

Saccade–Pursuit Interactions

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Introduction

Saccades are typically evoked by target steps, whereas pursuit eye movements are initiated by a moving target of interest. These two types of eye movements have been studied separately for years because it was thought that pursuit and saccadic systems were independent and were controlled by distinct cortical and subcortical networks (see [Figure 1](#)). Initially, scientists developed paradigms to elicit one of the two types of eye movements without any disruption by the other; that is, saccades were directed to stationary targets and the Rashbass paradigm was used to elicit pure smooth eye movements. Indeed, if a visual target first steps in one direction before moving in the opposite direction (this typical motion of the target is called the Rashbass paradigm), the probability of occurrence of saccades is strongly reduced during pursuit initiation. In contrast, if a target suddenly moves from the center in one direction, a catch-up saccade (saccade made during pursuit of a target to reduce the position error between the eye and the moving target) is necessary to foveate the target.

The Rashbass paradigm is essentially used in species, such as primates, that have a pursuit gain close to unity (the ratio between eye and target velocity). This high gain allows primates to pursue a moving target smoothly. In contrast, the smooth eye velocity of cats saturates at lower velocities (around 25°s^{-1}), and their pursuit gain is much more variable. As a consequence, cats usually rely on a combination of smooth and saccadic eye movements to pursue a moving target. In addition, cats have difficulties to make large saccades but, instead, usually perform series of small saccades to achieve large gaze shifts. During the intersaccadic intervals, postsaccadic slow eye movements directed toward the stationary target help reduce the residual error at the end of saccades. Thus, cats need a combination of both saccadic and smooth eye movements either to shift their gaze or to pursue a moving target.

After some preliminary observations of saccade–pursuit interaction in primates, major progress was achieved with cat studies. Indeed, the low gain of eye movements in this species forces the two subsystems to cooperate in order to foveate the target. Thereafter, scientists began to design new paradigms to test the

hypothesis of cooperation between the two oculomotor subsystems in primates. We now focus on these paradigms and the evidence of interactions they provided. We first describe evidence for shared velocity and position inputs to the saccadic and pursuit systems. We then examine the different mechanisms that are common to both oculomotor subsystems. Finally, we review the brain areas that were proven to contain signals related to the planning and execution of both pursuit and saccades.

Velocity Input to the Saccadic System

In contrast with the classical view of independent saccadic and pursuit systems (see [Figure 1](#)), lesions and behavioral studies demonstrated that there is a velocity input to the saccadic system. Lesions in brain areas (the middle temporal area (MT) or dorsolateral pontine nuclei (DLPN)) that are known to be prominent for motion processing disrupt the accuracy of saccades to moving targets without impairing saccades to stationary targets. Furthermore, the accuracy of catch-up saccades during pursuit initiation and maintenance implies that target motion is taken into account in their programming. Finally, the Rashbass paradigm itself shows that a prediction about future target motion (based on target velocity) is taken into account by the saccadic system. Indeed, after an initial step, the target moves toward the center of the visual field and the oculomotor system predicts that no saccade is necessary to catch the target but, instead, that a purely smooth movement is sufficient. Indeed, if the saccadic system did not have access to motion signals, it would trigger a saccade to the target in the direction opposite to target motion. All these experiments contributed to the accumulation of evidence showing that motion signals play a role in saccade programming and trigger but did not discriminate which parameter related to target motion (target velocity or velocity error) is taken into account. Indeed, these two parameters are highly correlated during pursuit initiation because eye velocity is very small in comparison with target velocity.

The first evidence for a prominent role of the retinal slip (RS, velocity error) came from cat studies and was confirmed later in humans. Cat experiments took advantage of the large variability of pursuit gain in this species, which yields a large range of RS for the same target velocity. Because the pursuit gain of primates is much larger and less variable, an original paradigm involving both position and velocity steps of the moving target was used to elicit catch-up

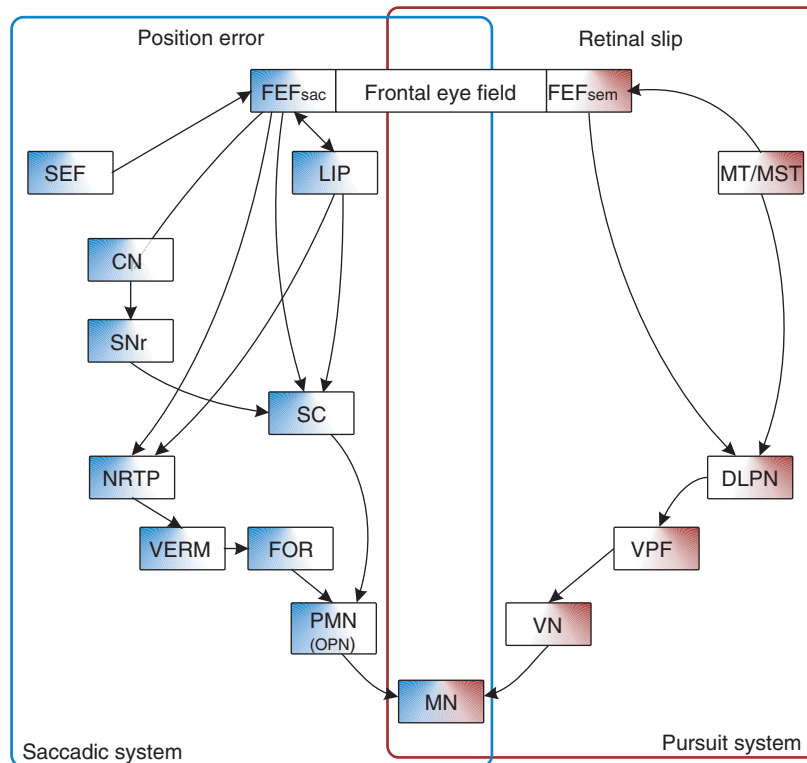


Figure 1 Diagram of the traditional view of saccadic and pursuit systems. Blue boxes are part of the saccadic system. Red boxes belong to the pursuit system. Two-color boxes are part of both systems. CN, caudate nucleus; DLPN, dorsolateral pontine nuclei; FEF_{sac}, saccadic region of the frontal eye field; FEF_{sem}, pursuit region of the frontal eye field; FOR, fastigial oculomotor region; LIP, lateral intraparietal area; MN, motor neurons; MST, medial superior temporal area; MT, middle temporal area; NRTTP, nucleus reticularis tegmenti pontis; OPN, omnipause neurons; PMN, brain stem premotor nuclei; SC, superior colliculus; SEF, supplementary eye field; SNr, substantia nigra pars reticulata; VERM, vermis; VN, vestibular nuclei; VPF, ventral paraflocculus.

saccades during pursuit of a moving target. This paradigm (ramp–step–ramp paradigm) consisted in a first ramp that was followed by a step of the target and a second ramp. During the step, both target position and velocity varied instantaneously and randomly before the second target ramp. The position and velocity steps created both position error (PE) and RS. To compensate for these errors, the oculomotor system combined catch-up saccades and pursuit responses.

In cats and primates, the amplitude of catch-up saccades results from the addition of two components: one related to PE that represents the proportion of PE that is taken into account by the catch-up saccade (on average, 90%) and another proportional to RS that compensates for target motion during the saccade. Some electrophysiological recordings suggest that the contribution of PE might be conveyed by the superior colliculus (SC), whereas the contribution of RS originates from the motion-processing pathway (through the MT).

The processing of the two components by different networks was confirmed by the asynchrony of signals related to PE and RS. This asynchrony has been

demonstrated separately with the ramp–step–ramp paradigm in two dimensions, on one hand, and by the shape of catch-up saccade velocity profiles, on the other hand. The two-dimensional ramp–step–ramp paradigm yielded curved catch-up saccades (large differences between the initial and final orientation of saccades). The asynchrony between PE and RS could be inferred from the difference between initial and final orientations of saccades that were aligned with the PE and RS vectors, respectively (see [Figure 2](#)). Similarly, the asymmetry of the shape of the velocity profile of catch-up saccades highlighted the asynchrony between PE and RS. The acceleration phase was related to PE and the deceleration phase to RS. These two results show that PE is available to the saccadic system earlier than RS because in both cases saccades take first PE into account and subsequently RS.

In addition, it has been demonstrated that both PE and RS influence the mechanism leading to the initiation of a catch-up saccade (trigger system) during ongoing smooth pursuit ([Figure 3](#)). The combination of PE and RS determines the time-to-contact between eye and target (eye-crossing time: $T_{XE} = -PE/RS$),

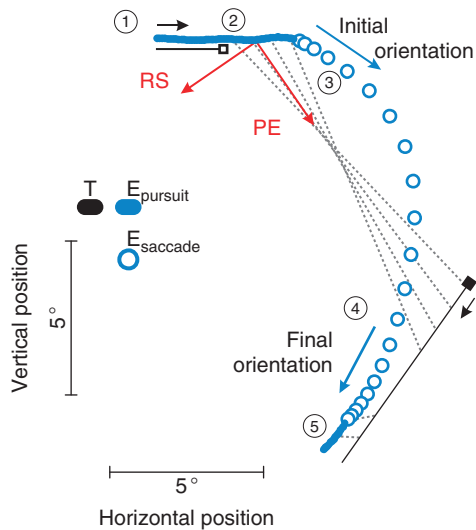


Figure 2 Velocity input to the saccadic system. A curved saccade (blue circles) occurring after both position and velocity steps of the target (black solid lines) is presented in two dimensions. The target position just before and after the target step is represented by the open and closed squares. Before and after the saccade, smooth pursuit eye movements (solid blue lines) are present to track the target. The gray dotted lines represent isochronic lines that connect eye and target at the same moment in time. Red arrows give the position error (PE) and retinal slip (RS) orientation before the saccade; blue arrows give the initial and final orientation of the eye at the start and end of the saccade, respectively, and black arrows indicate the direction of motion of the pursuit target. (1) Start of the trial: The eye smoothly pursues the rightward moving target. (2) Target step: From target step to the onset of the saccade, PE and RS are evaluated. (3) The saccade is elicited with an initial orientation close to the orientation of PE. (4) The saccade ends with a final orientation close to the orientation of RS. (5) After the saccade, pursuit is engaged to the target and the eye is very close to the target, as shown by the isochronic lines after the saccade. T, target; E, eye.

that is, the time that the eye trajectory would need to cross the target at constant velocity, which is used as a criterion to switch from pursuit mode to saccade mode. As long as the value of this sensory parameter remains in the smooth zone (between 40 and 180 ms), no saccade is needed to track the target. However, when the eye-crossing time takes values outside the smooth zone (i.e., inside the saccade zone), the decision to trigger a saccade is taken because the smooth pursuit system cannot compensate anymore for the position mismatch between eye and target. Therefore, a saccade takes place, on average, 125 ms later.

Finally, it has been shown that the saccadic and smooth pursuit systems cooperate despite the absence of retinal signals. For example, when directing gaze toward the remembered position of a flashed target, the saccadic system is able to take into account the smooth eye displacement (the integral of smooth eye velocity). This has been demonstrated during ongoing

pursuit of a moving target but also in the dark during anticipatory smooth eye movements. In this case, the estimation of the smooth eye displacement is based on extraretinal information about the smooth eye movement. Furthermore, it has also been shown that during the temporary occlusion of a moving target, the saccadic system takes into account and can compensate for the modulation of the smooth response in complete darkness. These observations are evidence for the role of extraretinal signals and the existence of a velocity input to the saccadic system.

In conclusion, the saccadic system has access to retinal information about relative eye and target velocity (RS), as well as to extraretinal information about smooth eye velocity. This velocity input is available later than the position input, and these signals are combined to estimate the eye-crossing time, which determines whether a catch-up saccade should be triggered or not. The velocity input used by the saccadic system originates from the motion-processing pathway.

Position Input to the Smooth Pursuit System

The first reports of a position input to the smooth pursuit system in primates were based on indirect evidence because stationary targets do not evoke smooth eye movements in this species. In contrast, cats use a combination of small saccades and slow correcting eye movements to shift their gaze to an eccentric stationary target. Thus, studies in this species provided direct evidence of a position input to the smooth pursuit system. In primates, new paradigms needed to be developed to address this question specifically.

PE, either induced by target stabilization on to the retina or by target steps during ongoing pursuit, gave the first evidence of a position input to the primate smooth pursuit system. Target stabilization consists in making the target move at the same velocity as the eye, which stabilizes the projection of the target on to the retina. The stabilization of the target with a small offset with respect to eye position evokes slow eye movements directed toward the target either during fixation or ongoing pursuit. Similarly, target steps provided evidence of slow eye movements in response to a position error. If during smooth pursuit the target steps but continues to move at the same speed, slow eye movements are modulated by the amplitude of the step (i.e., the amplitude of the position error).

However, in these studies, the influence of PE was not direct or could be perturbed by other factors, such as concurrent RS. The first direct evidence of a

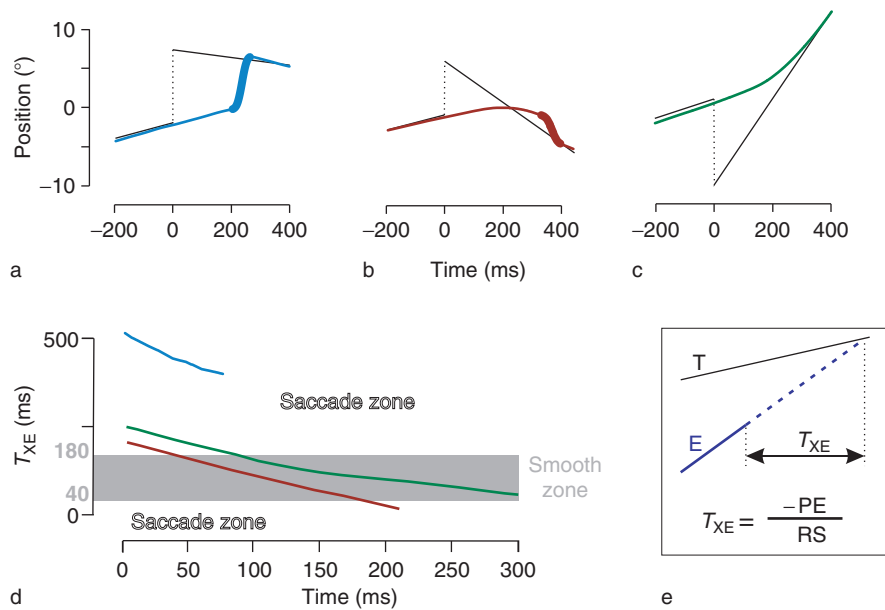


Figure 3 Saccade trigger: (a) early-saccade trial; (b) late-saccade trial; (c) smooth trial (no saccade); (d) the evolution of the eye-crossing time (T_{XE}) versus time for the three trials; (e) T_{XE} , the time that the eye trajectory would need to cross the target at constant velocity. Panels (a)–(c) show the position versus time representation of eye and target (black traces) during three different trials of a ramp–step–ramp paradigm along the horizontal axis. This paradigm consists of a moving target (first ramp) followed by a target jump (position step, represented by the dotted black lines) and a change in target velocity (velocity step) occurring at the same time (time zero on figure). The target then continues to move at constant velocity (second ramp). In panel (a), the latency of the saccade is around 200 ms; in panel (b), the latency of the saccade is around 350 ms. Panel (d) shows how the decision to trigger a catch-up saccade is taken based on T_{XE} . The T_{XE} is represented until 125 ms before the saccade. The smooth zone corresponds to the values of T_{XE} that do not trigger catch-up saccades because the pursuit system can compensate for position error (PE). In contrast, the saccade zone contains values of T_{XE} that trigger a catch-up saccade. For the early-saccade trial, T_{XE} lies far from the smooth zone and the decision to trigger a saccade is taken quickly. In contrast, for the late-saccade trial, T_{XE} lies outside the smooth zone at target step but soon enters the smooth zone for 150 ms before leaving it. As soon as the parameter leaves the smooth zone, the decision to trigger a saccade is taken. Finally, for the smooth trial, T_{XE} quickly enters the smooth zone but never leaves it; therefore, no saccade is triggered. E, eye; RS, retinal slip; T, target.

position input to the pursuit system was provided by flashing a target aside from the pursuit target path (see Figure 4). In this paradigm, subjects pursued a spot moving along a straight line. During pursuit maintenance, a second target was briefly flashed aside from the target path. This flash created a position error with a component orthogonal to the target path. This component of position error generated by the flash evoked smooth eye movements orthogonal to the direction of pursuit, directed toward the flash and scaled to the position error created by the flashed target.

Apart from all the behavioral experiments conducted to assess the influence of a position input on the smooth pursuit system, it has been shown that the stimulation of the cat SC, an area classically involved in the saccadic pathway, produces such postsaccadic slow eye movements. In addition, it has been demonstrated that the saccadic and smooth pursuit systems share a PE signal at the level of the SC in primates. In this species, recordings in the rostral SC showed that

it codes small PEs during both smooth pursuit and saccades. Apart from well-established role of the SC in saccades, this shows evidence for the implication of the SC in saccade pursuit interaction.

In conclusion, evidence from several behavioral studies shows that PE influences the smooth pursuit system. Moreover, SC was proven to be the place where both saccade and pursuit systems share the PE signal, highlighting the role of SC in saccade-pursuit interaction.

Common Mechanisms for Initiation and Cancellation

Up to now, we have shown that both systems share common inputs. Indeed, PE and velocity error are used by both oculomotor subsystems. These two subsystems may either process their inputs independently or share some processes in transforming visual inputs into motor commands. We now review which processes are likely to be shared by both systems.

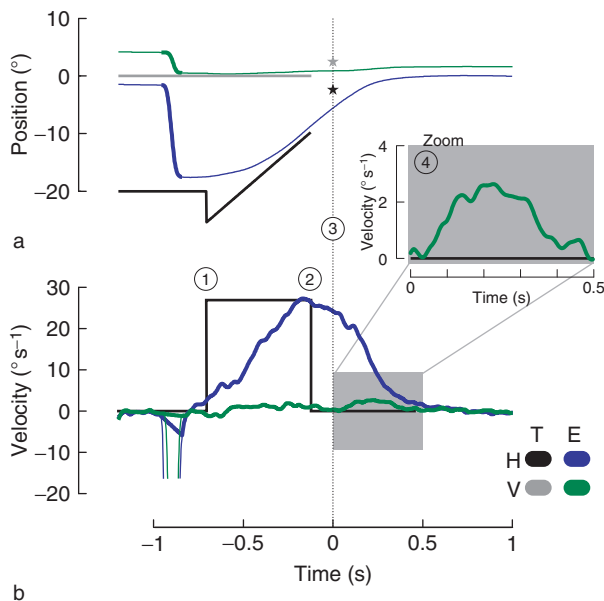


Figure 4 Position input to the pursuit system: (a) horizontal and vertical position of the eye and the target are presented as a function of time; (b) velocity of the eye and the target are presented as a function of time. The inset represents a zoom of the vertical eye velocity profile. (1) The pursuit target starts moving rightward. (2) The pursuit target disappears. (3) A target is flashed for 10 ms above the target path (slight vertical offset, see the gray (black) star that represents vertical (horizontal) flashed target position). (4) The vertical offset of the flash elicits a vertical smooth eye movement, which is orthogonal to the pursuit path. E, eye; H, horizontal; T, target; V, vertical.

Initiation

The latency of saccadic and pursuit eye movements have always been shown to differ. On average, the latency of saccades to stationary targets is around 200 ms, whereas the latency of smooth pursuit eye movements is around 100 ms. This discrepancy between smooth pursuit eye movements and saccades suggests that the initiation mechanisms are different. However, several paradigms have shown similar effects on the latency of both saccades and smooth pursuit. Their latency is shortened when the fixation point is extinguished prior to the appearance of the target (gap paradigm). The reduction in latency caused by the gap paradigm is very similar (around 50 ms) for both oculomotor subsystems. Neuronal correlates of the gap effect have been found in the SC for both types of eye movements when the buildup activity that occurs before saccade or pursuit is increased by the presence of a gap. Similar to the gap effect, the presence of a second moving target (a distractor) also modulates the latency of both pursuit and saccades in the same way (an increase in latency). Finally, when a first target is extinguished after the appearance of a new target (overlap paradigm), latencies of pursuit and saccades

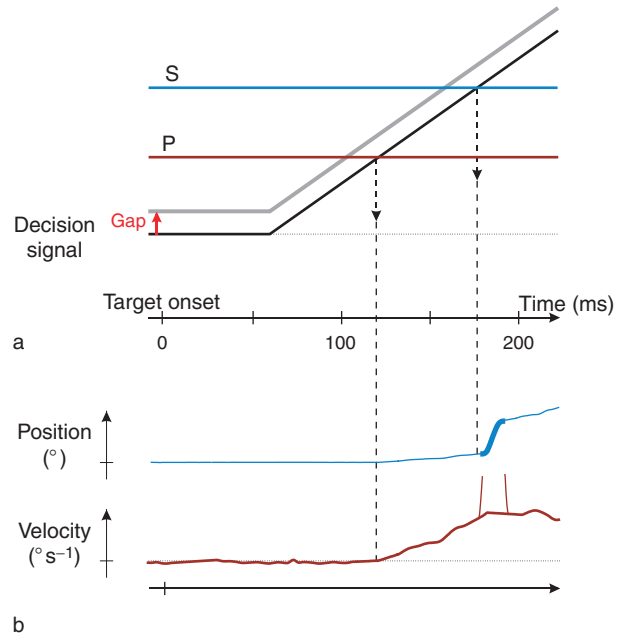


Figure 5 (a) Initiation mechanism; (b) corresponding eye position and velocity as a function of time. In panel (a), the initiation mechanism is represented by a linear rise to threshold process. After a given delay following target onset, the decision signal (black curve in no-gap condition) rises to two different thresholds (pursuit (P) in red and saccade (S) in blue). After the decision signal has reached a specific threshold, the corresponding eye movement is triggered (panel (b)). In the gap condition, the initial level of the decision signal is increased at target onset (gray curve).

are comparable and highly correlated. These similar changes in latency suggest a common mechanism for the initiation of pursuit and saccades.

A linear rise to threshold model, in which a decision signal evolves toward a threshold, makes good prediction of saccade latency. As soon as this threshold is reached by the decision signal (see Figure 5), the intended action is initiated. In the case of saccade and pursuit initiation, a similar model can be used. A common decision signal linearly rises to two different thresholds (one for pursuit and a second higher one for saccades) to elicit eye movements. The crossing of one of the thresholds implies the trigger of the corresponding eye movement after some motor delay (different for pursuit and saccades). This model can account for the gap effect if it is assumed that the presence of a gap increases by the same amount the initial level of the decision signal and, hence, reduces the time needed to reach the threshold for both pursuit and saccades.

Cancellation

In a complex environment, it is often necessary to inhibit an action as circumstances that led to its

planning can change rapidly. In the oculomotor domain, a stop signal could be issued before the initiation of a movement, requiring the cancellation of the prepared eye movement. For both the saccadic and smooth pursuit systems, the probability of cancellation of the planned eye movement depends on the delay between the go signal (stimulus onset) and the stop signal. If the stop signal arises just after the go signal, the eye movement can easily be canceled; however, if it arises 200 ms later, it cannot. On average, the stop signal must be issued 60 ms before pursuit initiation for it to be canceled. Similarly, the interval between the stop signal and saccade initiation must be 80 ms to be efficient. In sum, it was found that it takes an additional 20 ms to cancel a saccade compared with smooth pursuit cancellation, suggesting that cancellation mechanisms are different for saccades and smooth pursuit.

At the neurophysiological level, cancellation of both saccadic and pursuit eye movements is mediated through omnipause neurons (OPNs, located in the brain stem). Indeed, OPNs exert an inhibitory control on the excitatory burst neurons that generate saccades, and their stimulation interrupts ongoing saccades. OPNs are also modulated during smooth pursuit eye movements, and their electrical stimulation reduces ongoing smooth eye velocity. Therefore, these results suggest that a common inhibitory group of neurons could regulate the cancellation of both saccades and pursuit. The common inhibitory neuronal population makes us think that there is a common cancellation mechanism, but it does not explain the additional delay required to cancel a saccade compared with canceling a pursuit.

Thus, the discrepancy between the cancellation delay for both saccades and smooth pursuit is probably not due to different cancellation mechanisms. Indeed, saccadic latency is measured with an eye acceleration or velocity threshold. However, 20 ms before saccade initiation, there is a point of no return for saccades. Indeed, around 20 ms before saccade onset, the OPNs are inhibited and excitatory burst neurons are activated. Therefore, under natural conditions, it is not possible to cancel saccades during this 20 ms interval. Such point of no return does not exist for pursuit. Therefore, when we take the point of no return into account instead of saccadic latency, the time needed to cancel any eye movement (either saccade or pursuit) is comparable (around 60 ms). In sum, the same inhibitory neurons could be involved in canceling saccades and pursuit eye movements. However, the details of the inhibitory process might differ between oculomotor subsystems.

Common Processes

In addition to shared inputs, saccade and pursuit systems share common processes. The initiation mechanism was proven to be common for saccades and pursuit on the basis of the similar modulation of saccade and pursuit latencies in different paradigms and on the basis of neurophysiological recordings in the SC. The proof of a common cancellation mechanism was yielded by a behavioral study on action inhibition and by a neurophysiological study in the brain stem. A third mechanism is also shared by saccadic and pursuit systems – the target-selection mechanism. This was demonstrated on the basis of target-selection paradigms and recordings in the SC (and not described here).

Other Brain Areas Subserving Both Saccades and Pursuit

In contradiction with the classical view of totally segregated systems (see [Figure 1](#)), the cortical networks of pursuit and saccades are anatomically overlapping. Among the cortical overlapping areas, some contain distinct neuronal populations for pursuit and saccades, such as the frontal eye fields (FEFs); others contain a neuronal population conveying both saccadic and pursuit signals, such as the supplementary eye fields (SEFs).

Subcortical areas generally contain a population of neurons subserving both saccades and pursuit. A subset of these subcortical areas that contain shared neuronal populations takes part in the descending pathway from the cerebral cortex toward the motor nuclei: the substantia nigra (SNr), the DLPN, the SC, and other brain stem regions (vestibular nuclei, nucleus of the optic tract, and interstitial nucleus of Cajal). Other areas containing neurons that convey both position and velocity signals take part in the ascending pathway that relays signals from premotor/motor nuclei toward cortical areas and/or form an internal feedback pathway of the ongoing eye movement: the cerebellum (vermis and fastigial oculomotor region) and the thalamus. On the other hand, the caudate nucleus (CN) contains two mainly segregated populations that convey pursuit and saccade signals separately.

Brain areas subserving saccades and pursuit contain either distinct neuronal populations for pursuit and saccades (the FEFs and CN) or a single population of neurons that conveys both pursuit and saccade signals (e.g., SNr, dorsal pontine nuclei, cerebellum, and thalamus), corresponding either to parallel or

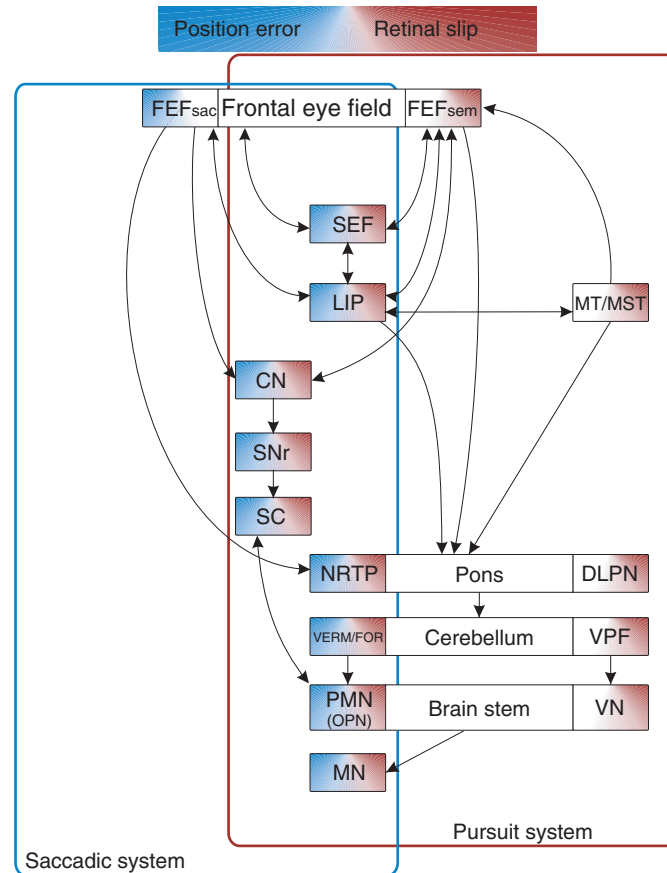


Figure 6 Diagram of the current view of saccadic and pursuit systems. Blue boxes are part of the saccadic system. Red boxes belong to the pursuit system. Two-color boxes are part of both systems. CN, caudate nucleus; DLPN, dorsolateral pontine nuclei; FEFsac, saccadic region of the frontal eye field; FEFsem, pursuit region of the frontal eye field; FOR, fastigial oculomotor region; LIP, lateral intraparietal area; MN, motor neurons; MST, medial superior temporal area; MT, middle temporal area; NRTP, nucleus reticularis tegmenti pontis; OPN, omnipause neurons; PMN, brain stem premotor nuclei; SC, superior colliculus; SEF, supplementary eye field; SNr, substantia nigra pars reticulata; VERM, vermis; VN, vestibular nuclei; VPF, ventral paraflocculus.

shared brain structures. The current view of the saccade and pursuit networks has thus evolved toward a more integrated network, subserving both oculomotor systems (see [Figure 6](#)).

Conclusion

In recent years, our view of the interaction between the smooth and saccadic systems has completely changed. From the two separate networks, a more unified scheme of the oculomotor system has emerged step by step. In this article, we highlight all the inputs, processes, and brain areas that are shared by the pursuit and saccadic systems. We emphasize that, even though they are computed by different networks, PE and RS influence both oculomotor subsystems. Finally, we underline the integration of common initiation and cancellation mechanisms and the numerous brain areas involved in both subsystems, even if, for the

majority of them, their precise role in the saccade-pursuit interaction needs to be further investigated.

See also: Attention and Eye Movements; Oculomotor Control: Anatomical Pathways; Oculomotor System: Models; Pursuit Eye Movements; Saccades and Visual Search; Saccadic Eye Movements; Superior Colliculus; Target Selection for Pursuit and Saccades; Vergence Eye Movements.

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