Role of Retinal Slip in the Prediction of Target Motion During Smooth and Saccadic Pursuit

SOPHIE DE BROUWER, MARCUS MISSAL, AND PHILIPPE LEFÈVRE. Role of retinal slip in the prediction of target motion during smooth and saccadic pursuit. J Neurophysiol 86: 550–558, 2001. Visual tracking of moving targets requires the combination of smooth pursuit eye movements with catch-up saccades. In primates, catch-up saccades usually take place only during pursuit initiation because pursuit gain is close to unity. This contrasts with the lower and more variable gain of smooth pursuit in cats, where smooth eye movements are intermingled with catch-up saccades during steady-state pursuit. In this paper, we studied in detail the role of retinal slip in the prediction of target motion during smooth and saccadic pursuit in the cat. We found that the typical pattern of pursuit in the cat was a combination of smooth eye movements with saccades. During smooth pursuit initiation, there was a correlation between peak eye acceleration and target direction. This correlation increased with the retinal slip and saturated at a value between 3.8 and 6 Hz (Goldreich et al. 1992; Robinson et al. 1986). During steady-state pursuit in primates, eye velocity oscillates around a mean value. The frequency of this oscillation varies between 3.8 and 6 Hz (Goldreich et al. 1992; Robinson et al. 1986) and could reflect the delays inherent in the operation of a visual feedback loop.

In cats, it has been previously suggested that the smooth-pursuit system is only poorly developed (Evinger and Fuchs 1978). The velocity of the eye during smooth pursuit of a small (~1°) spot of light was thought to be less than a few degrees per second in this species. These results were often interpreted as a consequence of the organization of the feline retina. The cat’s retina does not contain a fovea like primates and has only a limited area centralis (Hughes 1975). It was subsequently inferred that there is no possibility of real smooth pursuit in cats. Therefore smooth eye movements in cats were thought to be limited to smooth eye movements driven by large, full-field visual stimuli. This kind of stimulation leads to an optokinetic response (Evinger and Fuchs 1978). In contrast with this hypothesis, it has been shown that trained cats with the head immobilized are able to pursue a small moving target with smooth eye movements as fast as 40°/s (Missal et al. 1995). The velocity of the eye was correlated with the velocity of the target motion in this species. The analysis of catch-up saccades showed that prediction about future target motion is used in the programming of catch-up saccades. Altogether, these results suggest that pursuit systems in primates and cats are qualitatively similar, with a lower average gain in the cat and that prediction affects both saccades and smooth eye movements during pursuit.

INTRODUCTION

Pursuit eye movements allow primates to follow moving objects with the eyes (see reviews in Lisberger et al. 1987; Pola and Wyatt 1991). When a target of interest starts to move, after a latency period of ~120 ms, the eye accelerates smoothly in the direction of target motion to reduce the error between eye velocity and target velocity, i.e., retinal slip. Eye acceleration increases with the retinal slip and saturates at a value between 200 and 400°/s² for nonperiodic tracking in primates (Lisberger and Westbrook 1985; Lisberger et al. 1981). In the middle of this acceleration period, a “catch-up” saccade is generated to reduce the error between eye and target positions that accumulated during the latency period. The catch-up saccade brings the image of the target on the region of the retina where visual acuity is the highest, the fovea. In primates, smooth pursuit gain, the ratio of eye velocity to target velocity, is close to unity. This indicates that at the end of the acceleration period, eye velocity almost perfectly matches target velocity. The period during which eye velocity matches target velocity is often referred to as steady-state pursuit (Robinson et al. 1986). During steady-state pursuit in primates, eye velocity oscillates around a mean value. The frequency of this oscillation varies between 3.8 and 6 Hz (Goldreich et al. 1992; Robinson et al. 1986) and could reflect the delays inherent in the operation of a visual feedback loop.

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disappears during its trajectory. This phenomenon has been referred to as predictive pursuit (Becker and Fuchs 1985) and arises naturally when a moving target is temporarily occluded by other objects present in the environment. The velocity of the eye during predictive pursuit is related to the velocity of the target that preceded extinction. Higher predictive pursuit velocities are obtained for higher velocities of the moving target before extinction. Preliminary evidence suggests that cats also are able to continue pursuing a target that is transiently extinguished (Missal et al. 1995), but this phenomenon has never been quantitatively studied. The study of predictive pursuit in cats could reveal similarities with predictive pursuit in primates.

The influence of prediction during pursuit is not limited to the smooth part of the trajectory. Indeed, as the target continues to move during the preparation of the catch-up saccade, it has been suggested that the amplitude of the movement has to be corrected (increased) to take into account that displacement (in the monkey: Keller and Johnsen 1990; in human: Gellman and Carl 1991; Ron et al. 1989; but see Heywood and Churcher 1981 for an alternative interpretation). Without correction, the eye would fall short of the target, especially at high target velocities. This predictive adaptation of saccade amplitude could be based on the retinal slip of the target at the time the movement is planned. Because pursuit gain is ~0.5 in cats, saccades during pursuit are frequent (Missal et al. 1995). Therefore the contribution of prediction to the programming of saccade amplitude might be particularly important in this species.

The aim of this study was to evaluate quantitatively the characteristics of visually guided and predictive smooth eye movements in cats and to determine the role of prediction in the determination of saccade amplitude during pursuit. We found that visually guided smooth pursuit in cats is qualitatively similar to smooth pursuit in primates but with a lower average gain. During temporary disappearance of the target, predictive smooth eye movements were observed that are compatible with the hypothesis of a prediction of target motion. A new model to determine the amplitude of saccades during pursuit was proposed. It suggests that a predictive component estimated from the retinal slip contributes to the programming of catch-up saccades. Altogether, these results suggest that pursuit systems in primates and cats are similar and that prediction affects both saccades and smooth eye movements during pursuit.

METHODS

Experimental procedures

The results reported in the present study were gathered from recordings made in six adult cats trained to perform a saccade and smooth pursuit task. All procedures were approved by the Université Catholique de Louvain Ethics Committee and were in accordance with the National Institutes of Health Guide for Care and use of Animals.

Before training began, cats were surgically implanted, under general anesthesia (ketamine: 6–10 mg/kg and xylazine: 0.1 mg/kg im), with a scleral search coil to measure eye position (Robinson et al. 1986). A plastic rod was cemented on the skull and tilted 24° anterior in the sagittal plane. This rod was used to restrain head movements.

Behavioral procedures

Cats were held in a restraining box and faced a tangent screen 1 m away that spanned about ±35° of their visual field. They were trained to fixate a 1° target spot back-projected onto the screen. The fixation target was displayed at a position 10° opposite to the future direction of target motion; e.g., the target appeared 10° to the left of the fixation point before motion to the right. Cats had to maintain steady fixation for 500 ms. The target then started to move at a constant velocity (ramp paradigm); total target displacement was always 20°. Horizontal and vertical target motions were tested. During fixation and pursuit, the position of the eye had to remain within a square window of 4 × 4° centered on the target. Animals received a food reward if they pursued the target to its final position. Sessions of 1 h daily were divided in blocks of variable target velocity. Nine different target velocities were used (5, 7.5, 10, 12.5, 15, 20, 25, 30, and 38 deg/s). In 80% of blocks, target velocity was identical in all trials. In the remaining blocks (20%), target velocity was varied between trials. Up to five different values could be tested in one block. In each block, containing 20–30 trials, the two opposite directions of target motion (left-right or up-down) were randomly interleaved. Horizontal pursuit was quantitatively evaluated in three cats (1, 2, and 6) and vertical in three others (3–5).

Data acquisition and analysis

Vertical and horizontal eye position signals were low-pass filtered at 320 Hz and sampled at 2 kHz. They were stored on the hard disk of a PC for off-line analyses together with target position. MATLAB (Mathworks) was used to implement digital filtering, velocity, and acceleration estimation algorithms. MATLAB’s zero-phase forward and reverse digital filtering—using a Butterworth designed second-order low-pass, 55 Hz, cutoff filter—was applied to the position signals. The velocity and acceleration of horizontal and vertical components were derived from position signals using a central difference algorithm.

The typical pursuit response to a ramp stimulus was characterized by a combination of smooth eye movements and catch-up saccades. Saccade onset and offset were detected with an acceleration criterion of 500°/s². Before analyzing the smooth component of pursuit, all saccades were removed from trials, including 20 ms before saccade onset and 30 ms after saccade offset. Missing segments were replaced in the velocity profile with a linear interpolation based on the velocity before and after saccades. All pursuit traces were grouped by target velocity and moving direction, then aligned on the start of target displacement and finally averaged, with a minimum of 11 trials in each sample. Pursuit latency was detected by an absolute eye acceleration criterion of 25°/s² on the average velocity profiles. Pursuit initiation was followed by sustained pursuit that started after the first peak of eye velocity in the smooth response. Pursuit gain was estimated by computing the ratio between average eye velocity during the first 300 ms following the first peak velocity and target velocity.

Catch-up saccades were grouped into two classes: first saccades, i.e., saccades executed during pursuit initiation, and subsequent saccades, i.e., saccades executed during pursuit maintenance. The analysis was made separately on the two different classes of catch-up saccades because the range of eye velocity was very different in the two categories. The more general case of subsequent catch-up saccades was first described. The same analysis was then done on first catch-up saccades to verify whether the same mechanisms apply to the particular case of saccades during pursuit initiation when eye velocity is very low. After visual inspection, we excluded for quantitative analysis all abnormally slow saccades, saccades with a gain >1.75 and saccades occurring after target stop. For both types of saccades, saccade accuracy was estimated as the measured saccade amplitude divided by the amplitude of the ideal saccade that would have brought the eye on target (saccadic gain).
We studied the parameters that could determine saccade amplitude with a multiple regression analysis. The dependent variable was saccade amplitude (S_{AMP}). The following independent variables were used in the regression analysis: target velocity (T), position error (P_E), eye velocity (E_V), and retinal slip (R_S) or velocity error. Figure 1 illustrates how these variables were measured, together with saccade duration (S_{DUR}). We hypothesized that P_E was estimated 100 ms before saccade onset, as it has been shown that this is probably the last time at which P_E can influence saccade amplitude (Becker and Jurgen 1979). E_V is the slope of regression line fitted over the eye position trace on the 75 to 125 ms period before saccade onset. R_S is the difference T_V – E_V. All possible combinations of one, two, or three independent variables were tested. Given that R_S = T_V – E_V, any combination of two among these three variables gave identical correlation in the regressions.

We successively tested the first-, second-, and third-order regressions. For the third-order regression, P_E, E_V, and R_S constituted the single combination available. Indeed, there is only one combination of three independent variables to be chosen among four variables, three of them being linked by an explicit relation. Because every model with an additional variable always has a better correlation than a lower-order regression, it was important to check the validity of the addition of an independent variable in the fitting. Therefore we computed for second- and third-order regressions, the statistical level above which higher correlation coefficients meant that the associated model was significantly better than the best lower-order model. This was evaluated with a Student t-test ($P < 0.05$).

**Predictive smooth pursuit**

Predictive pursuit was studied in three subjects (4–6). Cats were trained to keep pursuing the target when it was switched off for a short period of time (target blinks). All subjects initially stopped working following the first target extinctions, probably because they were confused and interpreted the disappearance of the target as the end of the trials. Thus a spoon of food had to be presented near the location of target reappearance to make the subject understand the task. This had to be repeated at least 10–20 times before the subjects could understand the task and follow the target after its reappearance. Once the cats had understood the paradigm with extinction, no additional learning was necessary any more before each experimental session. After learning of the task, the target was extinguished during its displacement in 10–50% of the trials, depending on the performance of the animal. Animals learned to continue pursuing the target during its temporary disappearance, predicting its reappearance after the target extinction period. Target extinction lasted 160 to 400 ms. The timing of target extinction was kept constant within a block of ~20 trials but was varied from one block to another. The effect of target extinction on eye velocity was studied. Velocity traces were grouped according to extinction duration and were aligned on target blink onset. Eye velocity was normalized with the mean eye velocity observed during a 50-ms period, starting 25 ms before target extinction. Targets blinks evoked a decrease in eye velocity. The time course of decreasing velocity was approximated with an exponential function with a single time constant. The interval used for the exponential fitting was limited to the interval starting 100 ms after target disappearance to the time of target reappearance. The nonlinear estimation was performed using the nonlinear estimation procedures of a commercial software (STATISTICA, StatSoft). Estimation of the model was performed using the least squares method. The equation of the regression model was

$$V = \exp[-(t - t_0)/\tau]$$

where V is eye velocity during target blink; $\tau$ is the time constant of the exponential function; t is time; and $t_0$ is the time delay, an estimation of the latency of eye deceleration after target disappearance.

**RESULTS**

**Smooth pursuit in cats**

A typical example of pursuit eye movement in response to a target moving at 30°/s is shown in Fig. 2. A short time after target motion onset, the eye accelerates smoothly before a first catch-up saccade brings the eye close to the target. The target is then tracked by a combination of smooth movements and catch-up saccades (delimited by dark shaded bars in the central panel of Fig. 2). At the bottom of the figure, eye and target velocities are plotted together with the velocity of the smooth component. This latter eye velocity profile was obtained after removing saccades and interpolating smooth eye velocity during the period between the beginning and the end of the saccade (see METHODS).

For the six cats, the smooth component of pursuit was analyzed in a total of 1,635 trials. Smooth eye velocity was averaged for each target velocity as described in METHODS. Figure 3 illustrates average eye velocities and accelerations for three different target velocities (10, 15, and 20°/s) in one subject. Target motion onset is followed by an initial acceleration of the eye. The onset of the pursuit response was determined by an acceleration criterion (horizontal dotted line) and represented by vertical ticks on the velocity profiles. The average latency with respect to target motion onset was $65.5 \pm 37.8$ (SD) ms ($n = 29$ averaged profiles). The peak of eye acceleration occurs first (open triangle) and is followed by the peak of eye velocity (closed triangle). Smooth pursuit initiation is then followed by a period of sustained pursuit that can be characterized by its oscillations. For target velocities larger than 10°/s, the average smooth eye velocity responses show a
decay after the peak velocity. These responses could be interpreted as a transient onset smooth eye velocity response followed by a decay of smooth eye velocity toward a steady-state value near the response to 10°/s targets. In addition, the anticipation of the end of trials could also play a role in the decay of smooth eye velocity as has been shown in humans by Robinson et al. (1986). The ringing frequency of oscillations was estimated on the average velocity traces by Fourier analysis on the interval between the first velocity peak and target motion offset. For all cats, the ringing frequency depended very little on target velocity whereas the ringing amplitude increased with target velocity. Thus it was often difficult to estimate ringing frequency for target velocities, 10°/s because the ringing amplitude was too low. We found an average frequency of oscillations of 3.2 Hz for the six cats.

Figure 4 illustrates the relationship between target velocity and peak eye acceleration. This figure illustrates that the initial smooth acceleration of the eye is correlated with target velocity. Given that target velocity is close to the retinal slip during pursuit onset, this shows that the retinal slip is the important stimulus for smooth pursuit initiation as it is in primates. This is confirmed by the slope of the regression line described in Fig. 4, that is similar to that obtained by Robinson et al. (1986) in humans.

It was already clear from the example illustrated in Fig. 3...
that the gain of smooth pursuit in the cat is significantly smaller than unity. This is a major difference with smooth pursuit in primates. A consequence of this low gain is the large number of catch-up saccades during pursuit maintenance. We measured the gain of smooth pursuit in all subjects and found that it was not influenced by target velocity for the range of target velocities that were tested in our study (t-test, \( P < 0.05 \)).

The direction of pursuit movements had a slight influence on vertical pursuit gain in three subjects; however, this effect was not consistent across them (cats 3 and 4: faster up than down; cat 5: faster down than up). Figure 5 shows the distributions of pursuit gains for each subject (different target velocities and directions pooled together). The wide span of upper and lower quartiles around the median illustrates the large variability of smooth pursuit gain in the cat.

**Predictive smooth pursuit during target extinction**

When the target was temporarily extinguished during its trajectory, all subjects were able to continue to pursue, as shown in Fig. 6A. Trials were grouped on the basis of the duration of target extinction and averaged across subjects, target velocities, and directions. Figure 6B shows the normalized average responses for the three different durations of extinction. After 300 ms of target extinction, the residual eye velocity was still \( \sim 50\% \) of the initial eye velocity on average. Longer extinction durations could not be tested because subjects stopped to pursue the target. Subjects probably interpreted these longer durations as the end of the pursuit trial and not as a temporary target extinction. Thus we were not able to determine whether the eye velocity decayed to a nonzero steady-state residual velocity as has been shown to occur in human subjects (Becker and Fuchs 1985). We found no influence of target velocity or moving direction on the time course of the decay in eye velocity during target blink. The exponential fit estimated on the 400 ms extinction duration was characterized by a delay of 95 ms and a time constant of 325 ms \( V = \exp[-(t - 0.095)/0.325]; R > 0.84 \).

**Saccades toward moving targets**

Catch-up saccades play an important role in cats (see Fig. 2). They occur during both pursuit initiation (1st catch-up saccades) and pursuit maintenance (subsequent catch-up saccades). A total of 3,143 catch-up saccades were analyzed, including 990 first catch-up saccades. The mean saccadic gains and ranges for the two types of catch-up saccades (1st and...
Saccade amplitude (AMP), ° 4.25

Table 1. Mean values, standard deviations and ranges for different parameters of catch-up saccades

<table>
<thead>
<tr>
<th>Values Range for 75% of Data</th>
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<tbody>
<tr>
<td>A. Subsequent saccades</td>
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<tr>
<td>Saccade amplitude (SAMP), ° 3.19 ± 1.23 1.74–4.63</td>
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<tr>
<td>Saccade duration (Sdur), ms 89 ± 14 74–104</td>
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<tr>
<td>Position error (Pe), ° 1.02 ± 0.78 0.25–1.87</td>
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<tr>
<td>Target velocity (Tv), °/s 14.25 ± 7.12 4.99–19.88</td>
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<tr>
<td>Retinal slip (Rs), °/s 9.05 ± 4.25 4.22–13.82</td>
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<tr>
<td>Eye velocity (Ev), °/s 5.21 ± 4.51 0.93–10.06</td>
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<tr>
<td>B. First saccades</td>
</tr>
<tr>
<td>Saccade amplitude (SAMP), ° 4.25 ± 1.56 2.51–6.08</td>
</tr>
<tr>
<td>Saccade duration (Sdur), ms 97 ± 14 84–110</td>
</tr>
<tr>
<td>Position error (Pe), ° 1.16 ± 0.89 0.23–2.29</td>
</tr>
<tr>
<td>Target velocity (Tv), °/s 17.29 ± 7.62 9.97–29.49</td>
</tr>
<tr>
<td>Retinal slip (Rs), °/s 15.74 ± 7.54 7.97–26.36</td>
</tr>
<tr>
<td>Eye velocity (Ev), °/s 1.56 ± 1.67 0.23–3.40</td>
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Values are means ± SD; n = 2,153 and 990 for subsequent and first saccades, respectively.

mean of 3.19° and ranged from 1.74 to 4.63° for 75% of the data (Table 1A). Saccade duration had a mean of 89 ms and ranged from 74 to 104 ms for 75% of the data. Before making a multiple regression analysis on saccade amplitude, we verified that the independent variables were not correlated with each other. We found the following correlation coefficients for subsequent (respectively first) catch-up saccades: P_E/R_s, 0.14 (0.28); P_E/T_v, 0.02 (0.15); P_E/T_v, 0.1 (0.08); E_v/R_s, 0.32 (0.05). These correlation coefficients were sufficiently low to consider the variables as independent in a multiple regression analysis. The first-order regression for saccade amplitude gave the best result with retinal slip (Eq. 8, left). For the second-order regression, two combinations of variables gave a significant improvement compared with the best first-order regression. Both combinations used position error as one of the independent variables and the best correlation was obtained when target velocity was the second variable (Fig. 8, middle). We finally tested the multiple regression with a combination of three variables and found that it significantly improved the best second-order model (Fig. 8, right). The third-order model is represented by Eq. 2

\[
S_{AMP} = -0.09 + 0.92 \times P_E + 0.169 \times R_s + 0.068 \times E_v
\]
(0.169) can be interpreted as the retinal slip integrated over the 100 ms period of saccade preparation plus saccade duration (89 ms on average, see Table 1), whereas the coefficient of \( E_V \) (0.068) would correspond to an integration of eye velocity over saccade duration. On the basis of this interpretation, a new third-order regression was estimated using independent variables slightly modified from Eq. 2: \( P_E, R_S*(0.1 + S_{DUR}) \) and \( E_V*S_{DUR} \), where \( S_{DUR} \) represents the duration of individual saccades.

We obtained the following equation

\[
S_{AMP} = -0.05 + 0.80*P_E + 1.04*R_S*(0.1 + S_{DUR}) + 1.19*E_V*S_{DUR}
\]

All the coefficients of this equation can be interpreted as gains; they represent the proportion of the different variables that is corrected by catch-up saccades. This regression \((R = 0.98, n = 2,153)\) was significantly better than the third-order model described by Eq. 2.

For the first catch-up saccades, a similar study was performed. Table 1B summarizes the characteristics of the different saccade parameters. The best model that we found with the multiple regression analysis was a second-order model with position error and target velocity as independent variables \((R = 0.98, n = 990; \text{Eq. } 4)\)

\[
S_{AMP} = -0.01 + 0.86*P_E + 0.162*T_V
\]

The third-order regression did not give any statistically significant improvement. This could be explained by the fact that eye velocity was close to zero during pursuit initiation for the first catch-up saccades (correlation coefficient between \( T_V \) and \( R_S = 0.98)\).

**Discussion**

We found that cats pursued moving targets by using a combination of smooth eye movements and catch-up saccades. During smooth pursuit initiation, there was a correlation between peak eye acceleration and target velocity. During pursuit maintenance, we showed that eye velocity oscillated at ~3 Hz around a steady-state value. The average gain of smooth pursuit was ~0.5. We also demonstrated that smooth eye velocity decayed exponentially during temporary target extinction and that trained cats were able to continue pursuing in the absence of a visible target, suggesting a possible role of prediction in this species. Catch-up saccades during smooth pursuit initiation and maintenance were analyzed. We found that the smooth pursuit motor command is added to the saccadic command during catch-up saccades and that both position error and retinal slip are taken into account in their programming. This influence of retinal slip shows that prediction about future target motion is used in catch-up saccade programming.

**Smooth pursuit**

A previous report about smooth pursuit in cats revealed that smooth eye movements in this species reach velocities as high as 40°/s (Missal et al. 1995). However, the average gain of smooth pursuit in cats is lower than it is in primates. Therefore it was important to analyze smooth pursuit in details to assess whether several important characteristics of smooth pursuit in primates were present in cats.

During pursuit initiation, we showed that initial peak acceleration of the eye was correlated with target velocity. When target velocity increased, initial peak acceleration and velocity of the eye increased concomitantly. We found the same linear relationship between target velocity and peak eye acceleration that has been described in human subjects (Robinson et al. 1986). These findings clearly indicate that smooth-pursuit initiation in cats depends on target velocity in a similar way as it does in primates.

During pursuit maintenance, oscillations at ~3 Hz were observed on the eye velocity profile. These oscillations were superimposed on a steady-state velocity that varied with target velocity. Similar oscillations were previously described in human subjects (Robinson et al. 1986) and in monkeys (Goldreich et al. 1992). In fact, recent models of smooth pursuit (Krauzlis and Lisberger 1994; Robinson et al. 1986) reproduce these oscillations when steady-state pursuit is simulated. Oscillations during sustained pursuit in cats occur around the same frequency as in primates (~3 vs. [3.8–6] Hz), thus it is reasonable to suggest that a similar mechanism might be involved in their occurrence. The small difference in oscillation frequency could be related to sensory (visual) or internal delays that are specific to each species. Again, these findings suggest that cat and primate pursuit systems are similar. Both species probably use retinal slip on the retina as the dominant stimulus to control sustained pursuit.

When the target was temporarily extinguished, cats learned to maintain smooth pursuit until it reappeared. During target blink, eye velocity decreased exponentially with a time constant that was estimated to 325 ms on average. In fact, it is remarkable that cats learned to continue pursuing in the absence of the target. This suggests that a predictive mechanism about future target motion exists in cats as has been suggested to exist in humans (Becker and Fuchs 1985). Indeed, in a natural environment, moving targets often temporarily disappear behind occluding objects. Prediction might be necessary in order catch a prey at the appropriate velocity when it reappears. When a target disappears, eye velocity normally decreases with an exponential time course. The time constant of the decay that we report is larger than what was found in humans (~100 ms in Becker and Fuchs 1985). One possible interpretation of this difference is the presence of an internal positive feedback loop that increases the time constant after learning of the task in the cat. The existence of such an internal positive feedback loop has already been suggested to account for larger time constants during foveal stabilization of a target compared with normal pursuit offset response (500 vs. 100 ms) (Polis and Wyatt 1997). Whatever the mechanism, our results suggest that prediction during smooth pursuit is present in cats. Therefore prediction during pursuit cannot be considered as a distinctive criterion between this species and primates.

Because pursuit initiation, oscillations during pursuit maintenance, and prediction are characteristics that are common to both cats and primates, the only major difference in smooth pursuit between these species remains the lower and more variable gain of feline smooth pursuit.

**Catch-up saccades**

The most important consequence of the low gain of smooth pursuit in cats is the large proportion of pursuit trials that contain several catch-up saccades. In addition, the large vari-
ability of pursuit gain yields a wide range of position error, retinal slip, and eye velocity at saccade onset for a given target velocity. This is an advantage of the cat as experimental model when studying catch-up saccades. In primates, saccades usually occur only during pursuit initiation (1st catch-up saccades).

The multiple regression analysis for saccade amplitude gave a third-order equation (Eq. 3), which describes the best correlation found with three variables: position error ($P_E$), retinal slip ($R_S$) multiplied by 0.1 plus saccade duration ($S_{DUR}$), and mean smooth eye velocity ($E_V$) multiplied by $S_{DUR}$. The contribution of position error ($P_E$) to saccade amplitude is rather straightforward. Since $P_E$ was measured 100 ms before saccade onset, it corresponds to a saccadic command identical to what could happen for saccades to stationary targets. In fact, if cats were neither capable to pursue smoothly nor to predict future target motion on the basis of retinal slip, saccade amplitude should have been proportional to only $P_E$.

The second term in Eq. 3 is proportional to retinal slip [$R_S^*(0.1 + S_{DUR})$]. This finding is important because it shows that $R_S$ is evaluated and used to predict future target motion. This prediction is necessary to compensate for the delay between the measure of $P_E$ and the end of the saccade (100 ms + $S_{DUR}$), otherwise, the eye would always fall very short of the target, especially when $R_S$ is large. Indeed, for a retinal slip of 20°/s, a 2° error accumulates only during saccade preparation (100 ms). Equation 3 suggests that there is a prediction of future target motion during both saccade preparation and execution.

Previous studies of catch-up saccades in primates reported correlations of saccade amplitude ($S_{AMP}$) with position error ($P_E$) and target velocity ($T_V$) only (Gellman and Carl 1991; Keller and Johnsen 1990; Ron et al. 1989). These studies included only the first catch-up saccades. Before and during these saccades, the velocity of the eye ($E_V$) was small and its contribution to the amplitude of the movement can be considered as negligible. Consequently, target velocity ($T_V$) and retinal slip ($R_S$) were similar, making a distinction between these variables impossible in a multiple regression analysis. In humans, Kim et al. (1997) studied catch-up saccades during pursuit maintenance, when eye velocity is close to target velocity. These saccades were obtained by triggering sudden steps in the position of the target without varying its velocity. Because these steps were introduced during pursuit maintenance, target velocity ($T_V$) was close to eye velocity ($E_V$) and the retinal slip ($R_S$) was therefore very small. Once again, evaluating the contribution of these different variables to the programming of catch-up saccades was not possible. In our study, the fourth equation (Eq. 4), which describes the results obtained for the first catch-up saccades, shows the same correlations with $P_E$ and $T_V$ as obtained in primates (Gellman and Carl 1991; Keller and Johnsen 1990; Kim et al. 1997; Ron et al. 1989). However, the third equation (Eq. 3), which describes the results obtained for subsequent saccades, shows clearly the role of the other components. Indeed, there was a wider range of retinal slip ($R_S$), target velocity ($T_V$), and eye velocity ($E_V$) at the time of occurrence of these movements.

The last term in Eq. 3 is proportional to smooth eye velocity ($E_V$) multiplied by saccade duration ($S_{DUR}$). It indicates that the smooth pursuit motor command is not interrupted during saccade execution but is added to the saccadic motor command. The faster the smooth eye movement and the longer the saccade, the larger the contribution of the smooth motor command to the catch-up saccade. Therefore the smooth pursuit contribution has to be subtracted from the saccade to measure the contribution of the saccadic system in isolation, as suggested by Keller and Johnsen (1990).

Prediction of target motion plays a pervasive role during pursuit of a moving target, in cats as well as in other species. We found evidence of prediction of target motion during both smooth-pursuit epochs and catch-up saccades. Prediction is needed to allow a precise estimation of the trajectory of the target and to compensate for delays present in the visual and oculomotor systems. The finding that qualitatively similar predictive capacities exist in cats and in primates suggests that prediction plays a major role in orientation, independently of the position of the organism on the evolutionary ladder.

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