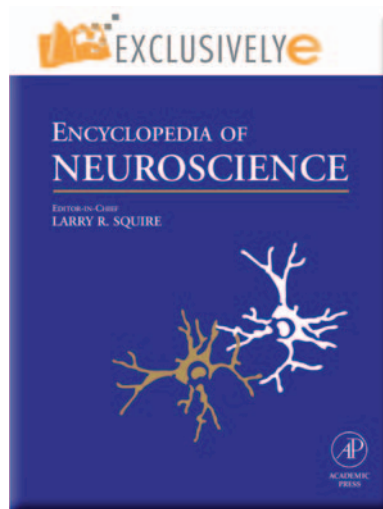


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Krauzlis R J and Chukoskie L (2009) Target Selection for Pursuit and Saccades. In: Squire LR (ed.) *Encyclopedia of Neuroscience*, volume 9, pp. 863-868. Oxford: Academic Press.

Target Selection for Pursuit and Saccades

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Introduction

When we visually inspect our surroundings, we typically direct our line of sight to objects or features of particular interest, even when those items move. These eye movements are under voluntary control and involve selectively sampling the visual environment because tracking one visual object typically causes the retinal images of other objects to become blurred. Accordingly, these voluntary eye movements are found only in animals that have retinal specializations, such as the primate fovea, that can be used to examine a limited region of visual space at a higher spatial resolution.

There are two types of voluntary eye movements used by animals with foveal vision (illustrated in [Figure 1](#)). The first type is saccadic eye movements, which act to quickly move the image of a visual target from an eccentric retinal location to the center of the retina, where it can be seen best. Saccades are rapid movements, reaching peak speeds of several hundred degrees per second and lasting only tens of milliseconds. Consequently, although saccades are typically evoked by stimulus events at latencies of 150–250 ms, the trajectory of saccades is not guided by sensory feedback. Instead, saccades follow a stereotyped profile that depends on the amplitude of the movement. Saccades are typically triggered by visual stimuli, but they can be evoked and guided by other stimulus modalities and can also be directed toward the location of imagined or remembered targets.

The second type of voluntary eye movements is called smooth pursuit, which slowly rotates the eyes to compensate for any motion of the visual target and thus acts to minimize the blurring of the target's retinal image that would otherwise occur. Smooth pursuit is a relatively slow movement whose trajectory is determined by the moving stimulus. Pursuit is triggered by visual stimuli at latencies similar to, but somewhat shorter than, the latencies of saccades (typically 100–200 ms) and generates eye velocities up to approximately 50°s^{-1} , continuously adjusted by visual feedback about the target's retinal image. Unlike saccades, pursuit cannot be generated in the absence of a stimulus, although moving targets that are sensed through modalities other than vision can also guide pursuit.

As this brief overview indicates, saccades and pursuit have very different properties. The neural mechanisms for the two types of movements have also been conventionally viewed as involving distinct neuroanatomical circuits. However, during normal behavior the two types of movements are tightly coordinated and almost always act to stabilize the same visual stimulus on the retina ([Figure 1](#)). Results from recent behavioral and physiological studies have provided insights into how the coordination between these two motor systems is achieved.

Gating of Pursuit and Saccades

The initiation of both pursuit and saccades involves a break from the state of fixation, which otherwise keeps the eyes from shifting to the new target. This break from fixation is controlled by similar factors for pursuit and saccades, and can be either facilitated or inhibited, depending on the circumstances. In the gap paradigm, the break from fixation is facilitated by manipulating the temporal sequence in which the visual stimuli are presented. In a typical simple eye-movement task, a second target is presented at an eccentric position immediately after the initial foveated target has been extinguished, and saccades and pursuit are evoked at latencies of approximately 150–200 ms. However, in the gap paradigm, the initial foveated stimulus is turned off a few hundred milliseconds before the eccentric target appears, and this simple change consistently reduces the latencies of saccades and pursuit, typically by approximately 20 ms. The decreases in pursuit and saccade latencies show the same dependency on the duration of the gap, suggesting that the release of fixation for the two movements depends on a shared preparatory signal.

Conversely, the inhibition of pursuit and saccades also appears to involve a shared mechanism. In the countermanding paradigm, the break from fixation is inhibited by presenting a stop signal indicating to the subjects that they should cancel the movement that had been previously planned. By varying when this stop signal is presented relative to the go signal (e.g., the appearance of the eccentric visual target), it is possible to calculate how much time is required to cancel the movement. The calculation is complicated by the fact that the final motor pathways for pursuit and saccades are different – in particular, the generation of saccades appears to include an approximately 20-ms ballistic interval that is not present for pursuit. However, once these differences are taken into account, it has been found that the time

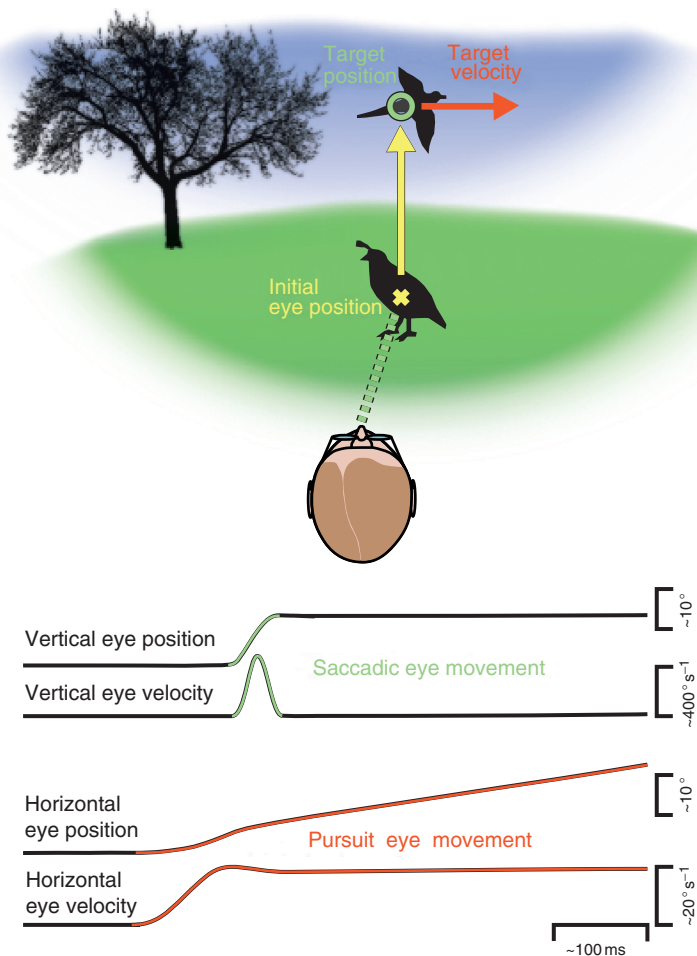


Figure 1 The selection of targets for saccades and pursuit is normally tightly coordinated. In this example, the observer's initial eye position is aligned on a quail standing in the grass. To stabilize the image of the dove flying overhead, the observer makes a coordinated combination of saccadic and pursuit eye movements. The saccade rapidly changes eye position (in this case, primarily vertically) based on the position of the new target, as highlighted in green in the traces of eye position and velocity. The pursuit movement smoothly adjusts the velocity of the eyes (in this case, primarily horizontally) based on the velocity of the same selected target, as highlighted in red in the traces.

taken to stop either a pursuit or saccadic eye movement is approximately 50–60 ms. Moreover, both movements show an effect of trial sequence. Pursuit and saccade latencies are longer if the previous trial contains a stop signal than if it does not. These differences occur regardless of whether the previous trial involves the same or different type of eye movement response, showing that the effect involves a shared inhibitory mechanism.

Target Selection for Pursuit and Saccades

In addition to determining whether and when to break fixation, saccades and pursuit also depend on selecting one visual target from among the various candidates within the visual scene. It is well established that the latencies of saccades increase when observers must search the visual field for a unique

target among a set of stimuli and that these increases depend on the difficulty in finding the target. Similar increases in latency have been observed for pursuit eye movements when an observer must choose between two stimuli moving in opposite directions. These latency effects suggest that a target selection process might precede the initiation of both pursuit and saccades, but they do not resolve whether these effects are due to a single process or to similar but independent processes. To address the linkage between the two movements, it is necessary to consider the two movements together during the process of selection. Recent studies have addressed this challenge and have produced evidence in favor of two different hypotheses about how target selection for pursuit and saccades is coordinated.

One possibility is that target selection for pursuit is determined by the generation of saccades. When

pursuit of a moving target is initiated, it is typically accompanied by saccades that eliminate the mismatches between eye and target position that were left uncorrected by the pursuit movement. The pursuit eye velocity after the corrective saccade is usually much closer to target velocity than it was prior to the corrective saccade and higher than that observed at comparable times in trials without corrective saccades. This postsaccadic enhancement of pursuit suggests that the execution of the saccade improves the ability of the pursuit system to track the target. A closely related finding occurs when subjects initiate pursuit in response to two stimuli that move in orthogonal directions but subjects are not told at the outset which of the two will be the target. Because the target identity is not known initially, subjects begin smooth pursuit in a direction that tends toward the average of the two motions. After a brief period of this vector-average pursuit, subjects make a saccade toward one stimulus or the other and then pursue that one selectively. Once again, the execution of the saccade is closely related to the ability of the pursuit system to selectively track the target, supporting the suggestion that pursuit target selection is serially linked to the execution of the saccade.

Another possibility is that targets are selected in common for pursuit and saccades. By using a discrimination task that requires subjects to select the target using a combination of horizontal pursuit and vertical saccades, it is possible to compare the pursuit and saccade choices on a trial-by-trial basis. Even though they are aimed in orthogonal directions, pursuit and saccade choices agree on the target much more frequently than expected by chance. In the minority of trials in which they initially disagree (1–13%), pursuit eye velocity reverses direction producing turn-around pursuit that anticipates the choice made by the saccade that follows. These findings suggest that the two choices are guided by the same decision process but that saccades might use a somewhat more stringent decision criterion. Consistent with this view, when performance (e.g., discriminability) is considered as a function of reaction time, pursuit and saccades exhibit nearly the same trade-off between speed and accuracy but saccades tend to be delayed and somewhat more accurate.

How can this evidence of a shared decision process be reconciled with the observations of postsaccadic enhancement of pursuit? One possibility is that the decision signal evolves fairly abruptly but stochastically during single trials. In this case, the occurrence of the saccade provides a temporal marker for when the decision signal reaches a critical level, and we would expect the selectivity of pursuit to increase

markedly at about this same time if it is guided by the same decision signal but used different criteria. As expected from this interpretation, there is a telltale correlation between the absolute latencies of the saccades and the differences in latency between pursuit and saccades on each trial. This correlation between relative and absolute latencies is what is expected if two different response thresholds were applied to the same decision signal. On the other hand, it is evident that saccades are not strictly necessary for pursuit target selection because pursuit can selectively follow one stimulus in the presence of distracters even when no corrective saccades are generated.

It may not be initially evident how such a shared decision signal operates because saccades depend on selecting the correct stimulus location, whereas pursuit depends on selecting the correct stimulus motion. However, there is evidence that spatial information has a surprisingly large influence on target selection for pursuit, even though stimulus motion is the crucial signal for driving pursuit eye movements. When subjects are given prior information about the location of the target but not its motion, this reduces the latencies of pursuit much more than when subjects are given prior information about the motion of the target but not its location (Figure 2). Thus, for triggering pursuit eye movements, it is more important to know where the target will be than to know in which direction it will be moving. These findings suggest that spatial attention may play a prominent role in target selection for eye movements. They also provide hints about the likely neural sites and mechanisms involved in coordinating target selection for pursuit and saccades.

Neural Mechanisms of Target Selection for Pursuit and Saccades

The neural mechanisms of target selection for saccades have been studied for many years and involve cortical areas such as the frontal eye fields, lateral intraparietal area, and subcortical brain regions such as the superior colliculus (SC). The mechanisms of target selection for pursuit have not been as thoroughly studied. The middle temporal (MT) area provides the visual motion signals that are most important for driving pursuit, and although neurons in MT area show a preference for the motion of the target, this effect appears to be too small to fully account for the selectivity of the pursuit eye movement. The pursuit area in the frontal eye fields also plays an important role in the control of pursuit and is the only area identified in the cerebral cortex where electrical stimulation can directly evoke smooth eye movements.

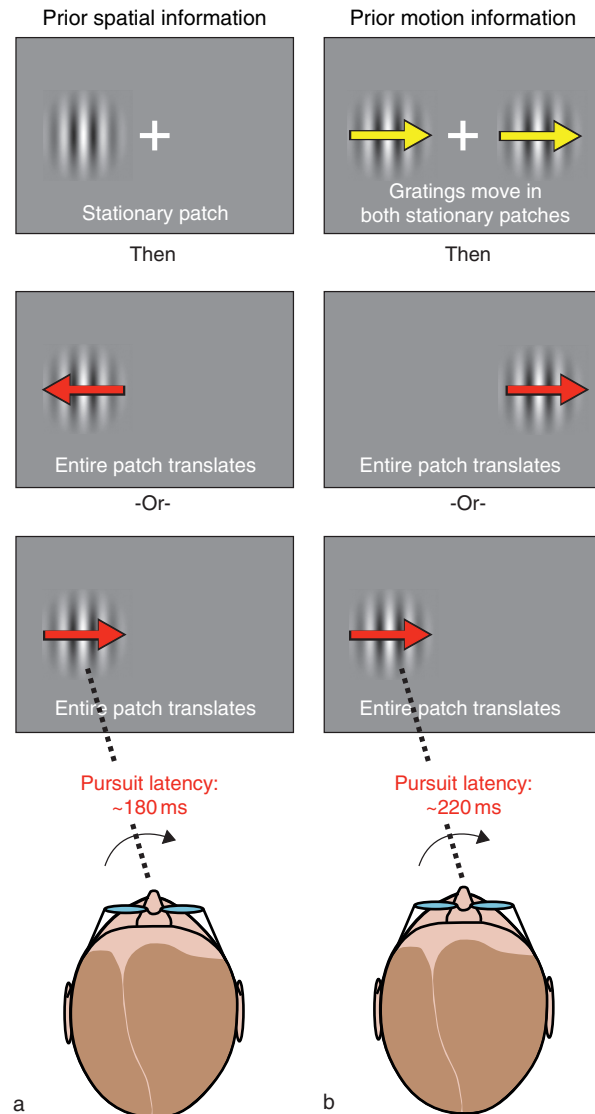


Figure 2 Spatial information influences target selection for pursuit more than motion information: (a) trial in which subjects were given prior spatial information; (b) trial in which subjects were given prior motion information. On trials with prior spatial information, a single stationary gabor patch indicated the location of the upcoming target but not its direction of motion. On trials with prior motion information, two stationary gabor patches both displayed drifting gratings that indicated the direction of motion of the upcoming target but not its location. Surprisingly, the average latency on trials with prior spatial information was shorter (~ 180 ms) than on trials with prior motion information (~ 220 ms), even though visual motion is the primary driving signal for pursuit. This effect demonstrates the primacy of spatial information in guiding target selection for pursuit and saccades. Adapted from Adler SA, Bala J, and Krauzlis RJ (2002) Primacy of spatial information in guiding target selection for pursuit and saccades. *Journal of Vision* 2: 627–644.

However, in none of these areas is there clear evidence of a mechanism for coordinating the outputs of the pursuit and saccadic eye movement systems. In fact, although many of the same cortical areas are involved in the control of pursuit and saccades, each

area contains largely nonoverlapping subregions for the two types of eye movements. How are the outputs from these two different eye-movement systems coordinated? One possibility is that the coordination is accomplished by the same selection mechanisms that control visual attention. There is emerging evidence from physiological experiments supporting the idea that the selective processing of visual stimuli (i.e., visual attention) and the preparation of voluntary eye movements involve overlapping mechanisms. Another possibility, not necessarily excluding the first, is that the coordination is accomplished by subcortical brain regions. The brain stem pathways for pursuit and saccades have long been believed to remain separated until the final motor steps, but recent physiological experiments have identified two regions where signals from the two eye movement systems coincide: the reticular formation and the SC.

The brain stem reticular formation contains the special classes of neurons that make up the saccadic burst generator – the circuit that forms the motor command for saccades. However, parts of this classic brain stem circuit for saccades also appear to be involved in the control of pursuit. For example, one well-known type of neuron in this circuit emits a burst of activity that is related to the pulse of velocity that defines the saccade trajectory. Some of these burst neurons have activity that is related to the velocity of the eyes during pursuit as well as during saccades. The function of this activity related to pursuit velocity is not yet understood, but it might be related to the mechanisms that determine when to trigger corrective saccades during pursuit eye movements.

Even more surprising is the finding of pursuit-related modulation in the activity of omnipause neurons (OPNs). It is well known that OPNs discharge steadily during fixation but stop firing during all saccades. Because this pause in activity is believed to disinhibit the saccade burst generator, OPNs are considered to act as the gatekeepers for saccade initiation. Surprisingly, approximately half of the OPNs also decrease their activity during the onset of pursuit – they do not completely pause their activity but reduce their activity depending on the speed of pursuit. Moreover, microstimulation in the region of the OPNs not only stops saccades but also strongly decelerates pursuit eye movements. These results suggest that the brain stem reticular formation contains an inhibitory mechanism that acts on both pursuit and saccadic eye movements.

The intermediate and deep layers of the SC contain neurons that have long been implicated in the selection of targets for saccades. During the preparation

of saccades, many SC neurons show increases in activity that begin hundreds of milliseconds before the movement, and these increases appear to play a role in representing the possible targets. When the probability that a visual stimulus will be the target is changed, for example by adding extra distracter stimuli, the level of preparatory activity changes in ways that reflect the altered target probability. During a visual search task, when subjects search for a uniquely colored target stimulus amid other colored distracters, many SC neurons discriminate the target from the distracter with a delay that is time-locked to the stimulus onset (rather than saccade onset), suggesting that they play a role in target selection for saccades.

Many of these saccade-related neurons also show modulation in activity during pursuit eye movements. The SC has not classically been viewed as part of the pathways for pursuit eye movements, but this modulation was noted in passing in some of the earliest studies of the SC, and more detailed studies have shown that it depends on where the neurons are located within the retinotopically organized SC

map. During pursuit eye movements, each neuron may show a somewhat complicated temporal pattern of activity, but this pattern can be explained fairly simply by considering the position of the tracked target within the neuron's response field. The distribution of activity across the SC map thus provides a real-time estimate of the position of the target in oculocentric or retinotopic coordinates, not restricted to saccades but for orienting movements in general. This target position map hypothesis provides a parsimonious alternative to the widely discussed fixation zone/saccade zone hypothesis, although the issue has not yet been definitively settled.

In addition to indicating the position of the target, the activity of these SC neurons also reflects its behavioral relevance. During a visual search task, many SC neurons exhibit a preference for the rewarded stimulus over irrelevant (i.e., unrewarded) stimuli, and this preference emerges over the course of approximately 100 ms prior to the initiation of pursuit and saccades. By interpreting this preference for the rewarded target as a decision signal, it has been shown that this SC activity can account for the target

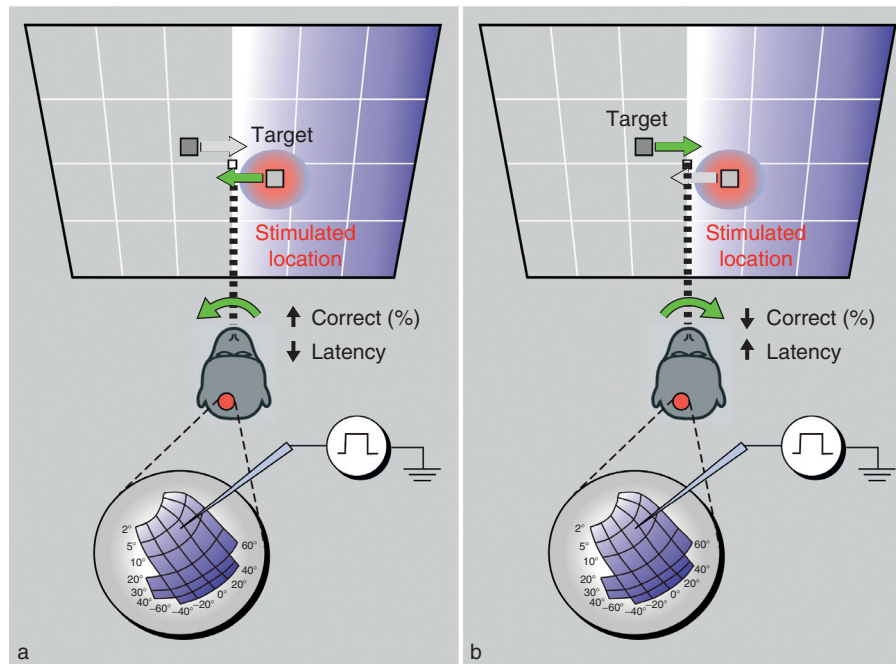


Figure 3 Experiment showing that subthreshold stimulation of the superior colliculus biases target selection for pursuit: (a) the site of stimulation matches the position of the visual target; (b) the site of stimulation is opposite the position of the visual target. An electrode placed in the intermediate layers of the superior colliculus is used to apply subthreshold electrical stimulation (i.e., currents too weak to directly evoke an eye movement) during a target selection task requiring a luminance discrimination. When the site of stimulation matches the position of the visual target (a), the percentage of correct responses increases (compared to no-stimulation control trials) and the latency of those correct responses decreases. In contrast, when the site of stimulation is opposite the position of the visual target (b), the percentage of correct responses decreases and the latency of the responses increases. Thus, activation of the superior colliculus biases target selection for pursuit eye movements, even though the required eye movements are directed away from the stimulation site. This experiment therefore demonstrates that the effect of stimulation in the superior colliculus is based on the location of the target and not the direction of the eye movement needed to acquire the target. Adapted from Carello CD and Krauzlis RJ (2004) Manipulating intent: Evidence for a causal role of the superior colliculus in target selection. *Neuron* 43: 575–583.

choices made by pursuit and saccades. Consistent with the behavioral results cited earlier, these results also imply that saccades use a more stringent decision criterion than pursuit, perhaps because errant saccades are more costly than mistakes by pursuit. These physiology results show that activity in the SC provides a neural correlate of target selection for both pursuit and saccades.

There is also recent evidence that the SC plays a causal role in target selection for pursuit and saccades. During a visual search task in which the subject should saccade to the oddball stimulus, it has been shown that, when the region of the SC representing the target is focally and reversibly inactivated, saccades are often misdirected to distracters appearing in unaffected areas of the visual field. During a luminance discrimination task, it has been found that electrical stimulation of the SC – at currents too weak to directly evoke an eye movement – nonetheless biases the selection of targets toward the stimulated location, regardless of whether the target is acquired with a pursuit or saccadic eye movement. The results for pursuit are especially revealing (Figure 3). Because the targets for pursuit initially appear at a location opposite to its direction of motion, the experimental design is able to identify effects based on the position of the target (i.e., which stimulus to follow) as distinguished from effects based on the motor commands (i.e., which direction to move). The results provide strong support for the idea that the SC plays a causal role in target selection itself, regardless of the type or direction of eye movement used to acquire the target.

Conclusion

Although pursuit and saccadic eye movements have been conventionally described as separate systems, their outputs are tightly coordinated during normal behavior. Recent findings indicate that this coordination is achieved by shared mechanisms for gating the movements and for selecting the visual target. The neural basis of these shared mechanisms includes the SC and possibly parts of the brain stem saccade generator. It is left for future work to clarify how these mechanisms of target selection for eye

movements are related to other types of visual selection, such as the allocation of spatial attention.

See also: Brainstem Control of Eye Movements; Cortical Control of Eye Movements; Frontal Eye Fields; Oculomotor Control: Anatomical Pathways; Pursuit Eye Movements; Saccade–Pursuit Interactions; Saccades and Visual Search; Saccadic Eye Movements; Sensorimotor Integration: Attention and the Premotor Theory; Superior Colliculus.

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