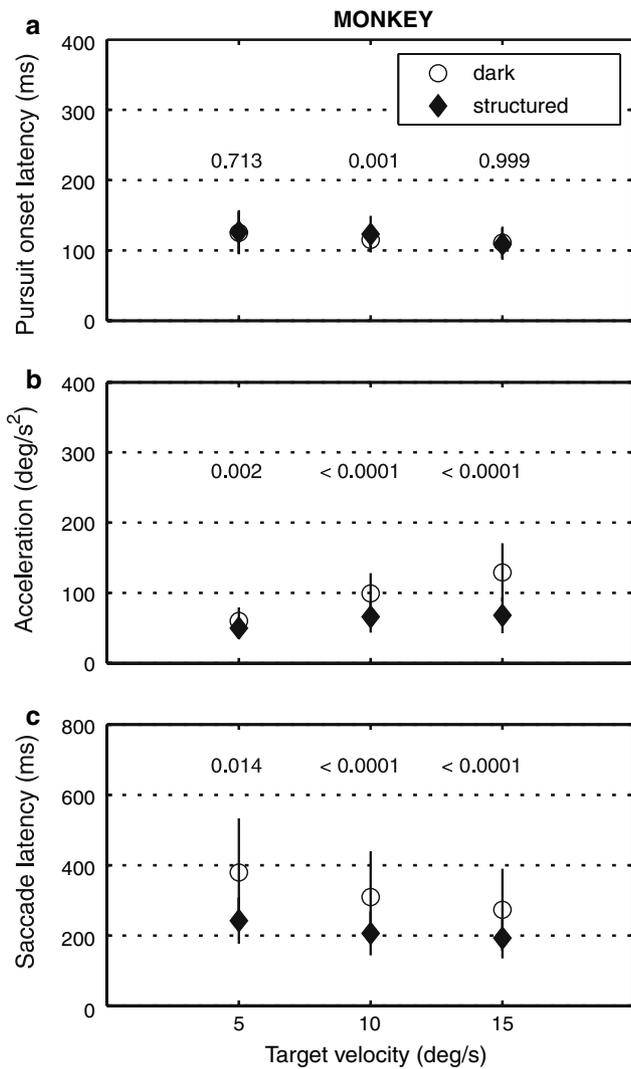
**Fig. 3** Median and mean deviation of the median (five human subjects) of pursuit onset latency (a), initial acceleration (b) and saccade latency (c) for the three different target velocities (5, 10 and 15°/s). The target either moved across a homogeneous dark background (open circles) or across a stationary structured background (filled diamonds). P-values resulting from KW tests of the factor *background* are shown for each velocity

tion, the subject performs visually-guided saccades to bring the eyes on target.

A very similar eye movement pattern is seen in the monkey data. Typical examples are shown in Fig. 6 for target movement across a dark homogenous background. As it is found for human subjects described above, high-gain smooth-pursuit is performed if the target is constantly visible (*visual*, see Fig. 6c). If the monkey is able to predict the direction of the target movement (*prediction*, see Fig. 6a), the eyes start to move to the right prior to the appearance of the target, resulting in  $V_{500} = 3.7^\circ/\text{s}$ . During the control condition without prediction (*control*,  $V_{500} = 1.1^\circ/\text{s}$ , see Fig. 6b), the eyes of this monkey deviate slightly to the right. Nevertheless, the  $V_{500}$  in this control condition is significantly smaller than in the predictive condition (KW test,  $P < 0.0001$ ). This monkey tends to move his eyes spontaneously to the right, independent of the actual eye movement task.

In order to quantify the ability to perform anticipatory pursuit, we calculated  $V_{500}$  as described above. To determine whether the factor *target velocity* significantly affects  $V_{500}$  in the different experimental conditions, we calculated separate KW tests on each set of  $V_{500}$ . Figure 7 shows the median values based on five human subjects for a homogeneous, dark background and a stationary, structured background, together with the P-values resulting from the KW test of the factor *background* (see below). *Target velocity* affects  $V_{500}$  significantly during predictive pursuit (*prediction*,  $P = 0.0009$ ) and during visually-guided control (*visual*,  $P < 0.0001$ ) if the background is dark and homogeneous. In the control condition, the influence of target velocity on  $V_{500}$  is not significant (*control*,  $P = 0.457$ ).

Figure 8 shows the  $V_{500}$  values for both background types obtained from our monkeys. The results of the KW tests for the monkeys show the same pattern as for the human data.  $V_{500}$  is significantly affected by *target velocity* in case of visually-guided control (*visual*,  $P < 0.0001$ ) and there is a highly significant effect for the velocity in the predictive condition (*prediction*,  $P < 0.0001$ ), but not in the control condition (*control*,  $P = 0.111$ ).

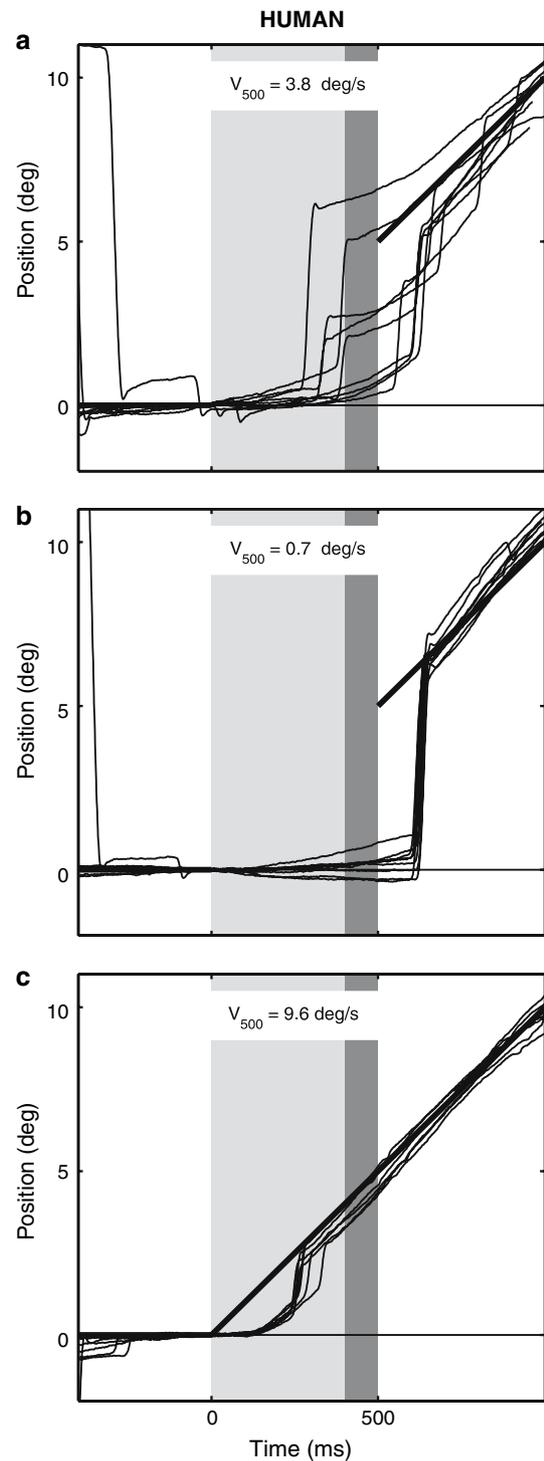


**Fig. 4** Median and mean deviation of the median (three monkeys) of pursuit onset latency (a), initial acceleration (b) and saccade latency (c) for the three different target velocities. The target moved across a homogeneous dark background (open circles) or across a stationary structured background (filled diamonds). P-values resulting from KW tests of the factor *background* are shown

Our data show that  $V_{500}$  is scaled to the expected target velocity in the predictive condition in both humans and monkeys. If valid prediction is abolished in our control condition,  $V_{500}$  is marginal and significantly different from the predictive condition ( $P < 0.0004$  for both species and all three target velocities) and never significant different from 0 ( $t$ -test;  $P > 0.02$ ).

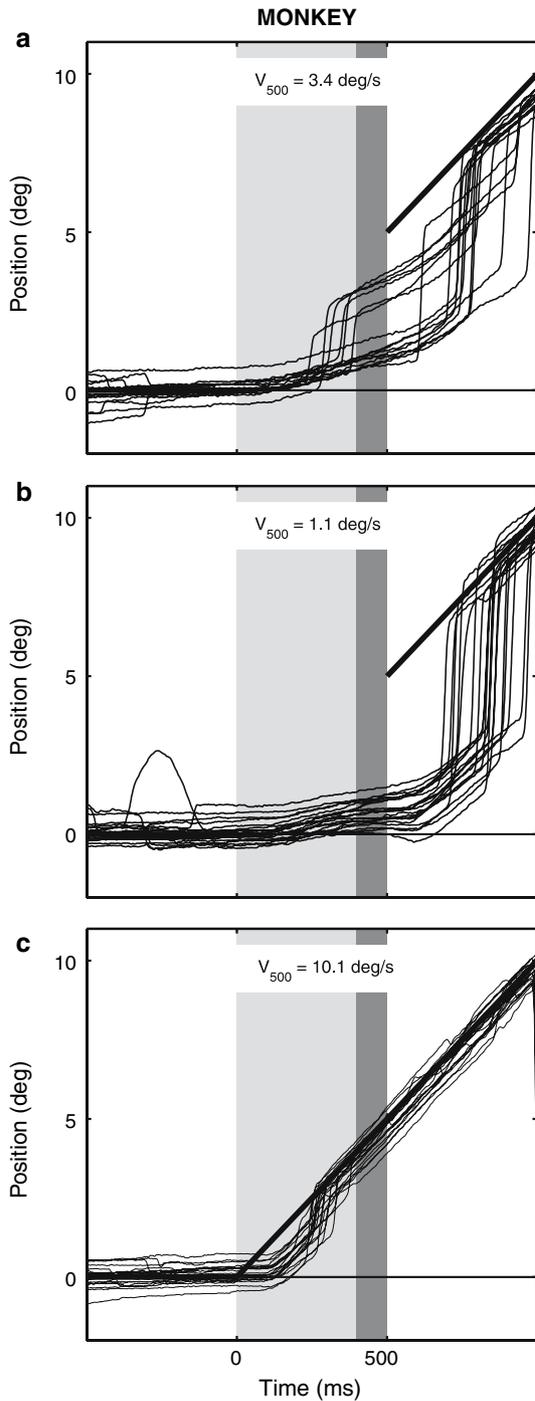
**Influence of structured background on anticipatory pursuit**

When our human subjects as well as our rhesus monkeys were asked to perform anticipatory pursuit across a structured background,  $V_{500}$  is significantly reduced ( $P$ -values



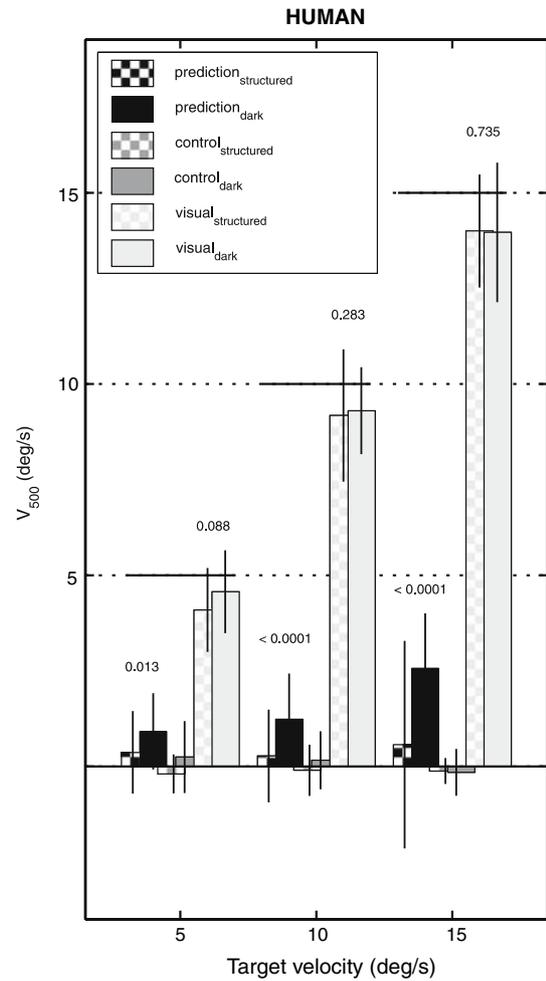
**Fig. 5** Target position (bold line) and eye positions (thin line) during single trials for the three conditions (a prediction, b control and c visual) recorded from a typical human subject (SF). The target moved at 10°/s to the right across a dark homogenous background. All eye position profiles were aligned in time with respect to the disappearance of the fixation target ( $t = 0$ )

see Figs. 7, 8) compared to  $V_{500}$  without background and does not increase with expected target velocity (prediction, see Fig. 7 human and Fig. 8 monkey). In the human



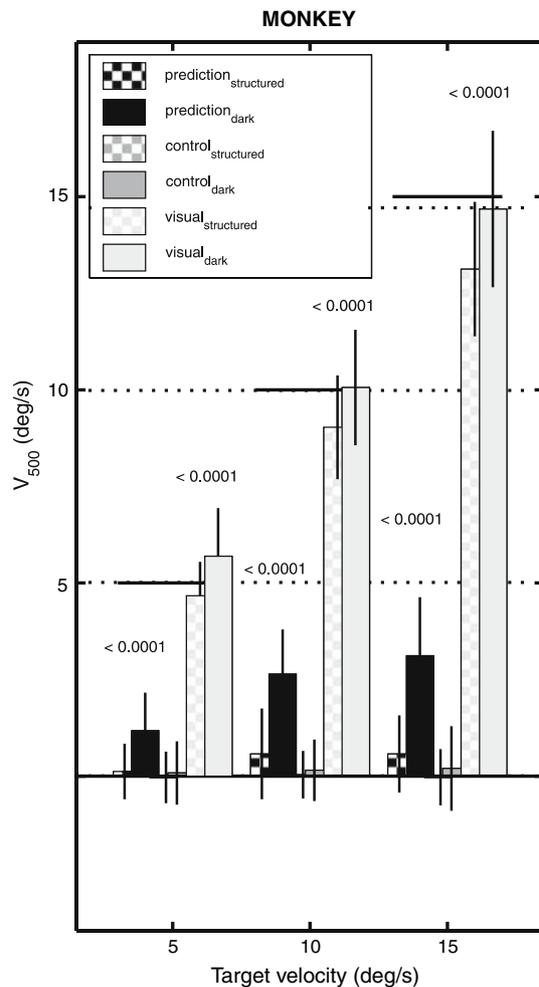
**Fig. 6** Target position (*bold line*) and eye positions (*thin line*) for single trials in the three conditions (**a** prediction, **b** control and **c** visual) recorded from a rhesus monkey (M). The target moved at 10°/s to the right across a dark homogenous background. For further details see Fig. 5

prediction trials in the presence of a structured background, no significant effect of *target velocity* on  $V_{500}$  is revealed by the KW test (*prediction*,  $P = 0.823$ ). In contrast, the influence of target velocity is significant in our



**Fig. 7** Median  $V_{500}$  and its mean deviation for the three different target velocities. The results represent data from five human subjects viewing a homogeneous, dark background (*filled bars*) and a stationary, structured background (*textured bars*). *Short horizontal bold lines* give the target velocities. *P-values* resulting from KW tests of the factor *background* are shown for predictive and visually-guided  $V_{500}$  and each velocity

monkey data (*prediction*,  $P < 0.0001$ ) in the presence of a structured background. However,  $V_{500}$  does not monotonically increase with target velocity as it does in the dark background condition. As for the dark background, the difference in  $V_{500}$  obtained in the predictive and control condition for structured background is significant for human and monkeys (KW test,  $P \leq 0.01$ ) and  $V_{500}$  in the control condition is never significant different from 0 (*t-test*,  $P > 0.02$ ). The effects of the structured background on visually-guided pursuit are different in human subjects and monkeys: the background presence does not influence  $V_{500}$  in humans (*visual*, see Fig. 7 for *P-values*) while the visually-guided pursuit of the monkeys is reduced significantly for all velocities (*visual*, see Fig. 8 for *P-values*).



**Fig. 8** Median  $V_{500}$  and its mean deviation for the three different target velocities. For further details see Fig. 7

One might speculate whether the amount of  $V_{500}$  is subject of learning, i.e. whether  $V_{500}$  in early trials is different from late trials. A comparison between the first and last trials of all sessions (human subject three trials and monkeys five trials per block) reveals no significant difference in the anticipatory smooth-pursuit eye movement in both species (KW test,  $P = 0.691$ ,  $P = 0.178$ ).

These results strongly suggest that human and monkeys are able to produce smooth-pursuit eye movements when an upcoming target is expected. The anticipatory pursuit responses are adjusted to the expected target velocity. However, a stationary structured background reduces the ability to generate anticipatory pursuit in both species. In order to emphasise the similarity of anticipatory pursuit of human and monkey, we performed a two-factorial ANOVA with the factors species and experimental condition on the median values presented in Figs. 7 and 8. This analysis reveals a highly significant effect of experimental condition ( $P < 0.0001$ ). However, the effect of species is not significant ( $P = 0.06$ ).

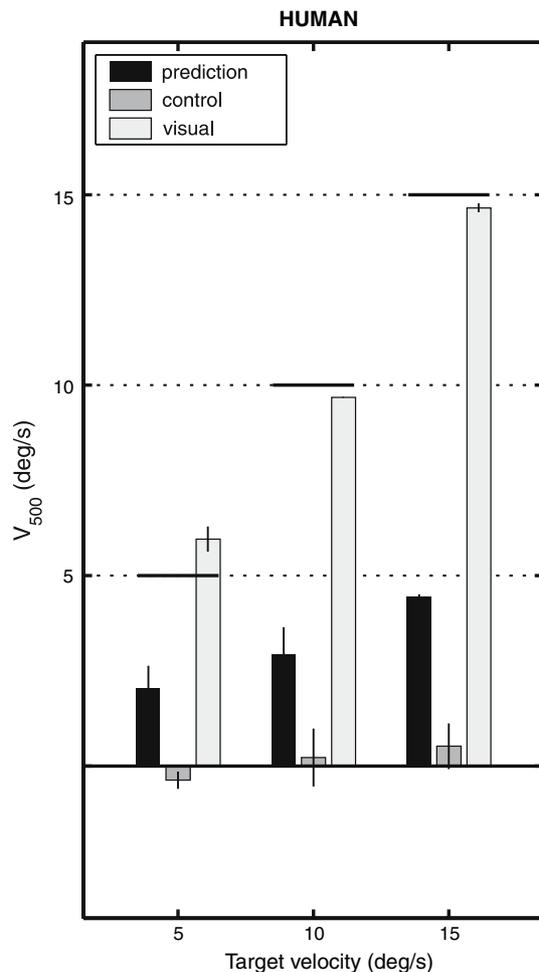
## After-pursuit test

In a supplementary experiment (see Fig. 1d) we wanted to answer the question whether the anticipatory pursuit can simply be explained as pursuit afternystagmus of the previous trial? To clarify this question, we slightly modified the target trajectory. At the end of each trial, the target turned its direction and moved for another 500 ms at the same speed in opposite direction. Visual inspection of the eye movement profile of every single trial reveals that the subjects followed this reversal of pursuit direction. The target moved over a homogenous, dark background. This manipulation does not prevent our subjects from performing anticipatory pursuit;  $V_{500}$  is still significantly scaled to the expected target velocity (KW test of factor target velocity  $P < 0.0001$ ) and reaches comparable values as in the standard condition (*prediction*, see Fig. 9). We can therefore dismiss the notion that anticipatory pursuit could be explained as pursuit afternystagmus.

## Discussion

Our results show that human subjects and rhesus monkeys were both able to produce anticipatory smooth-pursuit when they expected a moving target. These eye movements were appropriately scaled to the velocity of the expected target. A structured background impaired the ability to perform anticipatory pursuit. Additionally, we could show that the anticipatory pursuit is not an after-pursuit of the previous trial.

Initially, there were doubts in the literature as to whether rhesus monkeys were able to perform predictive eye movements at all (Fuchs 1967). The present results, together with the results of others (Badler and Heinen 2006; de Hemptinne et al. 2006, 2007), provide convincing evidence that monkeys are indeed able to generate anticipatory pursuit, provided that they were trained appropriately. Human subjects were simply instructed to generate eye movements in anticipation of the target; monkeys had to be trained to do so. The critical issue of training might explain why the older study (Fuchs 1967) failed to demonstrate predictive eye movements in monkeys. Having said this, we would like to emphasise that we do not think that motor learning or adaptation plays a major role in anticipatory pursuit. As in other pursuit studies, it is necessary to familiarise the subjects with the set-up and the task in order to minimise variability in oculomotor responses. However, there are two arguments against the idea that the results reported here were consequences of learning. First, learning depends critically on the existence of an error feedback signal. Over the course of a typical learning session, this error signal gradually decreases. However, we did not provide feedback to



**Fig. 9** Median  $V_{500}$  and its mean deviation for the three different target velocities in the after-pursuit test. Five human subjects participated in this experiment. Targets were presented on a homogeneous, dark background. Note that the *error bar* for the 10°s target velocity in the visual condition is too small to be visible

our human subjects. The monkeys did receive a feedback since they were rewarded for every trial during which the gaze did not deviate from target position. Without this reward, the motivation to participate in these experiments would have decreased rapidly. If a feedback signal related to the ongoing eye velocity was provided (coded in the pitch of an auditory signal), human subjects were able to maintain high-speed pursuit even if the target was removed temporally (Madelain and Krauzlis 2003) emphasising the importance of the feedback signal. Second, we did not observe any dynamics in the ability to produce anticipatory pursuit. When we compared the  $V_{500}$  of the first and last trials of a given block, we did not find any significant differences. Thus, we believe that the ability to perform anticipatory pursuit develops in a way similar to the ability to perform visually-guided pursuit, both in humans and monkeys.

### Visually-guided pursuit initiation

Both humans and monkeys performed high-gain smooth-pursuit when the target was constantly present. Pursuit latencies and acceleration values from humans and monkeys are comparable with those from the literature (human: Tychsen and Lisberger 1986; Carl and Gellman 1987, monkey: Lisberger and Westbrook 1985). The faster the target, the shorter the saccade latency and the higher the acceleration (human: Tychsen and Lisberger 1986; Carl and Gellman 1987; Kao and Morrow 1994, monkey: Keller and Khan 1986). The pursuit latency was constant with increasing target velocity in human (Carl and Gellman 1987), but decreased in monkey. It is questionable whether this is a real difference between both species. It might be possible that the decreasing pursuit onset latency in monkeys is an artefact due to the fact that initial acceleration increases with target velocity. Since pursuit onset latency was determined by an eye velocity threshold criterion, the dependency of pursuit latency might be a consequence of acceleration. With respect of the human pursuit initiation, the increase in acceleration with target velocity is not as pronounced as in the monkey data.

### Structured background

When a target moves in front of a structured background, two different problems occur. First, the salience of the target during pursuit initiation is vigorously reduced. The target itself has to be identified within distractor elements. This explains the increased pursuit onset latency (Mohrmann and Thier 1995) which is also present in our data from human subjects. The reduced salience also explains the decreased initial acceleration (Kimmig et al. 1992; Masson et al. 1995) which is present in our data from monkeys. Second, the executed eye movements produce self-induced retinal image motion opposite to the direction of target movement. With respect to self-induced retinal image motion, it has been shown that the presence of a structured background slightly reduced steady-state smooth-pursuit of a moving target in humans (Collewyn and Tamminga 1984) and monkeys (Mohrmann and Thier 1995). The fact that pursuit is possible despite the large amount of self-induced retinal image motion is explained by mechanisms which suppress the processing of self-induced motion signals (Schwarz and Ilg 1999; Lindner et al. 2001). In contrast to the heterogeneous effects of a structured background on  $V_{500}$  during visually-guided pursuit found in the two species, the effect on anticipatory pursuit was quite clear: anticipatory pursuit was significantly reduced in the presence of a stationary structured background. We speculate that the presence of a focussed image of the background on the retina is responsible for this. If

these speculations were true, blurring the image should result in a loss of the suppressive effect; a prediction which could be tested in future experiments.

## Conclusions

We developed a simple paradigm in which the disappearance of the fixation target signalled the onset of an initially invisible moving target. All of our human subjects and the monkeys were able to generate smooth-pursuit eye movements during that time interval. These anticipatory pursuit eye movements were scaled according to the expected velocity of the moving target and were not influenced by previous trial history. The presence of a structured background considerably impaired the ability to generate anticipatory pursuit.

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