

Quantitative Analysis of Catch-Up Saccades During Sustained Pursuit

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de Brouwer, Sophie, Marcus Missal, Graham Barnes, and Philippe Lefèvre. Quantitative analysis of catch-up saccades during sustained pursuit. *J Neurophysiol* 87: 1772–1780, 2002; 10.1152/jn.00621.2001. During visual tracking of a moving stimulus, primates orient their visual axis by combining two very different types of eye movements, smooth pursuit and saccades. The purpose of this paper was to investigate quantitatively the catch-up saccades occurring during sustained pursuit. We used a ramp-step-ramp paradigm to evoke catch-up saccades during sustained pursuit. In general, catch-up saccades followed the unexpected steps in position and velocity of the target. We observed catch-up saccades in the same direction as the smooth eye movement (forward saccades) as well as in the opposite direction (reverse saccades). We made a comparison of the main sequences of forward saccades, reverse saccades, and control saccades made to stationary targets. They were all three significantly different from each other and were fully compatible with the hypothesis that the smooth pursuit component is added to the saccadic component during catch-up saccades. A multiple linear regression analysis was performed on the saccadic component to find the parameters determining the amplitude of catch-up saccades. We found that both position error and retinal slip are taken into account in catch-up saccade programming to predict the future trajectory of the moving target. We also demonstrated that the saccadic system needs a minimum period of approximately 90 ms for taking into account changes in target trajectory. Finally, we reported a saturation (above 15°/s) in the contribution of retinal slip to the amplitude of catch-up saccades.

INTRODUCTION

In natural conditions, it is very common that objects are moving in the environment. Pursuit eye movements allow primates to maintain the image of moving targets on the fovea, the highest acuity zone of the retina. However, smooth pursuit eye movements are controlled by visual feedback and thus the delays present in the visual system influence their characteristics (see reviews in Lisberger et al. 1987; Pola and Wyatt 1991). When object motion is unpredictable, these delays cause the accumulation of retinal error when the target velocity varies rapidly. In this condition, the strategy used by primates to track moving objects is to combine smooth eye movements with catch-up saccades that are rapid eye movements executed without visual feedback. Of course, the precision of these saccades is very important because they largely influence the performance of pursuit. The goal of this study is to investigate

the mechanisms underlying the programming and execution of catch-up saccades in humans.

Catch-up saccades are typically preceded and followed by smooth eye movements. It has never been clearly demonstrated whether the smooth pursuit motor command was interrupted or maintained during the execution of catch-up saccades. An early study by Jürgens and Becker (1974) concluded that there was no linear addition of saccades and smooth eye movements. However, in more recent studies (Keller and Johnsen 1990; Smeets and Bekkering 2000), the smooth pursuit component was removed from catch-up saccades before analysis because the assumption was made that there was a linear addition of saccades and pursuit during catch-up saccades. The first objective of this study will be to address this issue by comparing the characteristics of catch-up saccades with control saccades made to stationary targets. Given that saccades can be characterized by their main sequence, a relationship that tightly relates their duration (or peak velocity) to their amplitude (Bahill et al. 1975), the hypothesis of linear addition between saccades and pursuit could be unambiguously tested. Indeed, if the smooth component is added to the saccade, the main sequence of catch-up and control saccades should be distinct.

For saccades to stationary targets, the sensory signal determining their amplitude is the position error, i.e., the retinal error between the target and the fovea. In addition, it has been demonstrated by Becker and Jürgens (1979) that a step in target position occurring less than 100 ms before saccade onset did not affect saccade amplitude. This period reflects the delays present in the sensory visual pathways and the time necessary for saccade preparation. When the target is moving, position error continuously varies if the eye and target velocity are different, i.e., if there is a retinal slip. To overcome the delay present in the saccadic system, it has been suggested that the oculomotor system uses prediction of future target motion to program catch-up saccades to moving targets (in the monkey: Keller and Johnsen 1990; in human: Gellman and Carl 1991; Ron et al. 1989). However, the exact nature and origin of the predictive component of catch-up saccades has never been clearly demonstrated. In particular, previous studies did not allow the relative role of retinal slip and target velocity estimation in saccade programming to be clearly distinguished. The second objective of this study will be to investigate which

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parameters determine the amplitude of catch-up saccades. The influence of position error, target velocity, and retinal slip in catch-up saccade programming will be specifically assessed. For this purpose, we have specifically chosen a paradigm that uses large ranges of combined position and velocity steps of the target during sustained pursuit.

METHODS

Subjects were seated and faced a tangent screen 1 m away that spanned about $\pm 45^\circ$ of their visual field. Their head was restrained by a chin rest. A visual target spot of 0.2° was back-projected onto the screen and moved horizontally under the control of a motor-driven mirror. Movements of one eye were recorded with the scleral coil technique (Collewijn et al. 1975; Robinson 1963). Healthy subjects without any known oculomotor abnormalities were recruited after informed consent. Among the six subjects, two authors participated and two subjects were completely naive of oculomotor experiments. Mean age was 29, ranging from 24 to 35. All procedures were conducted with approval of the Université Catholique de Louvain Ethics committee.

Each trial started with a fixation period of 1 s at a position 20° from center in the direction opposite to the future direction of target motion (e.g., the target appeared 20° to the left before target motion to the right). Then, a first step-ramp started (target velocity TV1) to initiate smooth eye movements. The initial step amplitude was controlled in such a way that the target crossed the initial fixation point 200 ms after the step. This step reduced the probability of occurrence of the first catch-up saccade during pursuit initiation (Rashbass 1961). TV1 was randomly chosen among 10, 20, or $30^\circ/\text{s}$, and the direction of target motion (rightward or leftward) randomly varied from trial to trial. In each block, the duration of the first ramp randomly varied in a range of 500 ms and was always larger than 600 ms. Following the first step ramp, a second step in position and velocity occurred. The step in position randomly varied from -20 to 20° and the step in velocity (TV2-TV1) from -50 to $50^\circ/\text{s}$. The duration of the second ramp varied between 500 and 700 ms. All variations of parameters were continuous. The complete randomness of the second ramp in its initial position, velocity, direction, and duration reduced the influence of cognitive expectation. Trials ended with a fixation period of 1 s at the final position of the second ramp. Sessions of maximum one half hour were divided into blocks of 25 trials.

Data acquisition and analysis

Eye and target position were sampled at 1,000 Hz. They were stored on the hard disk of a PC for off-line analyses. MATLAB (Mathworks) was used to implement digital filtering, velocity, and acceleration estimation algorithms. Position signals were low-pass filtered by a zero-phase digital filter (cutoff frequency: 50 Hz). Velocity and acceleration were derived from position signals using a central difference algorithm.

We analyzed only the first saccade occurring after the second target step. Saccades were detected by an acceleration threshold ($750^\circ/\text{s}^2$) and then were visually inspected. Their latency was measured with respect to the second target step. We measured all the parameters necessary to construct the saccadic main sequence, i.e., saccade amplitude (S_{AMP}), duration (S_{DUR}), and peak velocity (V_{MAX}). We estimated also the mean pursuit velocity observed before and after each saccade (V_{PURS}). This average velocity was calculated over the interval from 75 to 25 ms before saccade onset (V_P) and from 25 to 75 ms after saccade offset (V_N): $V_{\text{PURS}} = (V_P + V_N)/2$. These parameters are illustrated in Fig. 1. Multiple regression analysis was used to determine the parameters that influenced S_{AMP} (de Brouwer et al. 2001). The following independent variables were used in the multiple regression analysis: target velocity (T_V), position error (P_E), and

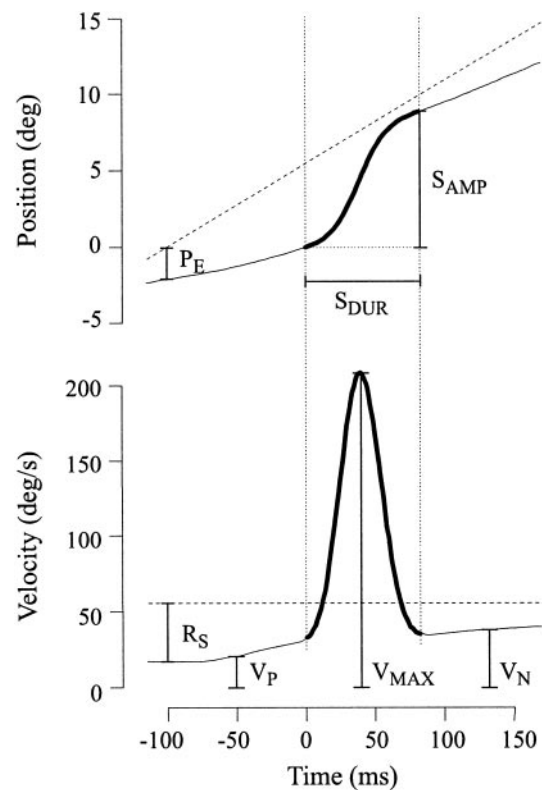


FIG. 1. Example of a catch-up saccade during a smooth pursuit eye movement. All parameters that were analyzed in this study are illustrated on the figure. *Top*: position traces; *bottom*: velocity traces. Solid lines and dashed lines, the eye and target, respectively. Vertical dotted lines, delimit saccade onset and offset. *Time zero* defines saccade onset. S_{DUR} corresponds to saccade duration and S_{AMP} to saccade amplitude. The position error (P_E) and the retinal slip (R_S) are measured 100 ms before saccade onset. The smooth eye velocities 50 ms before saccade onset (V_P) and 50 ms after saccade offset (V_N) are illustrated. The mean smooth pursuit eye velocity during the catch-up saccade (V_{PURS}) is estimated as the mean of V_P and V_N [$V_{\text{PURS}} = (V_P + V_N)/2$]. V_{MAX} corresponds to the maximum eye velocity during the catch-up saccade.

retinal slip (R_S) or velocity error. 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 Jürgens 1979). R_S is the difference between target and eye velocities, estimated over a 50-ms interval centered around 100 ms before saccade onset. Control saccades, i.e., saccades toward a stationary target, were recorded in separate blocks of trials to compare them with catch-up saccades.

RESULTS

Two typical examples of visual tracking of a moving target are illustrated in Fig. 2. All trials started with a first ramp of constant target velocity. Because target motion onset was combined with a backward step of the target, the oculomotor response usually started with a purely smooth eye movement and the eye velocity reached a value near target velocity before the end of the first ramp (Rashbass 1961). This study focused on the analysis of the second part of the trials, after the second step in position and velocity. Shortly after that time, the error between target and eye position was significant and a catch-up saccade was triggered by the oculomotor system to catch the target (Fig. 2). When the direction of the saccade was the same as the direction of the preceding smooth eye movement, the catch-up saccade was defined as a forward saccade (Fig. 2A),

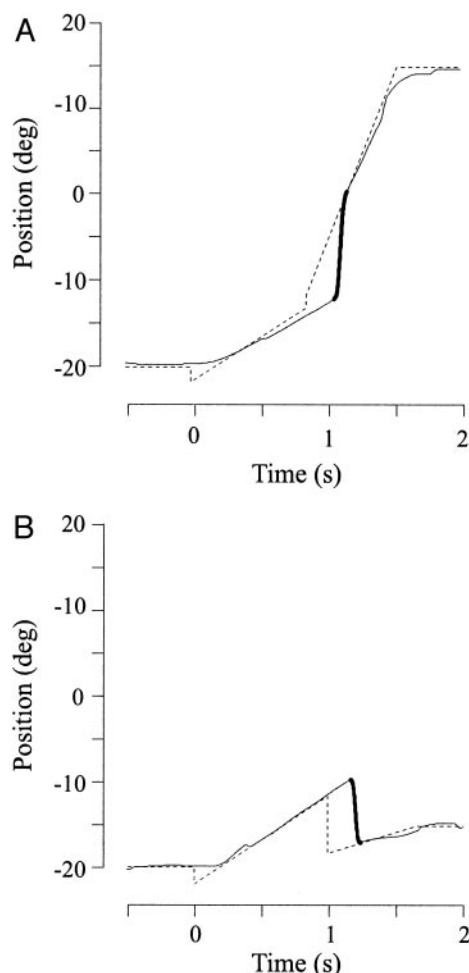


FIG. 2. Typical examples of forward and reverse saccades. Solid and dashed lines, the eye and target position traces, respectively. Catch-up saccades are illustrated by the thick segments on the solid traces. Depending on the values of the position and velocity steps of the target, a forward saccade (A) or a reverse saccade (B) is observed. Catch-up saccades were defined as forward saccades when they were in the same direction as the preceding smooth eye movement, whereas it was the opposite for reverse saccades.

whereas it was defined as a reverse saccade when the direction was opposite (Fig. 2B). A total of 1,367 reverse saccades, 2,899 forward saccades, and 345 control saccades were analyzed.

We first quantified the main sequences of catch-up saccades and compared them with control saccades. Figure 3A shows the relationship between saccade duration (S_{DUR}) and saccade amplitude (S_{AMP}) for control (●), forward (◐), and reverse saccades (○) for all subjects pooled together. It clearly appears that the three populations of saccades are characterized by different main sequences. When saccades of identical duration are compared in the three populations, reverse saccades are smaller than control saccades and forward saccades are larger than control saccades. This is compatible with the hypothesis that a smooth eye movement is added to the saccadic command during catch-up saccades. Because smooth and saccadic commands are in the same direction for forward saccades, they are larger than control saccades of the same duration. For reverse saccades it is the opposite. We tested quantitatively the hypothesis of linear addition of saccade and smooth eye movement by constructing the main sequences of catch-up saccades

after removing the putative smooth eye movement integrated over saccade duration. This was done by evaluating the main sequences with the corrected amplitude of catch-up saccades.

$$S_{\text{AMP}}^* = S_{\text{AMP}} - S_{\text{DUR}} \cdot V_{\text{PURS}}$$

After this correction, the three populations of saccades were merged so that variance was reduced (Fig. 3B). For each subject, the effect of saccade correction on the variance of the main sequence was tested. We pooled the data from the three populations and compared the mean square deviation of the classical main sequence (Fig. 3A) with the mean square deviation of the corrected main sequence (Fig. 3B). For all subjects, the variance significantly decreased after correction (Fisher test, $P < 0.01$). Moreover, we statistically compared the linear models of the main sequence for the reverse and forward saccades (Graybiel 1976). Before correction, the main sequence for reverse saccades was significantly different from the main sequence for forward saccades (for each subject, $P < 0.01$). After correction of the smooth pursuit contribution, both the slope and intercept of the main sequences for reverse and forward saccades were not significantly different (for all but 1 subject, $P < 0.01$). The same analysis was done with the main sequence between peak velocity (V_{MAX}) and amplitude of

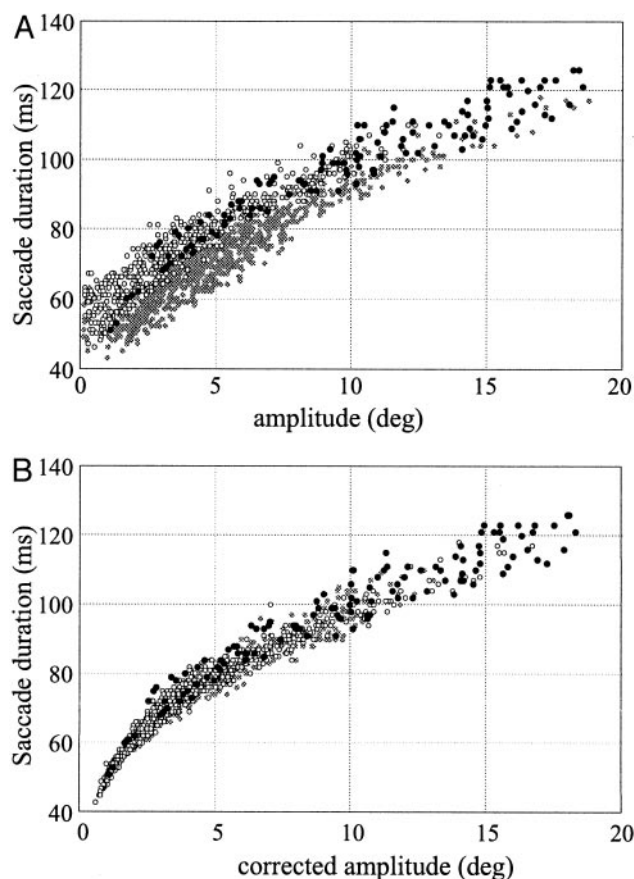


FIG. 3. Main sequence relationship between saccade duration and amplitude. A: the main sequence between duration (S_{DUR}) and amplitude before correction (S_{AMP}). Forward saccades (◐, $n = 2,899$), reverse saccades (○, $n = 1,367$), and control saccades to stationary targets (●, $n = 345$) correspond to distinct populations in the graph. B: the same main sequence after correction of saccade amplitude for the smooth component ($S_{\text{AMP}}^* = S_{\text{AMP}} - S_{\text{DUR}} \cdot V_{\text{PURS}}$). Forward, reverse, and control saccades are represented by the same symbols as in A. They are now concentrated in a single population.

saccades (Fig. 4). Again, three distinct main sequences could be observed for the three populations of saccades (Fig. 4A). In this case, the evaluation of the corrected main sequences required a correction for both saccade amplitude (as in the preceding text) and peak velocity. Corrected peak velocity was evaluated by removing the mean pursuit eye velocity

$$V_{MAX}^* = V_{MAX} - V_{PURS}$$

After this correction, the three populations of saccades were merged in a single main sequence (Fig. 4B). The same statistical test as for the first main sequence was performed. For all subjects, the global mean square deviation of the main sequence decreased significantly after correction (Fisher test, $P < 0.01$). Moreover, by comparing the linear models of the main sequence, we found that for all subjects, the main sequence for reverse saccades was statistically different from the main sequence for forward saccades before correction. After correction, the main sequences for reverse and forward saccades were not significantly different (for all but 2 subjects, $P < 0.01$). The results of the analysis of the main sequences suggest that there is a linear addition of saccades and smooth

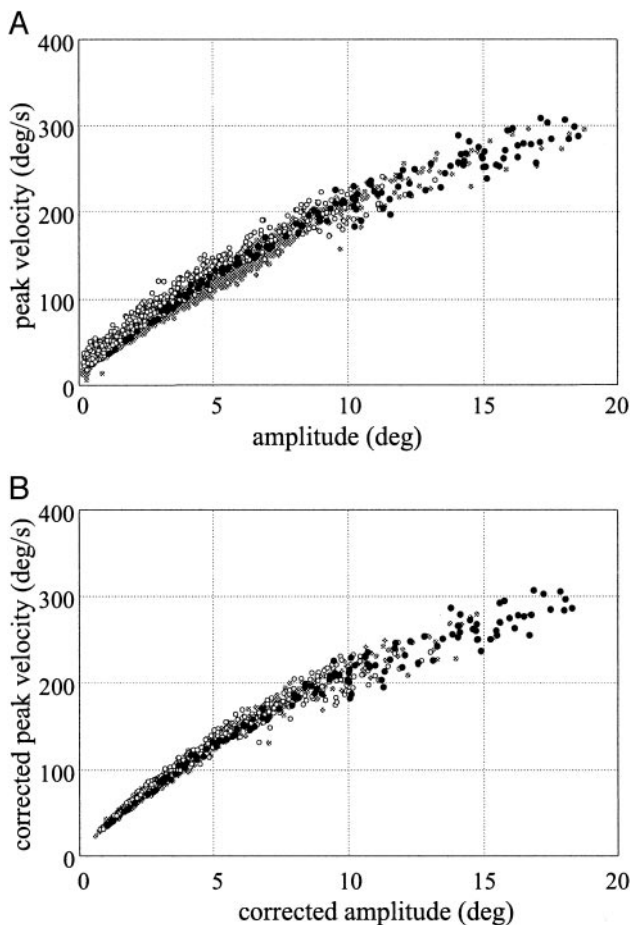


FIG. 4. Main sequence relationship between saccade peak velocity and amplitude. A: the main sequence between peak velocity (V_{MAX}) and amplitude before correction (S_{AMP}). Forward saccades ($\circ$, $n = 2,899$), reverse saccades ($\bullet$, $n = 1,367$), and control saccades to stationary targets ($\bullet$, $n = 345$) correspond to distinct populations in the graph. B: the same main sequence after correction of saccade amplitude ($S_{AMP}^* = S_{AMP} - S_{DUR} \cdot V_{PURS}$) and peak velocity ($V_{MAX}^* = V_{MAX} - V_{PURS}$) for the smooth component. Forward, reverse, and control saccades are represented by the same symbols as in A. They are now concentrated in a single population.

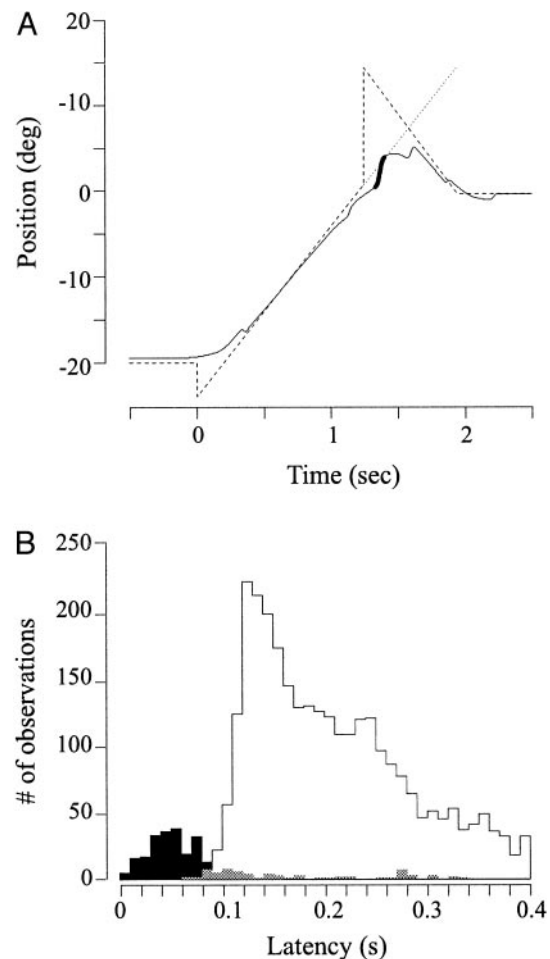


FIG. 5. Minimum latency of catch-up saccades. A: solid and dashed lines, the eye and target position traces, respectively. It shows an example of a catch-up saccade (thick segment) occurring shortly after the target step. In this case, the saccade brings the eye near the first ramp (dotted line) because the latency (87 ms) was probably too short to take into account the step in catch-up saccade programming. B: a histogram of the total number of trials for which the catch-up saccade brought the eye closer to the 1st ramp (black histogram) or to the 2nd ramp (white histogram) as a function of saccade latency with respect to the target step. Bins of 10 ms are used.

pursuit during catch-up saccades. Thus catch-up saccades are composed of two components: the “smooth pursuit component” and the “saccadic component.”

For the first catch-up saccade after the second target step, we also evaluated whether the visual information used for its programming was based on sensory signals preceding or following the step. This was done to quantify the minimum saccade latency to consider in our analysis. For this purpose, we measured two different errors for all catch-up saccades. The first error was the final error between target and eye position at the end of the catch-up saccade (Err1). The second error was the difference between the putative target position if the second target step had not occurred and actual eye position (Err2). For trials with small Err2, it is likely that the oculomotor system did not take into account the second target step. This is illustrated by the example in Fig. 5A, where the first catch-up saccade occurring after the second target step brings the eye near the dotted line, which corresponds to the prolonged first target ramp. For each catch-up saccade, we evaluated whether the saccade was pointing to the first ramp [$\text{abs}(\text{Err1}) >$

TABLE 1. Mean values and ranges for different parameters of catch-up saccades

	Mean	Range [25–75]%
Forward		
S_{AMP}^* , °	6.64 ± 2.93	[4.57–8.01]
P_E , °	5.30 ± 4.49	[1.70–8.18]
$V_{PURS} \cdot S_{DUR}$, °	1.28 ± 0.77	[0.63–1.85]
R_S , °/s	23.55 ± 11.99	[14.31–32.34]
T_V , °/s	29.68 ± 17.46	[15.00–44.06]
S_{DUR} , ms	74 ± 10	[67–79]
Final error, °	1.42 ± 1.20	[0.50–2.07]
Saccadic gain	0.91 ± 0.24	[0.76–1.01]
Reverse		
S_{AMP}^* , °	4.62 ± 2.70	[2.58–6.26]
P_E , °	6.01 ± 3.89	[2.72–8.50]
$V_{PURS} \cdot S_{DUR}$, °	0.80 ± 0.58	[0.33–1.20]
R_S , °/s	20.97 ± 12.65	[10.05–30.49]
T_V , °/s	22.31 ± 14.33	[10.98–32.13]
S_{DUR} , ms	74 ± 10	[66–80]
Final error, °	1.28 ± 1.16	[0.45–1.78]
Saccadic gain	0.94 ± 0.41	[0.71–1.05]
Control		
S_{AMP}^* , °	10.09 ± 4.34	[6.55–13.96]
P_E , °	10.64 ± 4.66	[6.66–14.64]
S_{DUR} , ms	91 ± 15	[79–101]
Final error, °	0.75 ± 0.61	[0.30–1.05]
Saccadic gain	0.94 ± 0.068	[0.90–0.98]

$n = 1,850, 975$, and 345 for forward, reverse, and control, respectively. Values are means $\pm$ SD.

$\text{abs}(\text{Err2})$] or the second ramp [$\text{abs}(\text{Err1}) < \text{abs}(\text{Err2})$]. Figure 5B reports histograms of the number of trials in the two categories of catch-up saccades as a function of saccade latency. To avoid ambiguous situations where the first ramp was relatively close to the second ramp at the time of saccade execution, Fig. 5B reports only trials for which the difference between $\text{abs}(\text{Err1})$ and $\text{abs}(\text{Err2})$ was larger than 2° . The example of Fig. 5A had a latency of 87 ms and was counted in the black histogram (saccades to the first ramp, $n = 273$). The trials of Fig. 2 are two typical examples of saccades to the second ramp (white histogram, $n = 2,790$); their latencies were 203 ms (Fig. 2A) and 157 ms (Fig. 2B). Figure 5B illustrates that when catch-up saccade latency was shorter than 90 ms, most saccades pointed to the first ramp, whereas it was the opposite for latencies larger than 90 ms. We made the same kind of analysis when restricting the data to trials with small values of R_S [$\text{abs}(R_S) < 5^\circ/\text{s}$], i.e., to evaluate the timing of P_E evaluation; we found that the transition was also around 90 ms. For data restricted to small values of P_E [$\text{abs}(P_E) < 2^\circ$], i.e., to evaluate the timing of R_S evaluation, we found that the transition was around 80

ms. This justifies our assumption that both P_E and R_S are evaluated around 100 ms before saccade onset (see METHODS).

Table 1 summarizes the principal parameters of forward, reverse, and control saccades. The saccadic gain was defined as the ratio between the measured saccade amplitude and the amplitude of the ideal saccade that would have brought the eye on the target. Our detailed analysis of saccades was restricted to forward and reverse catch-up saccades with a minimum corrected amplitude of 2° and a minimum latency of 125 ms ($n = 2,825$). We hypothesized that this latency was sufficient to make sure that catch-up saccades were responses to the step and not responses to the first ramp (Fig. 5B). For forward and reverse catch-up saccades, the pursuit component was removed before the analysis (corrected saccades). We tried to determine the parameters that influenced catch-up saccade amplitude by performing a multiple regression analysis. The dependent variable was corrected saccade amplitude (S_{AMP}^*), and we considered position error (P_E), retinal slip (R_S), and target velocity (T_V) as the independent variables. Table 2 gives the correlation coefficient between S_{AMP}^* and each of the independent variables. All correlations were significant (Student's t -test, $P < 0.01$). The best first-order regression was obtained with position error (P_E) as the independent variable. Table 2 also reports the second-order correlation coefficients for the two combinations improving the first-order regression. Position error was the first independent variable and either retinal slip (R_S) or target velocity (T_V) was the second. The best correlation was obtained with position error and retinal slip. Because adding a variable in a regression systematically increases the correlation coefficient, we tested the significance of each additional variable with the partial correlation, i.e., the correlation between one independent variable and S_{AMP}^* after accounting for the influence of the other independent variable. All partial correlation coefficients were significant (Student's t -test, $P < 0.01$), which means that both second-order regressions significantly improved the determination of S_{AMP}^* . To distinguish the respective roles of the retinal and extraretinal velocity signals (R_S vs. T_V) in the saccade programming, we compared the correlation coefficients of the two second-order regressions ($R = 0.9816$ vs. $R = 0.9705$, $n = 2,825$). We found that the model using R_S as second independent variable was significantly better than the model using T_V as second independent variable (Student's t -test, $P < 0.01$). The high correlation coefficient obtained when T_V is used as second variable can be explained by the correlation between R_S and T_V ($R = 0.87$).

Equation 1 yields the results of the best second-order regression

TABLE 2. Correlation coefficients for the multiple regression analysis between the dependent variable (S_{AMP}^*) and different independent variables

	Independent Variable		R	Partial Correlation	
	1	2		Variable 1	Variable 2
First-order regression	P_E	—	$0.9079 (P < 0.01)$	—	—
	T_V	—	$0.2477 (P < 0.01)$	—	—
	R_S	—	$0.1494 (P < 0.01)$	—	—
Second-order regression	P_E	R_S	$0.9816 (P < 0.01)$	$0.9812 (P < 0.01)$	$0.8904 (P < 0.01)$
	P_E	T_V	$0.9705 (P < 0.01)$	$0.9686 (P < 0.01)$	$0.8182 (P < 0.01)$

$n = 2,825$ for first- and second-order regressions.

$$S_{AMP}^* = 0.09 + 0.86 * P_E + 0.091 * R_S \quad (R = 0.9816, n = 2825) \quad (1)$$

The two coefficients of Eq. 1 can be interpreted as follows. The coefficient of P_E (0.86) represents the proportion of position error that is corrected by catch-up saccades. Similarly, as R_S is a velocity, its coefficient (0.091) corresponds to the duration by which it is multiplied. Another way of looking at Eq. 1 is to consider what its coefficients should be for catch-up saccades to bring the eye exactly on the target. In that case, it is necessary to take into account the observation that we made that, on average, the eye accelerates smoothly during the period between 100 ms before saccade onset until the end of the saccade. We quantified the influence of smooth acceleration on average retinal slip and found that: mean $R_S = R_S * 0.77$, $n = 2,825$. Under these assumptions, the amplitude of a putative "exact" catch-up saccade can be described by the following equation

$$\text{Exact } S_{AMP}^* = 1 * P_E + (0.1 + S_{DUR}) * 0.77 * R_S \quad (2)$$

This means that for accurate catch-up saccades, the saccadic system corrects the position error (P_E) and integrates the mean retinal slip over the period of saccade latency plus saccade duration. The comparison of Eq. 1 with Eq. 2 clearly shows that both coefficients of P_E and mean R_S are smaller in Eq. 1 (mean $S_{DUR} = 0.074$). This indicates that, on average, catch-up saccades do neither fully compensate for position error nor for retinal slip.

Thus we addressed specifically the issue of the precision of catch-up saccades in Fig. 6 by showing the average final error at the end of catch-up saccades as a function of retinal slip. In Fig. 6, we considered that saccade amplitude was always positive and thus reversed all leftward saccades accordingly. This allowed us to distinguish between undershooting (positive final error) and overshooting saccades (negative final error). Figure 6 reports separately data from forward and reverse saccades, showing that the two populations are almost identical (in terms of both mean and SD). This means that the mechanisms of catch-up saccade programming are likely very similar

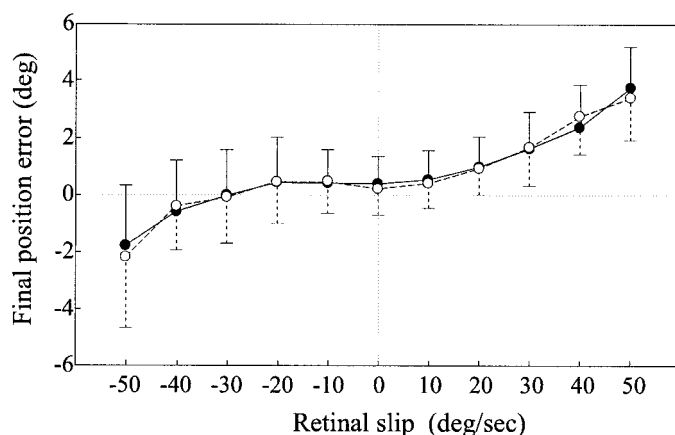


FIG. 6. The influence of retinal slip on the precision of catch-up saccades. Representation of mean $\pm$ SD of final position error (i.e., target–eye position at the end of catch-up saccade) as a function of retinal slip (R_S). Final position errors were illustrated separately for forward saccades (black dots, solid lines) and reverse saccades (open circles, dashed lines). For the analysis, we considered that saccade amplitude was always positive and thus positive final errors correspond to undershoot and negative final errors to overshoot (see text). Bins of 10°/s are used.

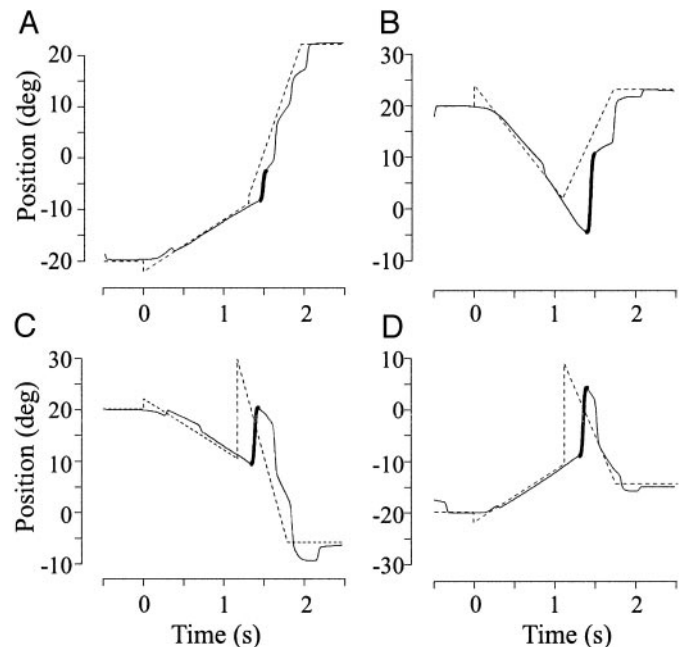


FIG. 7. Examples of catch-up saccades for large values of retinal slip. Solid and dashed lines, the eye and target position, respectively. Catch-up saccades are illustrated by thick segments. A and B: trials for which the sign of R_S and S_{AMP} are the same. They are both undershooting saccades. In A, it is a forward saccade, whereas in B, it is a reverse saccade but the target changes direction after the step. C and D: trials with R_S and S_{AMP} of opposite signs. They are both overshooting saccades. In C, it is a reverse saccade, whereas in D, it is a forward saccade, but the target changes direction after the step.

for forward and reverse saccades. In Fig. 6, a positive final error can be unambiguously interpreted as an undershoot whereas a negative final error corresponds to an overshoot. For moderate values of retinal slip [$\text{abs}(R_S) < 15^\circ/\text{s}$], the average final error does not vary with retinal slip: it is rather small and positive (undershoot). This can be compared with control saccades that show a similar undershoot (Table 1). For values of R_S that are positive and large, the final error increases with retinal slip (undershoot). This can be explained by the fact that the proportion of retinal slip taken into account in saccade programming decreases as R_S increases (Fig. 6). For values of R_S that are negative and large, the final error decreases and changes sign for very large values of R_S (overshoot). Again, this is compatible with the hypothesis that a smaller proportion of R_S is used to program saccades (Fig. 6). This influence of R_S on final error is not an indirect influence of saccade amplitude or position error as we found that the correlation between R_S and S_{AMP} and between R_S and P_E were very small ($R_S|S_{AMP}$: $R = 0.14$; $R_S|P_E$: $R = 0.02$).

Figure 7 illustrates four individual examples of catch-up saccades for large values of retinal slip that illustrate the effects shown in Fig. 6. In Fig. 7, A and D show forward saccades, whereas B and C show reverse saccades. When the value of R_S is positive (Fig. 7, A and B), the final error is positive (undershoot, Fig. 6, right), whereas when the value of R_S is negative (Fig. 7, C and D), the final error is negative (overshoot, Fig. 6, left).

In conclusion, our data show that large values of retinal slip are poorly estimated by the saccadic system and thus there is a nonlinearity in the way R_S is taken into account. Consequently, we separated our data into two groups [$\text{abs}(R_S) < \text{or} > 15^\circ/\text{s}$]

and made two separate multiple regression analyses. *Equations 3 and 4* summarize the results

$$\text{If } \text{abs}(R_S) \leq 15^\circ/\text{s}: S_{\text{AMP}}^* = 0.05 + 0.90 * P_E + 0.109 * R_S \\ (R = 0.986, n = 850) \quad (3)$$

$$\text{If } \text{abs}(R_S) > 15^\circ/\text{s}: S_{\text{AMP}}^* = 0.10 + 0.85 * P_E + 0.090 * R_S \\ (R = 0.980, n = 1975) \quad (4)$$

The coefficient of R_S is about 20% smaller in *Eq. 4*, which is compatible with the interpretation that R_S is underestimated for large retinal slips (Figs. 6 and 7). For small retinal slip data, it is possible to interpret the coefficients of *Eq. 3* by comparing them to the coefficients of *Eq. 2*, which describes an “exact” catch-up saccade. Indeed, under the assumption that the saccadic system has an undershooting strategy of 90% for catch-up saccades, the coefficients of P_E and R_S have to be multiplied by 0.9 in *Eq. 2*. This yields 0.9 for the coefficient of P_E and 0.12 for the coefficient of R_S (mean $S_{\text{DUR}} = 0.074$, cf. Table 1), which are very close to the values reported in *Eq. 3*.

DISCUSSION

Main sequence of catch-up saccades

The analysis of the main sequence of catch-up saccades showed that these movements are composed of two independent components, smooth and saccadic (Figs. 3 and 4). Indeed, the smooth motor command is clearly not interrupted during catch-up saccades but is linearly added to the saccade. Thus when forward, reverse, and control saccades of the same duration are compared, reverse saccades are smaller than control (the smooth command is subtracted) and forward saccades are bigger than control (the smooth command is added). This finding is important because it demonstrates that it is necessary to subtract the smooth contribution to catch-up saccades before their analysis. In contrast, a preliminary report by Jürgens and Becker (1974) showed that there is not a linear addition of saccades and pursuit movements, but these authors did not test a large range of eye velocity and did not include control saccades to fixed targets in their analysis. Two previous studies corrected the amplitude of catch-up saccades by removing the smooth component before analysis (Keller and Johnsen 1990; Smeets and Bekkering 2000), whereas the other studies did not correct catch-up saccades (Gellman and Carl 1991; Heywood and Churcher 1981; Kim et al. 1997; Ron et al. 1989). The results of the present study clearly show that the correction of catch-up saccades is necessary before their analysis. Of course, this correction is typically moderate for catch-up saccades during pursuit initiation because smooth eye velocity is usually low for these movements. In contrast, this correction can be very large for catch-up saccades during sustained pursuit, where the smooth eye velocity is much larger.

Catch-up saccade latency

In our multiple regression analysis, we showed evidence that position error and retinal slip determine catch-up saccade amplitude. The estimation of these two parameters is based on visual signals, and it takes some time to have them available for catch-up saccade programming. For saccades to stationary targets, Becker and Jürgens (1979) used double-step stimuli

and reported that 100 ms is the shortest latency for the second step to influence saccade amplitude. In our study, the target was moving and the value of this minimum latency might have been different. However, we found that this minimum latency was very similar to what has been reported for stationary targets. We based our analysis on the precision of catch-up saccades by comparing the error between final eye position and first- or second-ramp target position (Fig. 5). We specifically tested trials with different ranges of P_E and R_S and reported latency values between 80 and 100 ms. This shows that both P_E and R_S are available to the oculomotor system around 100 ms before catch-up saccade onset.

Catch-up saccade programming

Classically, it has been suggested that target velocity is taken into account in the programming of catch-up saccades. This assumption was based on the observation that catch-up saccades during pursuit initiation are rather precise (Robinson 1965). Several behavioral studies investigated the issue of catch-up saccade programming. First, Heywood and Churcher (1981) could not find any influence of target velocity on catch-up saccades, whereas all subsequent behavioral studies demonstrated that target motion was taken into account in catch-up saccade programming. Indeed, Gellman and Carl (1991) and Keller and Johnsen (1990) studied first catch-up saccades during pursuit initiation and found an influence of target velocity on the amplitude of saccades. Ron et al. (1989) and Kim et al. (1997) studied both first and subsequent catch-up saccades (during pursuit maintenance) and found a contribution of target velocity. However, in these studies, it was never possible to clearly identify the relative role of target velocity, retinal slip, and eye velocity in catch-up saccade programming. Indeed, either the eye velocity was very low (pursuit initiation, i.e., 1st catch-up saccades) and target velocity was highly correlated with retinal slip or the retinal slip was very low (pursuit maintenance, i.e., subsequent catch-up saccades) and target velocity was highly correlated with eye velocity. More recently, de Brouwer et al. (2001) showed in the cat that the amplitude of catch-up saccades was correlated with position error and retinal slip. Because of the large range of pursuit gain in the cat, it was possible in this study to distinguish the role of target velocity, retinal slip, and eye velocity in a multiple regression analysis. In the present human study, it was necessary to combine position steps and velocity steps of the target to evaluate the contribution of target velocity, eye velocity, and retinal slip to catch-up saccade programming. The conclusion of this investigation was that catch-up saccade amplitude was correlated with both position error and retinal slip.

Link with physiology

Several lesion studies reported deficits in the ability of subjects to make accurate catch-up saccades during smooth pursuit. It was hypothesized that these lesions were located in the visual motion pathway such that the capability to evaluate target velocity (or retinal slip) and to integrate it in the programming of catch-up saccades was impaired. In the monkey, Newsome et al. (1985) made lesions in the middle temporal visual area (MT) and showed a reduction of smooth pursuit

gain together with a deficit in catch-up saccade accuracy. May et al. (1988) made lesions in the dorso-lateral pontine nuclei (DLPN) and reported deficits in steady-state pursuit and pursuit initiation. After lesion, their monkeys made hypometric saccades to moving targets, whereas saccades to stable targets were accurate. A clinical study by Thurston et al. (1988) investigated patients with unilateral cerebral lesions in occipito-temporal cortex (the probable homologue of MT) and reported an inability to make accurate saccades to moving targets in the hemifield contralateral to the lesion, a result very similar to the effects of MT lesions in the monkey.

The contribution of retinal slip to catch-up saccades is probably conveyed by the motion processing pathway which involves MT, MST, DLPN, and the cerebellum. At the level of subcortical structures, Keller et al. (1996) recorded saccade related burst neurons in the superior colliculus (SC) during catch-up saccades and showed that those neurons do not encode the full amplitude of catch-up saccades but only the term proportional to position error. This seems to indicate that the addition of the position error and retinal slip contributions to catch-up saccades occurs downstream from the SC. However, it cannot be excluded that this is performed by other types of SC cells. Two other areas are good candidates for the integration of position error and retinal slip contributions to catch-up saccades. First, there is the nucleus reticularis tegmenti pontis (NRTP), which is known to be involved in the control of saccades (Crandall and Keller 1985). Chemical lesions (Suzuki et al. 1999) and microstimulation studies (Yamada et al. 1996) indicated that NRTP could also affect the smooth pursuit response. Second, another possible site of integration of P_E and R_S components is the cerebellar vermis, which receives strong projections from NRTP (Matsuzaki and Kyuhou 1997) and has been proposed to play a central role in the control of saccades (Lefèvre et al. 1998; Quaia et al. 1999). Moreover, microstimulation studies have shown that the oculomotor vermis could evoke both saccade and smooth eye movement responses (Krauzlis and Miles 1998) and lesions in the vermis affect both saccades (Takagi et al. 1998) and pursuit (Takagi et al. 2000).

Catch-up saccade accuracy

In this study, we showed, on the basis of a multiple regression analysis, that both position error (P_E) and retinal slip (R_S) are used to program catch-up saccades (Eq. 1). In this analysis, P_E and R_S were evaluated 100 ms before saccade onset as we showed that both sensory signals are adequately estimated by the oculomotor system for catch-up saccades with a latency larger than 90 ms. However, it is important to notice that the influence of both P_E and R_S was significant when these variables were evaluated over a very wide range of time delays (from 150 ms before saccade onset to saccade onset, $P < 0.01$). Thus the role played by R_S in catch-up saccade programming seems to be a robust observation.

For values of R_S in the range of $\pm 15^\circ/\text{s}$, the amplitude of R_S did not influence saccade precision (Fig. 6) and catch-up saccades slightly undershot the target. This observation was similar to what has been classically described for normal saccades to stable targets (Becker 1991). However, for values of R_S beyond the range of $\pm 15^\circ/\text{s}$, the precision of saccades was dramatically influenced by R_S (Fig. 6). For R_S larger than $15^\circ/\text{s}$, the undershoot increased with R_S , whereas for R_S smaller than

$-15^\circ/\text{s}$, the undershoot decreased and became an overshoot for very large values of R_S (Fig. 6). Given the format of Eq. 1, this observation is compatible with the hypothesis that there is a saturation in the evaluation of R_S for large values of this physical parameter. Indeed, this would lead to saccades that are too short for positive R_S and saccades that are too large for negative R_S (Eq. 1, Fig. 6). This putative saturation in the evaluation of R_S could be explained by several observations of saturation at different levels in the visual and motion processing pathways. Saturation has been reported at the level of the retina (Barlow et al. 1964; Oyster 1968), of the nucleus of the optic tract (NOT) (Collewijn 1975) and of the visual cortex (Orban et al. 1981). In addition, smooth pursuit eye movements, for which retinal slip is the prominent input, also exhibit a saturation in the motor response for large values of retinal slip (Lisberger et al. 1981).

The first finding in this paper establishes that there is a continuous superposition of both saccadic and pursuit commands. This observation is compatible with the classical view that the two components of voluntary tracking eye movements, saccades and smooth pursuit, are distinct oculomotor subsystems with very different control mechanisms. However, the second major finding of this study, that sensory signals (such as the retinal slip) are shared by both systems, confounds the strict dichotomy between smooth pursuit and saccadic systems. In conclusion, this paper, in complement with recent neurophysiological and behavioral studies (de Brouwer et al. 2001, 2002; Missal et al. 2000), reveals many interactions existing between the two systems.

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