


REVIEW

Control of Movement

Visual selective attention and the control of tracking eye movements: a critical review

 **David Souto¹ and Dirk Kerzel²**

¹Department of Neuroscience, Psychology and Behaviour, University of Leicester, Leicester, United Kingdom and ²Faculté de Psychologie et des Sciences de l'Education, University of Geneva, Geneva, Switzerland

Abstract

People's eyes are directed at objects of interest with the aim of acquiring visual information. However, processing this information is constrained in capacity, requiring task-driven and salience-driven attentional mechanisms to select few among the many available objects. A wealth of behavioral and neurophysiological evidence has demonstrated that visual selection and the motor selection of saccade targets rely on shared mechanisms. This coupling supports the premotor theory of visual attention put forth more than 30 years ago, postulating visual selection as a necessary stage in motor selection. In this review, we examine to which extent the coupling of visual and motor selection observed with saccades is replicated during ocular tracking. Ocular tracking combines catch-up saccades and smooth pursuit to foveate a moving object. We find evidence that ocular tracking requires visual selection of the speed and direction of the moving target, but the position of the motion signal may not coincide with the position of the pursuit target. Further, visual and motor selection can be spatially decoupled when pursuit is initiated (open-loop pursuit). We propose that a main function of coupled visual and motor selection is to serve the coordination of catch-up saccades and pursuit eye movements. A simple race-to-threshold model is proposed to explain the variable coupling of visual selection during pursuit, catch-up and regular saccades, while generating testable predictions. We discuss pending issues, such as disentangling visual selection from preattentive visual processing and response selection, and the pinpointing of visual selection mechanisms, which have begun to be addressed in the neurophysiological literature.

catch-up saccade; premotor theory of attention; smooth pursuit; vision; visual attention

INTRODUCTION

“Vision is knowing what is where by looking” (1)

Tracking eye movements allow for good visibility of moving targets in human and primate vision. They are composed of smooth pursuit eye movements (pursuit for short) and catch-up saccades. The primary goal of pursuit eye movements is to avoid retinal motion of objects of interest by stabilizing their retinal image. Retinal motion, resulting from either body or object movement, has adverse consequences on perception, since a moving retinal image is blurry even at moderate speeds (2, 3). Retinal motion is also likely to degrade performance on a range of everyday tasks requiring a high-resolution input, such as recognizing the faces of walking people, estimating the trajectory of moving cars, or localizing appropriate grasping points on a moving object.

The aim of this review is to examine the coupling between visual selection and the control of tracking eye movements. Visual selective attention is an essential brain function allowing for the selective processing of only part of the overwhelming amount of visual information. The brain achieves visual selection through various mechanisms, which are jointly driven by the goals of the observer (also called top-down, endogenous, or voluntary control) and the physical salience of visual stimuli (also called bottom-up or exogenous control). The main function of visual selection is to gate access to capacity-limited processes, such as action planning (e.g., saccades), memory, and consciousness. Visual attention can also be seen as a limited resource that can be shared between visual objects, spatial locations, or visual features (4, 5). We need to bear in mind that even within top-down and bottom-up control modes, the term “selective attention” does not refer to a unitary mechanism (e.g., 6) and there is no sufficiently clear definition of visual attention to distinguish



between what belongs to visual selection or to other cognitive constructs, such as a decision-making (7). It is not clear, for instance, whether a choice bias induced by the presentation of a cue indicates visual selection or not. Response selection could take place without changing the nature of visual processing but still facilitating the access to this information, which may be called visual selection (6). However, other authors may consider this nonvisual processing, involving a decisional stage (4, p. 180).

The question of whether there is an overarching sensorimotor selection system that directs visual resources and orients gaze toward the same objects has been the subject of vigorous investigations over the past 30 years (e.g., 8, 9). Since we generally look at attended objects for scrutiny, it is plausible that our brains would have evolved an overarching selection mechanism for eye movements and the visual information at the location targeted by the eye movement. This idea was most prominently expressed in the premotor theory of attention (10). The theory claims that the orienting of attention is nothing more than a covert plan for an eye movement and that no voluntary eye movement is made without visual selection of the target, commonly referred to as a shift of attention. Since then, many behavioral and physiological studies have supported a strong coupling of visual attention and eye movements. In the now classic study from Deubel and Schneider (11), observers were unable to ignore saccade targets for a period of time before and after saccade execution, indicating an impossibility of diverting attentional resources from the saccade target. Conversely, drawing attention away from the target by cuing attention to the periphery affects saccadic reaction times (10) and their trajectories (12).

Much of the research concerning the coupling of attention and eye movements crystallized around testing the premotor theory with saccadic eye movements. For this reason, reviews on the topic focused almost exclusively on saccadic eye movements and left smooth pursuit eye movements aside (but see 13). The present review attempts to fill this gap in view of recent behavioral and physiological findings, offering a counterpoint to what we know from saccadic target selection. Initially, the pursuit system has at times been cast as a reflexive movement (14), unfolding without top-down influence other than the choice of the target to which it is locked. However, numerous cognitive influences over pursuit have been uncovered, such as the influence of visual attention, prediction (15), and reward (16). Similar to saccades, the voluntary execution of smooth pursuit eye movements requires a process to filter out irrelevant information and gate the visual signals that drive the eye movement. Even though the idea that pursuit target selection requires visual selection is uncontroversial, it is not clear by which mechanisms visual selection is achieved and to which extent visual and motor selection form a tight couple, or, conversely, can be dissociated.

We structure this review by first focusing on behavioral evidence relating to the coupling of visual selection and pursuit target selection, separating pursuit initiation and maintained (or steady-state) pursuit. We will then review the relevant neurophysiology and propose a simple theoretical framework that could account for physiological and behavioral findings. Specifically, the coupling of top-down

visual attention to the pursuit target can be understood in the same way as the coupling of goal-driven visual selection and saccadic eye movements, except that pursuit can be initiated based on a smaller amount of sensory evidence. This distinction corresponds to the “two-stage mechanism” proposed by Erkelens (17) and to the race-to-threshold model of pursuit and saccade coordination proposed by Liston and Krauzlis (18). We suggest that the coupling in pursuit and saccades is determined by the evidence needed to reach execution, meaning that the coupling depends on the balance between salience- and goal-driven distribution of visual resources (e.g., neurons that are responsive to the target), and not on a fixed amount of visual resources. Finally, we will expand on the “known unknowns” and areas that have been little explored so far, such as the role of visual attention in the coordination of slow and fast eye movements that occurs in natural situations. As will become apparent later, the complementary role of catch-up saccades and pursuit eye movements in tracking a target leads us to consider them jointly in this review.

Elements of Visual Selection

Examining how eye movements relate to visual attention is made difficult by the variety of tasks that can be used to infer attentional modulation and also the variety of ways in which it can operate. There have been recent calls (6), rooted in signal-detection theory (19), for a distinction between different forms of visual selection, via changes in sensitivity, and changes in criterion or bias. When cueing effects are measured via reaction times, by a detection (yes or no) or discrimination task (selection of one among two or more stimuli), performance favoring one response can be explained by decision-making, rather than an enhanced stimulus representation. In a yes-or-no task, changes of criterion have similar effects on hit rate (reporting the target as correctly present) and false alarm rate (erroneously reporting the target as present). Under natural circumstances, and in certain tasks, a shift in criterion increases performance. For instance, the probability of seeing the stimulus to detect can shift response criteria (e.g., 20). As a result, one is more likely to correctly detect the presence of a car if one is more eager to respond to stimuli appearing in the middle of the road than to stimuli appearing in the sky (21, 22). The same can be observed with reaction time-measures of attention. People are laxer in responding to a target presented at a precued location when the cue is predictive of the target location. This change in criterion will translate into a speed-accuracy trade-off, such that a button is being pressed faster but also with more false alarms (e.g., 23). Conversely, a change in detection sensitivity corresponds to hit rates changing when false alarms remain the same or change in the opposite direction. Sensitivity can be increased by a variety of mechanisms, for instance, by enhancing the signal, suppressing distractor signals, suppressing internal noise, or any combination of those (24). Both aspects of visual selection, choice bias and sensitivity, are important to understand how humans exploit the regularities in the visual environment to generate adaptive behavior (21). Those last aspects (e.g., how do eye movement decisions alter response criteria in a perceptual task?) have been underresearched in testing

the premotor theory of attention, in favor of other distinctions, such as endogenous and exogenous visual selection. We show how those and further distinctions between visual selection mechanisms pave the way for future progress in specifying the important role of visual selection in tracking eye movements.

Open-Loop and Steady-State Pursuit

Before detailing how visual attention affects pursuit, we need to define the main features of pursuit dynamics and how pursuit is driven by visual stimulation. There are two distinct phases in smooth pursuit eye movements. Those two phases can be observed in a ramp paradigm, in which the target starts moving with a constant velocity (Fig. 1A). Typically, the first 100 ms of smooth pursuit is open-loop, meaning that once started, pursuit is not affected by visual feedback (25, 26). The open-loop phase is characterized by a constant acceleration to reach the target velocity and typically ends with a catch-up saccade to foveate the target, as the distance to the fovea increases over time. After the offset of the first catch-up saccade, pursuit velocity is enhanced (26). The ensuing phase is known as the steady-state or closed-loop phase, as movement is controlled by a negative visual feedback loop (14). Pursuit in this phase is characterized by a velocity slightly slower than the target but well above the one observed during the open-loop phase. That is, pursuit gain (eye velocity divided by target velocity) is

typically around 0.95 or lower (25). Pursuit gain is a simple way of characterizing pursuit performance but should not be confused with the gain of the feedback system or *internal* gain, which characterizes the strength of the eye movement response to velocity errors. Catch-up saccades during this phase have been shown to be triggered preferentially when the position error of the target relative to the fovea corresponds to a fixed time to reach the target at the current pursuit velocity. Therefore, the trigger signal takes into account target velocity (27), as does the amplitude and direction of the saccadic eye movement itself (28). In addition to the open- and closed-loop phases of pursuit, there is a distinct stopping phase, with pursuit velocity decreasing exponentially (29). We will leave this phase aside, because we know little about how it relates to visual attention. Earlier studies showed that the stopping phase is relatively insensitive to attentional states (30), although it depends strongly on the expectation that the target will stop (29, 31, 32).

Open and closed-loop pursuit are guided by different types of motion signals as demonstrated by the pursuit of oblique bars. When measured by detectors with small receptive fields (such as V1 cells), the motion of an oblique bar moving horizontally is ambiguous. Local motion information incorrectly indicates that the bar is moving orthogonally to its contour (e.g., 33). As shown in Fig. 1B, pursuit is initially driven by local motion as it follows the orthogonal direction first, before motion signals at different locations along the bar are integrated, including the unambiguous 2D

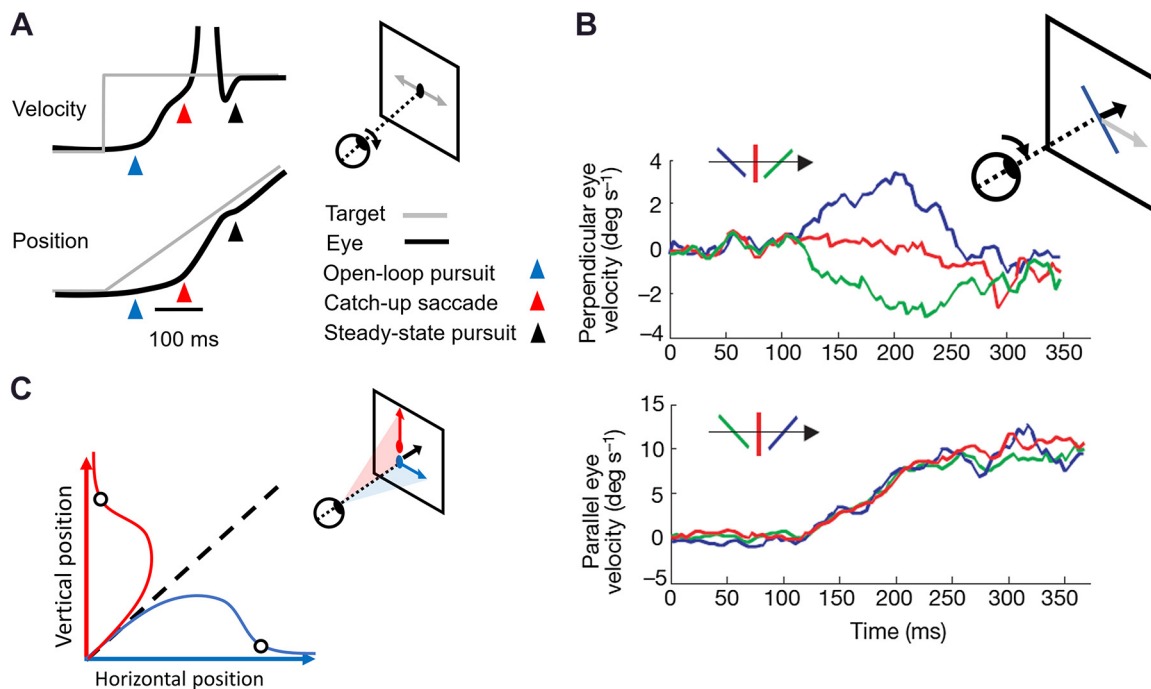


Figure 1. A: pursuit and catch-up saccades observed in a ramp paradigm. The first 100 ms of pursuit are open-loop (from the blue to the red arrow). As the distance to the fovea accumulates, a saccade (catch-up saccade, from the red to the black arrow) is executed to foveate the target. The black arrow indicates the transition to the steady-state (or closed-loop) phase of pursuit. From that point onward eye velocity is close to the target velocity, typically following the offset of the saccade. B: in the monkey, when tracking an obliquely oriented line moving horizontally (blue: -45° bar, red: vertical bar, green: 45° bar), pursuit initially follows a direction orthogonal (or perpendicular) to the orientation of the target bar, then its true horizontal direction of motion [gray arrow; adapted from Pack and Born (34)]. C: illustration of pursuit in the presence two stimuli moving in orthogonal directions. Open-loop pursuit tends to follow the average of motion vectors up to the first catch-up saccade (open dot). At this point pursuit becomes selective to the target direction. We show two conditions in which either the horizontal (blue) or vertical (red) motion is the target. In the inset, the shaded plane indicates an eye rotation that would be exclusively selective to either the blue or red target. The black arrow indicates the vector average.

motion at the bar edge. At this point, pursuit tracks the global motion direction (34). An initial *local* response has also been shown with ocular following a reflexive eye movement in response to a large moving stimulus, which may rely on neural computations similar to those used in the initiation of pursuit (35, 36). This computational stage seems impervious to cognitive factors, such as prior knowledge about the real target direction (37).

A further distinction between open and closed-loop pursuit phases, which may be related to stages in motion integration, is that they are driven differently by first- and second-order motion. Open-loop pursuit is driven by first-order motion signals (i.e., a pattern defined by luminance), whereas closed-loop pursuit can be driven by second-order motion signals, where motion is not defined by luminance, such as when motion is carried by a moving change in contrast (38). Further, intersubject variability in perceptual discrimination of second-order motion is correlated with the closed-loop phase of pursuit eye movements, whereas perceptual discrimination of first-order motion is correlated with the open-loop phase of pursuit eye movements, which confirms the dissociation of open-loop and closed-loop phases (39).

The fact that different motion signals drive pursuit differently would suggest that the open-loop stage is a preattentive stage driven by early motion signals, or at least that this phase is relatively insensitive to top-down attention or other cognitive factors. This could be a consequence of the time it takes to allocate attention (e.g., 40). In a ramp paradigm, with unpredictable movement direction, the open-loop stage may operate at a preattentive stage because it takes time to bring visual attention on the target motion. Although there is no consensual way to estimate the speed of voluntary and exogenous shifts of attention, estimates are in general commensurate with the idea that pursuit starts before attention is fully allocated to the target. For instance, effects of exogenous cues peak at ~150 ms post cue (41–45), whereas open-loop pursuit starts earlier, at around 100 ms. Consistently, whereas first-order motion processing can be preattentive, second-order motion is believed to involve attentional tracking of moving features (46, 47), such as a luminance contrast edge, thereby suggesting that steady-state pursuit requires attentional tracking, unlike open-loop pursuit.

In the next section, we will review more direct evidence from behavioral studies investigating the role of attention in selecting the pursuit target, by focusing first on pursuit initiation (open-loop and beginning of steady-state) and then on the steady-state phase. We then address investigations on the allocation of attention during steady-state pursuit in some depth because they raised a number of unresolved issues, such as whether target size affects the coupling of resources to the moving target, whether the coupling is asymmetric along the pursuit direction, and to what extent we can tell apart response biases, nonattentional changes in visual processing during pursuit, and modulations of visual processing by attention.

PURSUIT INITIATION: VECTOR-AVERAGING AND DUAL-TASK EXPERIMENTS

One way of ascertaining the role of voluntary attention in the control of pursuit is by analyzing target choice (i.e., the observed motor selection) in the presence of competing

motion signals. Target choice is indicative of voluntary (endogenous) attentive selection if a target is selected based on a predefined feature (e.g., color or location) while an equivalently salient distractor is ignored. When the target does not differ from the distractor in its bottom-up ability to drive pursuit (e.g., because of similar luminance contrast), target choice needs to be based on a top-down signal that may “bias” the competition between potential targets. A second way to ascertain the role of attention in pursuit control is to investigate dual-task performance when performing a perceptual task while pursuing a target in the presence or absence of distractors.

Vector Average and Winner-Take-All Behavior

The contribution of visual attention to pursuit target selection has been extensively studied in situations during which the subject is rewarded (monkey) or instructed (human) to pursue one of two stimuli moving at the same speed but in different directions (48–53). In the monkey, faced with stimuli moving in orthogonal directions, pursuit follows the vector average direction during the open-loop phase, as shown in Fig. 1C, and becomes selective to the target, the so-called winner-take-all response, within the start of the closed-loop phase (50). When moving in opposite directions, the competition results in a delayed pursuit latency (48). In line with the postsaccadic enhancement of pursuit velocity observed when using a ramp paradigm, winner-takes-all responses are more apparent after the initial saccade (see also 54). Ferrera and Lisberger (48) proposed a model of pursuit target selection based on the biased competition model of Desimone and Duncan (55) to explain the time-varying vector averaging behavior, going from vector averaging to winner-take-all target choice. In the biased competition model, visual attention is an emergent property of a competition between neural object representations. That is, when searching for an object, the enhancement of task-relevant information and the suppression of task-irrelevant information is the outcome of an evolving competition for representation between target and distractor objects. This model was proposed to stand in contrast to the notion of visual attention as a virtual spotlight, which would increase the visibility of the objects to which it is pointed, or which, in neural terms, would be the mechanism by which relevant representations are directly selected. Instead, the top-down signals originating in frontal cortical areas (the search template; 55) or bottom-up signals participate in biasing the outcome of the competition for representation based on any combination of target features (motion, color, direction), which ultimately leads to visual selection. In Ferrera and Lisberger’s (48) simple instantiation of this model (a four-unit network), neurons representing the target or distractor motion are mutually inhibited. The effect of endogenous cues is to strengthen the representation of the target, amounting to selection by signal enhancement, but it is the self-reinforcing network dynamics that reproduce the time-course of vector-averaging and winner-takes-all selection. Thus, selection is a by-product of a top-down signal but not its direct consequence.

In the biased competition model of pursuit target choice, any target feature can bias the competition for neural representation. Therefore, motion signals have no

privileged status. The prediction was in part borne out as a variety of different cues can be effective in biasing the initial vector average response toward the designated target. Garbutt and Lisberger (56) showed that directional cues are effective in biasing target choices, without an explicit instruction to pay attention to a given direction. Similarly, in human observers, precueing the target location can also bias the vector competition to some extent (57), as does cueing by shape or color (52, 57). As predicted by the biased competition theory, initial biases are unable to resolve the competition by themselves. Cueing experiments are consistent with this idea and suggest a mandatory averaging stage, with top-down and exogenous cues shifting the weights of target and distractor signals. One could argue that if the suggested dynamics of visual attention (as inferred from the time course of perceptual selection, for instance) explain vector averaging, then we should also see winner-takes-all responses from the start of pursuit whenever we are given sufficient time to visually select the target. On the other hand, averaging behavior despite pre-cueing target direction could be related to exogenous capture of attention by the motion onset of the distractor. We will show in the next section that in human observers, pursuit can indeed be selective from the start if the target is given sufficient priority (58).

A salient aspect of winner-takes-all behavior in ramp paradigms is that target selection starts by a catch-up saccade. This finding led to the idea that the saccade target selection itself controls pursuit target selection. The strongest evidence for a role of saccades in determining selection is based on microstimulation studies (54, 59), where pursuit target selection is solved by triggering a saccade to the target, and the postsaccadic enhancement of visuomotor gain, observed with a single moving object (26). These observations were taken to reflect a form of “motor attention,” where the saccade dictates spatial selection of the pursuit target (60). However, not only can winner-take-all selection occur in the absence of a catch-up saccade, but pursuit and saccade choices are coordinated even before the execution of the saccade, meaning that the pursuit target choice is gradually biased toward the saccade target choice even before saccade execution (18). These findings are compatible with the idea that visual attention is the spatial selection mechanism that coordinates target choices (18). As we will argue later (cf. A MODEL FOR VISUAL AND EYE MOVEMENT SELECTION), the apparent causal implication of saccades on pursuit target selection could be a consequence of both saccade execution and steady-state (winner-take-all) pursuit depending on visual selection of the target representation.

Dual-Task Experiments

The use of dual tasks to infer attentional demands has a relatively long history. It is based on the premise that the deterioration of performance in a primary task while carrying out a secondary task can tell us about how sensitive the primary task is to attentional resource allocation (61). An early use of the technique by Jeannette Welch (62) involved measuring the fluctuations in the force with which we can pull the handle of a dynamometer. The amount of force applied was reduced by concurrent mental tasks, depending

on how taxing they were. For instance, the task of multiplying two-digit numbers was one of the most disruptive.

In the context of visual attention, dual-task paradigms have been employed to ask whether different visual tasks use the same pool of attentional resources (e.g., 5) and to estimate to what extent attention can be drawn away from one task without altering performance (63, 64, 65).

We have used a dual task to uncover the dynamics of visual attention during open-loop and steady-state pursuit (66, 67). Figure 2A shows the time-course of a trial in an experiment testing pursuit initiation with a ramp paradigm. Observers were asked to pursue a dot while a central (endogenous) or peripheral (exogenous) cue indicated the presentation of a stimulus in the periphery that had to be attended (67). Our reasoning was that shifts of attention to the periphery should affect pursuit latency and gain if the movement relies on visual attention. Figure 2B shows that the initiation of pursuit was independent of whether the movement started when attention was shifted to the peripheral target or not. In contrast, catch-up saccade latencies were substantially prolonged when attention was shifted to the perceptual target. In another version, we used a step-ramp paradigm, meaning that the target stepped sideways before moving toward the location of the initial fixation point, which strongly reduces the probability of having an initial catch-up saccade (Fig. 2C). We found again that the initiation of steady-state smooth pursuit was delayed by the dual task (the pursuit gain was reduced), whereas pursuit initiation and the acceleration observed during the open-loop phase were not. Further, a reduction in gain at critical asynchronies was only observed when the perceptual target did not move with the pursuit target. When all stimuli moved in the same direction, the effect was much reduced, as shown in Fig. 2, B and C. Therefore, attentional selection of the correct motion signal is not necessarily constrained to the location of the pursuit target, provided that there is no conflict between motion signals relevant to both pursuit and perceptual tasks.

Earlier studies in which the effects of attention were measured by manual reaction times to peripheral targets suggest that more attention is allocated during a time period corresponding to pursuit onset and offset (68, 69). In those experiments, observers had to press a key on presentation of a probe stimulus presented in addition to the pursuit target. Reaction times were shorter to probes ahead of the pursuit target compared with its wake (cf. *The Distribution of Attention around the Pursuit Target*) and longer in onset and offset time periods compared with the steady-state phase, which was taken to indicate higher attentional demands during pursuit onset and offset. However, the pursuit target onset and offset itself competed for attention with the concurrent presentation of the probe stimulus, which could have led to overestimating the contribution of attention during onset and stopping compared with steady-state pursuit, where target onset or offset were absent.

In a follow-up study, observers were able to allocate attentional resources flexibly, depending on instructions to prioritize one task over the other. We displayed two oriented gratings moving in opposite directions. One of the gratings was pursued and the orientation of either the pursued grating or the nonpursued grating had to be discriminated (58). When the nonpursued grating had to be discriminated,

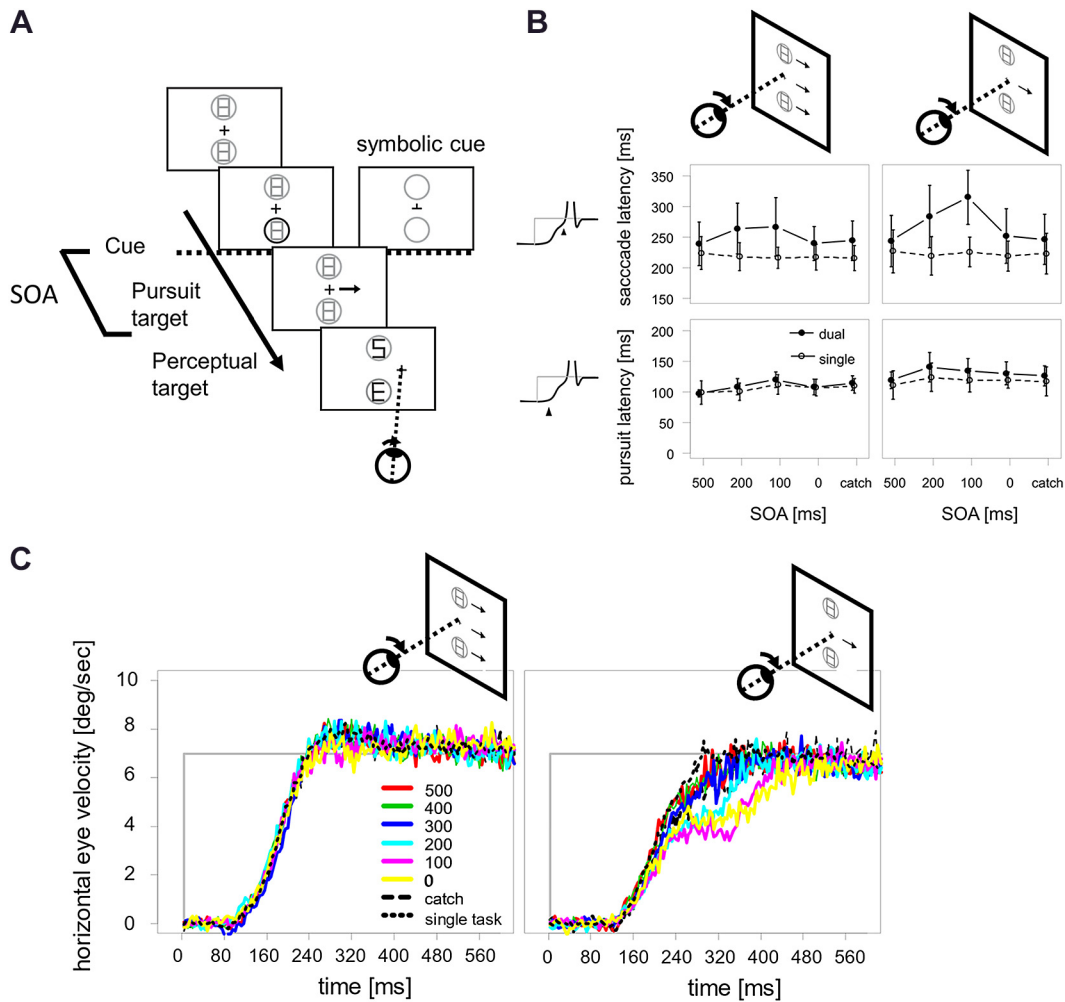


Figure 2. A: illustration of the dual-task paradigm used by Souto and Kerzel (67). The observer engages either in a single pursuit task or in a dual task where a stimulus presented at a precued location must be discriminated at the same time. The cue-target onset asynchrony (SOA) is varied. Some SOAs allow enough time to allocate visual resources to the periphery. Attention is summoned by endogenous cues (a missing bar in a plus sign presented at fixation) or exogenous cues (a darkening of a ring surrounding a placeholder in the periphery). B: average latencies of pursuit (bottom) and catch-up saccades (top) in a ramp paradigm ($n = 8$ subjects). There is a significant delay in the latencies of catch-up saccades at intermediate SOAs but not for pursuit latency. C: pursuit velocity in a step-ramp paradigm for different SOAs, in the absence of catch-up saccades ($n = 7$ subjects). A–C are adapted from Souto and Kerzel (67).

average pursuit latency reflected the distribution of resources, so that latencies increased with increasing attention to the discrimination task (58). Importantly, we could also test whether attentional resources were allocated to one task at a time, which is referred to as the “switch” model, or whether those resources were truly shared between tasks. The switch model applies to perception of briefly displayed letters at two different scales, where performance at one scale is traded for performance at the other scale, showing that only one scale can be attended at a time. In that case, the trade-off in performance between tasks is based on the number of trials one pays attention to one of the scales (5). In contrast, a hallmark of the resource sharing model is that errors or correct responses in one task are not predictive of errors or correct responses in the other, because on every block of trials there is a set amount of attentional resources for either task. To test the model with an oculomotor and perceptual task, we used pursuit latencies longer than the median and shorter than the median as an indicator of success and

failure in the oculomotor task. In both cases, our results were compatible with resource sharing and not a switch model (58, 67), emphasizing that humans are able to flexibly share attentional resources among the competing motion signals to control pursuit initiation.

To sum up, the analysis of pursuit initiation indicates that 1) pursuit latency and acceleration is mostly unaffected by endogenous or exogenous shifts of visual attention, 2) the beginning of steady-state pursuit and catch-up saccades are affected by those shifts but less so when paying attention to stimuli that move with the pursuit target, and 3) there is flexible resource allocation controlling target selection by voluntarily changing task priority (58).

STEADY-STATE PURSUIT: DUAL-TASK EXPERIMENTS

Focusing on the steady-state phase of pursuit, early studies have shown that visual attention is needed to support

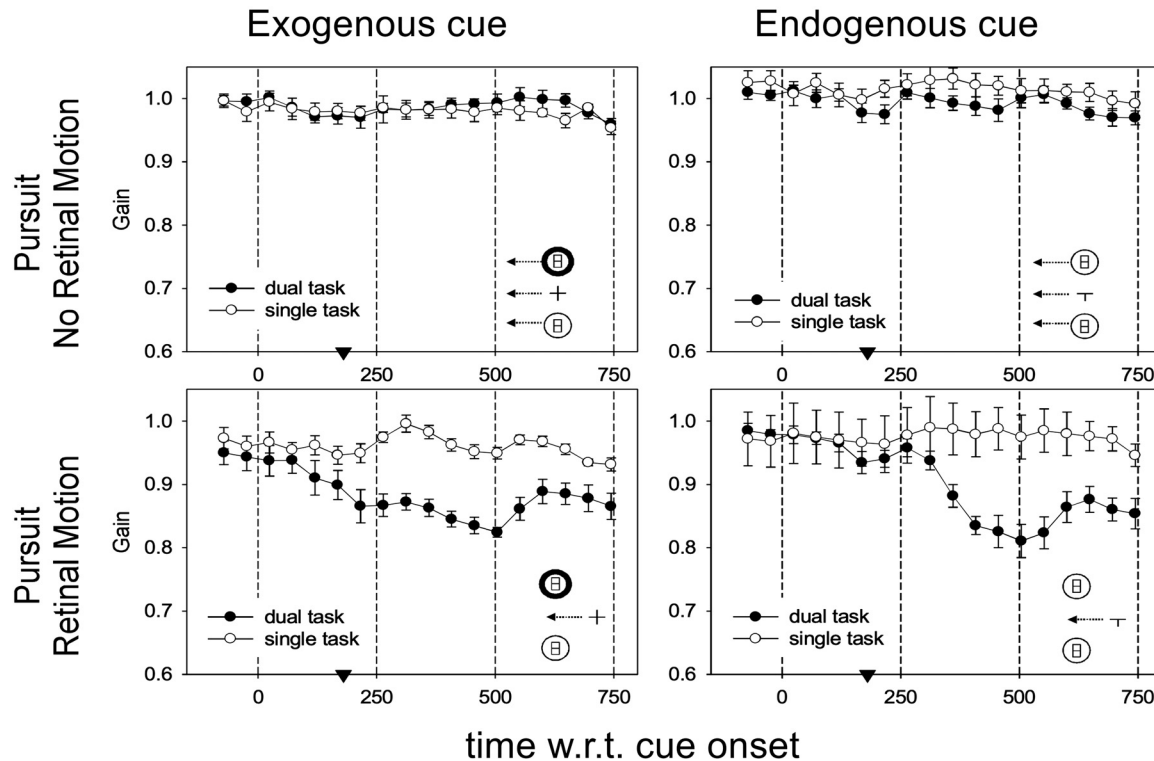


Figure 3. Effect of performing a peripheral perceptual task on pursuit gain during steady-state pursuit. *Top and bottom* contrast the effects of attending perceptual targets that moved with the pursuit target or were static in world coordinates (i.e., moving relative to the pursuit target and thereby generating retinal motion). *Insets* in the bottomright corner of each panel indicate stimulus configuration. A small triangle straddling the x-axis indicates when the target letter was presented. Error bars indicate between-subjects SE ($n = 6$ subjects). Adapted from Kerzel et al. (66). w.r.t., with respect to.

steady-state pursuit over structured backgrounds or with distractors moving apart from the target. In the classical dual-task study of Khurana and Kowler (70), attention was shown to be narrowly allocated to an object's motion. Their experiment emphasized selection by speed, not location, because observers had to track interleaved strips of letters. Observers were asked to pursue two rows of letters moving horizontally with the same velocity (as slow as 0.4, 0.6, and 1.6°/s), while two other rows were moving at a different velocity. Velocity differences were very small and the whole display subtended only a few degrees of visual angle. However, there was a clear trade-off between tracking a strip and detecting letter changes in the untracked strip, indicating the interdependence of target selection for pursuit and perception. Additional analysis showed that the trade-off was independent of the retinal speed of the perceptual target. Kowler et al. (71) also demonstrated the selectivity of steady-state pursuit as observers showed a near perfect ability to select the appropriate target when pursuing a cloud of dots moving very slowly over an equivalently salient and moving background.

We investigated the trade-off between pursuit and perception further by drawing attention away from the pursuit target during steady-state pursuit (66). The results in Fig. 3 show that pursuit gain was only affected in some conditions. Consistent with what we observed at the transition between open-loop and steady-state phases (67), pursuit was mostly affected when there was relative retinal motion between cue and target. When the peripheral and pursuit targets moved in concert the effects were much weaker, whether

the supplementary task involved perceptual discrimination (shown in Fig. 3) or speeded reaction times, and whether the cue was exogenous (Fig. 3, left) or endogenous (right). The reaction time task had less influence on pursuit gain than a perceptual task, but it is not clear that success in that task required a shift of attention away from the pursuit target. Therefore, we confirmed that attention is required in the direction of pursuit but is not necessarily coupled in space, as it is possible to shift attention to congruent motion signals at little cost in pursuit performance, confirming our earlier conclusions regarding the end of the closed-loop and start of the steady-state phase.

A smaller trade-off between pursuit and perception, depending on the task, was found when flashing perceptual targets during pursuit, thus reducing if not eliminating conflicting motion signals (72). We flashed a small grating in the periphery during pursuit and asked observers to discriminate its orientation. Importantly, observers had instructions to either prioritize pursuit or discrimination of the flashed perceptual target. Prioritizing the perceptual task over the pursuit task had little effect on perceptual performance but strongly decreased pursuit gain. In another version, observers were additionally required to discriminate the orientation of the pursuit target as an index of attention to the pursuit target. As expected, when the peripheral flash had priority, both perceptual discrimination of the pursuit target and pursuit gain decreased (72). This set of experiments indicates that there can be large effects of peripheral and localized transients on pursuit performance even when no

conflicting motion signals are present. However, interference from flashes is determined by top-down priority.

We have seen repeatedly that shifting attention away from the pursuit target only compromises pursuit performance when there is relative motion between the pursuit target and objects that are attentively tracked. We have also asked whether ongoing pursuit eye movements are affected by the allocation of feature attention to peripheral motion (73). Feature attention refers to our ability to select visual information based on specific features independently of spatial location. We tested whether feature attention can gate involuntary ocular tracking in the direction of the attended motion. The task was to pursue a dot horizontally while discriminating between subtle changes in the vertical trajectory of a field of randomly distributed dots (73). The dual-task paradigm is shown in Fig. 4, A–D. We balanced an upward and downward pulse of motion during horizontal pursuit (Fig. 4A), such that any involuntary responses to large-field motion (ocular following) would be cancelled out in the average to reveal the effect of voluntary attention. The explicit

instruction to attend to the dots of a particular color resulted in ocular following in the attended direction under some conditions (Fig. 4, B–D). Only the combination of motion direction and color cues indicating the background motion to attend were able to drive ocular following in the attended direction. One possible interpretation, consistent with our findings on pursuit initiation, is that feature attention cannot be allocated to a motion direction different from the pursuit target unless the conflicting motion signals share another distinctive feature, such as color, which allows for feature attention to be allocated in a voluntary fashion. The coupling of feature attention to the pursued target could contribute to perceptually group objects moving in the same direction (74). This is consistent with the possibility of paying attention to peripheral objects moving with the pursuit target. Those attention shifts could be supported by feature attention (attention being allocated based on a feature, such as motion direction) and spatial attention (attention being allocated based on stimulus location). An analysis of the trial-by-trial responses confirmed that the ocular following response

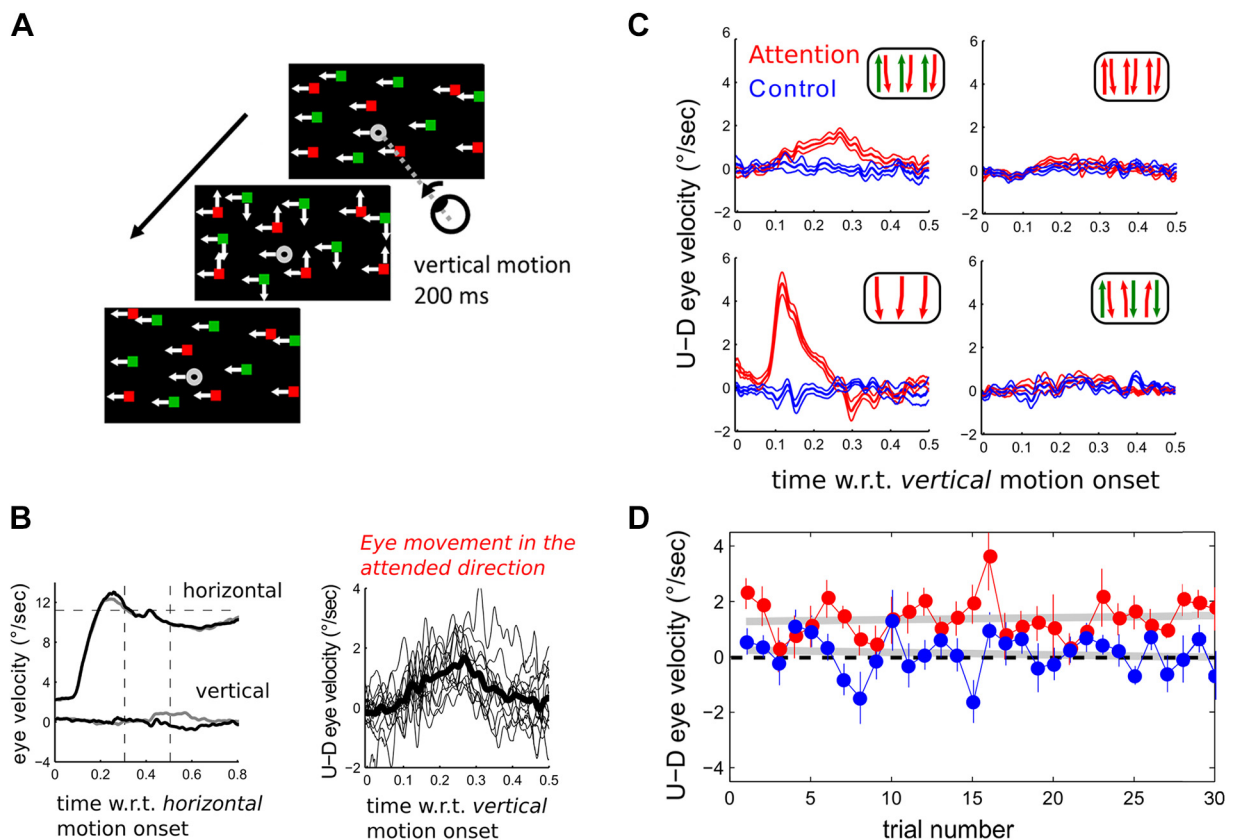


Figure 4. A: the display was composed of a pursuit target and two clouds of red and green dots moving in the same horizontal direction. For 200 ms, a vertical component was added to the motion of the background dots. Half moved up whereas the other half moved down. In a dual task condition (*attention condition*), observers had to discriminate a small change in the direction of motion of a predesignated group of dots. In the control condition, they had to ignore the background dots. B: the left shows horizontal and vertical eye movement velocity with respect to (w.r.t.) the onset of the pursuit target. In one observer, we can see the average vertical response in the direction of background motion when upward (gray line) or downward (black line) was attended. The right shows the average eye movement velocity (thick line, $n = 13$ subjects) in the direction of the attended vertical motion, with respect to the onset of vertical background motion, when subtracting upward and downward conditions (U, upward; D, downward). Eye movements are mirrored so that an eye movement in the attended direction is always shown as upward. Thin lines represent each observer's average. C: eye movements in the vertical direction in four conditions, as designated by insets. The motion to attend could either be designated by the color and motion direction of the dots (upper left, $n = 13$ subjects), motion direction (upper right, $n = 13$ subjects), or color alone (lower right, $n = 8$ subjects). In one condition, there were no distractor dots (lower left, $n = 15$ subjects). D: the peak response to vertical motion was averaged for every trial across observers when cued by motion direction and color (upper left condition in C), showing that observers could select target features from the start, with no noticeable effect of trial number. A–D are adapted from Souto and Kerzel (73).

resulted from a voluntary shift of feature-attention gating motion signals and not from the buildup of priming across trials (75). Indeed, trial-by-trial analysis showed significant ocular following from the first trial onward, as visible in Fig. 4D.

To sum up, during steady-state pursuit, 1) attention is closely coupled to the target velocity, although some of the attentional resources may be freed without an oculomotor cost. 2) There is flexibility in the *spatial* allocation of attention, which is consistent with the idea that motion signals provide the main drive to the pursuit system (e.g., 76). 3) Feature attention can be allocated to nontarget signals, as indicated by the gating of ocular following responses orthogonal to the direction of the pursuit target, but feature attention may not be allocated based on conflicting motion directions alone.

Pursuit of Small and Extended Objects

Most studies on the role of attention in pursuit have involved the pursuit of small stimuli, typically extending no more than a degree of visual angle. Investigating extended stimuli may bring us closer to natural conditions, where it is rare to track small targets, such as the proverbial dot on a black screen. In nature, tracked objects are formed of different features, which requires integration across space (33). Pursuing these objects requires an element of perceptual grouping (77), which may be supported by feature and spatial attention.

We know that attention to the pursuit target is not a fixed quantity with extended stimuli but depends on the top-down control of visual attention. Madelain et al. (78) showed elegantly how the size of the stimulus we attend to can affect the programming of catch-up saccades by using stimuli made up of concentric rings. Observers paid attention to the larger or smaller ring during pursuit while the target stepped or sped up during pursuit. When attending to the big ring, bigger perturbations of target motion were tolerated before triggering catch-up saccades, suggesting that tracking precision is adjusted to the size of the attentional window.

Tracking an extended object through an occluder (e.g., an animal through foliage) requires grouping of image points by shared visual features. For instance, participants are able to pursue an integrated motion signal in a random-dot-kinematogram (79). Remarkably, Jin et al. (80) investigated a multiple-object-tracking task and found that observers can pursue even a small number of dots as one integrated group. Moreover, they suggested that attentional resources are not bound to a particular dot direction, which contrasts strongly with the above conclusion that it is difficult to pay attention to objects moving relative to the pursuit target without cost (66, 70, 72).

Possibly, elements in a multiple-object-tracking task can be tracked as a single deforming entity (81) as indicated by the fact observers tend to pursue the centroid of the changing configuration (82, 83). In any case, this shows that we need to go beyond the single dot situation and consider the integration of motion signals for the guidance of pursuit. Therefore, our assumption that attention is coupled to the direction of motion may need to be updated to consider whether the elements that are attended cohere to be considered as a single entity, with a global direction or not (33). However, it remains to be tested whether perceptual

grouping is required to attend conflicting motion signals during pursuit with no oculomotor cost.

Another line of evidence was taken to suggest that the size of the stimulus has an impact on the amount of visual resources that can be freed from the pursuit target, which again could question the extent to which conclusions drawn from using impoverished stimuli transfer to more natural situations. The presence of background motion (a random-dot-kinematogram) in the same direction as a pursuit target was shown to improve pursuit performance by reducing the number of catch-up saccades, to improve the ability to discriminate parafoveal targets (moving with the pursuit target) and to reduce saccadic reaction times toward those targets (76, 79, 84). Although this pattern of results indicates that attentional resources can be freed to process the concurrent target, we will argue below (cf. A MODEL FOR VISUAL AND EYE MOVEMENT SELECTION) that the change in attentional demands is not necessarily indicative of a difference in attentional control when tracking small or large targets but is a consequence of an increase in the salience of the motion signal driving pursuit (through a change in size, luminance contrast, etc.), liberating attentional resources.

To sum up, the pursuit system can track the configuration of independently moving dots or individual dots alike, which indicates the importance of grouping mechanisms in determining the pursuit target. Extended targets may also free visual resources by boosting the driving signal (79).

The Distribution of Attention around the Pursuit Target

Thus far, we have reviewed the attentional requisites for performing pursuit eye movements. Many studies have also attempted to investigate how attention is naturally distributed during steady-state pursuit by probing perceptual or detection performance around the target location. This line of inquiry outlines the significant challenge of partialing out the influence of the secondary task on the strategic distribution of attention but also the difficulty in specifically attributing effects to visual attention. The use of different paradigms and measures lead to different conclusions, and we suggest that this could have something to do with using perceptual and reaction time measures as indices of visual selection.

It was first suggested by Van Donkelaar (69) that visual attention is asymmetrically allocated during pursuit, with more resources being allocated ahead of the target (68, 69, 85). This hypothesis was backed up by shortened latencies of manual responses to probe stimuli flashed ahead of the pursuit target compared with probes flashed behind the pursuit target, or probes flashed during fixation. Probes presented at the pursuit target location and 1–2 degrees of visual angle (°) ahead of the pursuit target led to similar reaction times (68). These data could indicate that attention is biased ahead of the pursuit target, at least for 10 and 15°/s pursuit target speeds. One may wonder what advantage could be derived from shifting attention in the pursuit direction, presumably removing visual resources off the target. The strategy would be broadly consistent with studies on saccades, where a pre-emptive shift of visual attention to future retinal target locations is observed (86), which has been related to the spatial

remapping occurring in some cells of the parietal cortex (87). The shift of spatial attention could benefit the remapping of receptive fields during saccades and pursuit, thereby contributing to visual stability (88).

Nonetheless, if attention is asymmetrically distributed during pursuit, perceptual discrimination should be shifted in the same way. However, data from Watamaniuk and Heinen (89) and Lovejoy et al. (90) indicate that this is not the case. In their experiments, observers tracked a strip of letters and showed perfectly symmetric perceptual performance around the pursuit target (see Fig. 5A), which stands in strong contradiction to claims from studies using reaction times. One interpretation is that extended stimuli require a different distribution of visual attention. Another is that reaction time-measures of attention are indicative of decision-making rather than the distribution of attentional resources. Next, we try to unpack evidence for either of those accounts.

Although reaction times are often interpreted within an attentional framework, they do not have a straightforward interpretation. To corroborate the hypothesis that attention is shifted ahead of pursuit, Van Donkelaar and Drew (68) analyzed the manual reaction time distributions. According to the LATER model (e.g., 91), differences in latency could be explained by differences in the rate of accrual of evidence (race-to-threshold) rather than a difference in execution threshold. However, the decision to respond is also dependent on postsensory factors. Indeed, when a target is well above the visual detection threshold, manual and saccadic reaction times are mostly determined by postsensory stages (92). To put it clearly, when a target is well above detection threshold, a difference in contrast adds a rather insignificant amount of sensory processing time as estimated by reaction times (<5 ms). If the effect of cuing is to speed up reaction times by 50 ms, then it would be unreasonable to ascribe the effect to the modulation of sensory signals by visual

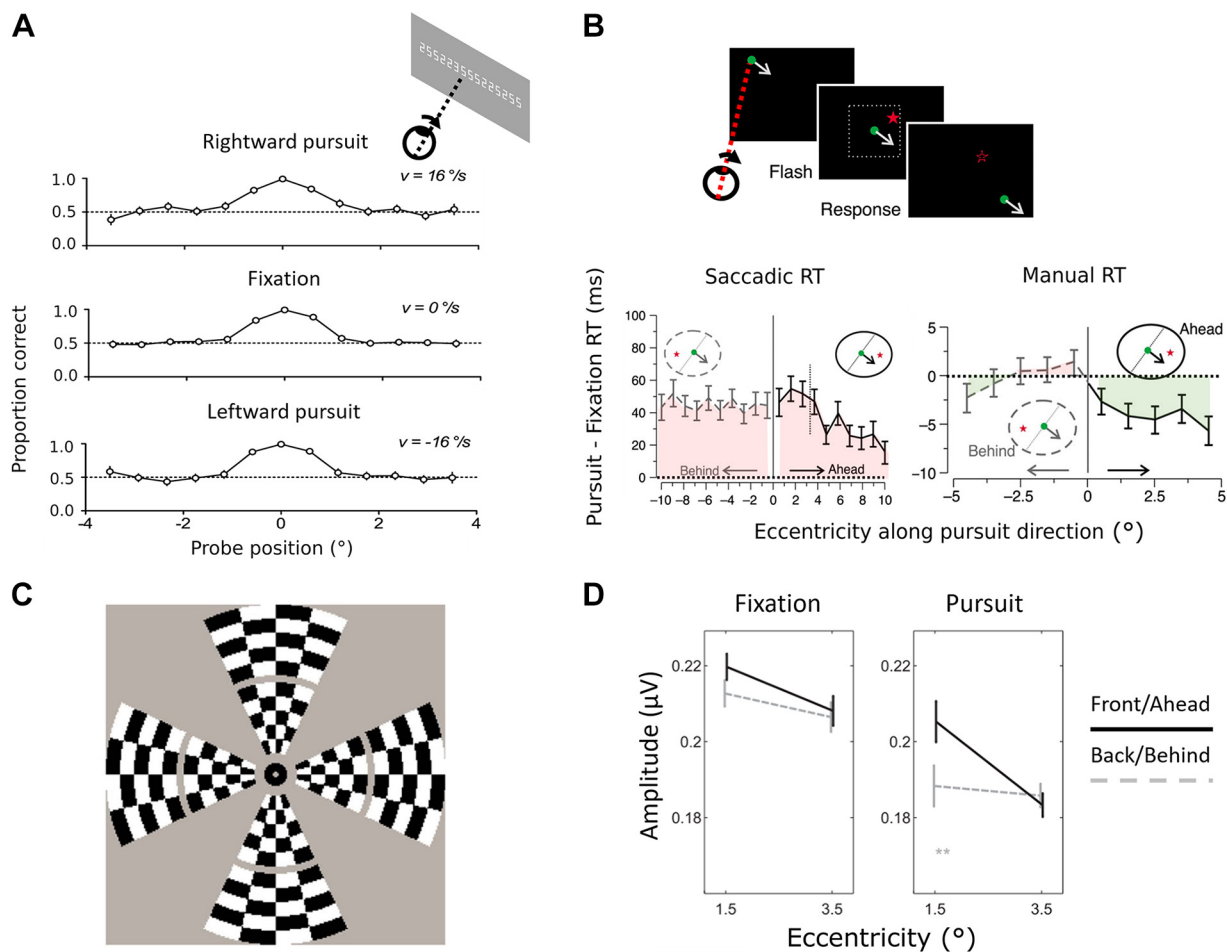


Figure 5. Is visual attention biased ahead of pursuit? **A:** Lovejoy et al. (90) asked observers to fixate the center of an array of placeholders. The probe was a briefly displayed letter at one of 13 locations. Perceptual performance in recognizing the letter is shown while pursuing a target moving at 16 or $-16^\circ/\text{s}$ (top and bottom, respectively, $n = 9$ subjects), or while fixating (middle). Adapted from Lovejoy et al. (90). **B:** Khan et al. (100) asked observers to execute a saccade toward a flashed target during pursuit eye movements. Saccadic reaction times (RT, left, $n = 8$ subjects) and manual reaction times (right, $n = 7$ subjects) in the pursuit condition compared with a fixation condition. Positive numbers indicate ipsiversive (i.e., in the direction of pursuit) peripheral targets, as shown in insets, whereas negative numbers indicate contraversive peripheral targets. The red area indicates prolonged reaction times during pursuit and the green area indicates reduced reaction times. Adapted from Khan et al. (100). **C:** stimulus used in experiment 2 of Chen et al. (112). Observers had to pursue the center disk. The surrounding checkerboards define different areas, including a wedge ahead or behind pursuit divided in two areas centered at 1.5° and 3.5° . **D** shows the amplitude of the response to the checkerboards extracted from the SSVP signal (see text) during pursuit and fixation for the checkerboards ahead of pursuit and behind ($n = 12$ subjects). **C** and **D** are adapted from Chen et al. (112). SSVP, steady-state visually evoked potential.

attention. Rather, the effect should be ascribed to decision-making (4, 22). Previous studies also indicated that reaction times can be sped up by exogenous cues without facilitating perception, indicating a choice bias in the absence of a change in sensitivity (93). Both effects may be deemed attentional but only one is related to the change in visual processing that is observed with discrimination tasks. Differences in reaction times may be caused by sensory, motor, attentional factors or their interaction (94). Therefore, we cannot take for granted that the bias in reaction times observed during pursuit implicates visual attention, at least not only.

The initial observation that saccadic reaction times are asymmetric during smooth pursuit eye movements is very robust and has been observed in a variety of conditions (95–105). The appeal of Van Donkelaar's proposal—that the asymmetries in reaction times reflects attention being biased ahead of the pursuit target—could have masked a more prominent feature in these data. The fact that latencies are prolonged opposite to the target direction compared with fixation (99) could have a different origin, such as the suppression of reafferent motion signals during pursuit (33, 106, 107), that is, the retinal motion signals that are the result of pursuit and not motion in the world. The most comprehensive data set documenting saccadic reaction times during pursuit is provided by Khan et al. (100). As summarized in Fig. 5B, saccadic reaction times are shorter over the whole ipsiversive hemifield (in the direction of pursuit) than for the contraversive visual field (opposite to the pursuit direction). Right ahead of the target, reaction times are prolonged, not shortened, which can be explained by responses merging into the population of catch-up saccades (which are not triggered by the same signals as normal saccades; 27). More importantly, saccadic reaction times are not shorter for targets ahead of pursuit compared with fixation. Rather, saccadic reaction times are longer for targets behind the pursuit target. Therefore, the pattern of a result is a suppression of saccadic reaction times in the reafferent direction on top of overall suppression compared with fixation.

Further evidence suggesting that visual attention is biased ahead of pursuit relied on manual reaction times (100). Relative to fixation, we see again an advantage for the ipsiversive over the contraversive hemifield. In that respect, the pattern is similar to the one observed with saccadic responses (Fig. 5B). However, manual reaction times show facilitation relative to fixation for the ipsiversive hemifield. The scale of the ipsiversive advantage over contraversive advantage is also at odds between response modalities: it is of ~5 ms for manual reaction times and ~20 ms for saccades. If the advantage for ipsiversive targets were due to a common sensory processing stage modulated by visual attention, then we should expect a similar delay in manual and saccadic responses. Actually, while fixating, Malienko et al. (108) report exogenous cueing effects (about a 10 ms reduction in RTs) in the same order of magnitude for manual and saccadic responses, confirming a common attentional benefit with either response mode. One anonymous reviewer argued that if we subtracted dual-task costs (i.e., the overall difference between pursuit and fixation tasks), we would see facilitation ahead of pursuit in saccadic and manual tasks. However, we would need to make the extra assumption that dual-task costs are higher in saccadic RTs compared with

manual RTs, for which evidence is missing. Therefore, we may interpret the findings in different ways, among the options, there could be an overall suppression of visual processing in any direction, but with stimuli ahead of pursuit benefitting from more attentional resources. Or there could be an overall suppression, but with stimuli opposite to pursuit receiving more suppression.

However, if it is not visual attention, then what is it that explains faster RTs in the direction of pursuit? As we have seen above, quantitative predictions indicate that those interpretations are only partially compatible with the data. Considering perceptual and response asymmetries during pursuit eye movements under the umbrella of attentional allocation can conceal the fact that vision during pursuit is not the same as during fixation (e.g., 109, 110). For instance, color discrimination is enhanced during pursuit compared with fixation (109), without visual attention having an obvious role. In the same vein, motor coordination may be facilitated in the pursuit direction or suppressed opposite to its direction without involving an attentional mechanism. Harrison et al. (111) sought to disentangle visual from attentional processes by using a crowding paradigm. Crowding is an impairment in the ability to recognize a visual target in the presence of surrounding elements (e.g., a letter flanked by other letters). The main finding was that crowding was stronger, as indexed by critical spacing (distance from flankers at which perception is impaired), for patterns in the contraversive hemifield compared with fixation and patterns in the ipsiversive hemifield. Knowledge about where the target would appear did not alter performance, suggesting that this asymmetry in crowding is insensitive to the endogenous orienting of attention. Whether we consider crowding to be an attentional phenomenon or not, this effect would indicate a reduced ability to resolve detail opposite to pursuit compared with fixation, and not an enhancement ahead of the target.

A further complication of the dual-task experiments seeking to evaluate the distribution of attention while pursuing a target is that we cannot exclude the influence of the secondary perceptual task on how attention is distributed. Chen et al. (112) avoided this problem, by measuring steady-state visually evoked potentials (SSVP) during pursuit. The method involved the presentation of visual patterns around the pursuit target flickering at different rates (shown in Fig. 5, C and D) to extract cortical responses to different parts of the visual field. Checkerboard patterns ahead and behind the pursuit target could be tagged with different flicker frequencies, allowing one to infer asymmetries in visual processing around the pursuit target. Figure 5D shows larger potentials ahead of pursuit, which is consistent with the idea that attention is allocated preferentially ahead of the target. However, they also show that the SSVP signal is overall of smaller amplitude compared with fixation. Consistent with the saccadic reaction time results, a prominent feature of the results is the suppression of visual processing during pursuit relative to fixation, selectively sparing patterns centered at 1.5 degrees of visual angle in the ipsiversive hemifield. The suppression of the contraversive hemifield may be accounted for by the same factors that cause the crowding asymmetry observed by Harrison et al. (111). If true, a testable

prediction is that this asymmetry should depend on the pattern scale, which determines whether crowding occurs.

To sum up, there are still several pending questions regarding the distribution of attention during pursuit. Reaction times and neural responses to stimuli presented in the contraversive hemifield during pursuit are suppressed compared with those presented in the ipsiversive hemifield and compared with fixation. It is not clear whether this effect results from the modulation of visual processing by visual attention or not. The studies that have used perceptual tasks showed perfectly symmetrical performance (89, 90), despite evidence that visual processing is asymmetric in the direction of pursuit, affecting our ability to resolve detail behind the pursuit target, as shown by crowding performance (111). Further research should seek to determine whether perceptual asymmetries reflect visual processes, their modulation by visual attention mechanisms, or both. This would allow telling apart rival interpretations, one proposing that attention is ahead of pursuit and thus benefits performance and another one which would account for asymmetries through the suppression of reafferent visual signals, which are overwhelmingly opposite to the pursuit direction.

THE NEUROPHYSIOLOGY OF SELECTIVE ATTENTION AND TRACKING EYE MOVEMENTS

Imaging studies in humans and single-cell neurophysiology in monkeys have shown a large degree of overlap in the activity elicited by saccades and endogenous shifts of attention, suggesting shared control via a fronto-parietal cortical network (113, 114) and a subcortical attentional network (for a review, 115), which may respectively contribute to visual selection by integrating top-down signals and computing physical saliency (116, 117). Although the frontal eye fields (FEF) may have a role in enhancing visual signals during voluntary pursuit and saccadic eye movements via projections to extrastriate cortical visual areas, the superior colliculus (SC) has been pinpointed as an important structure for understanding the coordination of target choice for pursuit and saccades (e.g., 54), vector averaging behavior during pursuit (118), and possibly the modulation of visual processing via noise exclusion (119). The latter is a point of contention, as it would indicate that subcortical and cortical areas contribute to eye movement target selection in fundamentally different ways (6). Specifically, monkey physiology, especially within the last 10 years, has indicated that voluntary visual selection can rely on subcortical pathways, beyond their traditional role in driving exogenous allocation of attention. The SC in the midbrain has been identified as an important site for target selection (20, 118–123), which may participate in the modulation of visual processing via different circuits, involving the thalamus, the brain stem, and the cerebellum, perhaps even bypassing the cortex (115).

Figure 6 provides a sketch of how cortical and subcortical structures control visual selection, saccades, and pursuit eye movements. The cortical control of voluntary pursuit and visual attention implicates several “eye fields” receiving visual inputs from early and later stages in the visual processing hierarchy, such as the middle temporal (MT) and medial superior temporal (MST) area (124). The supplementary eye

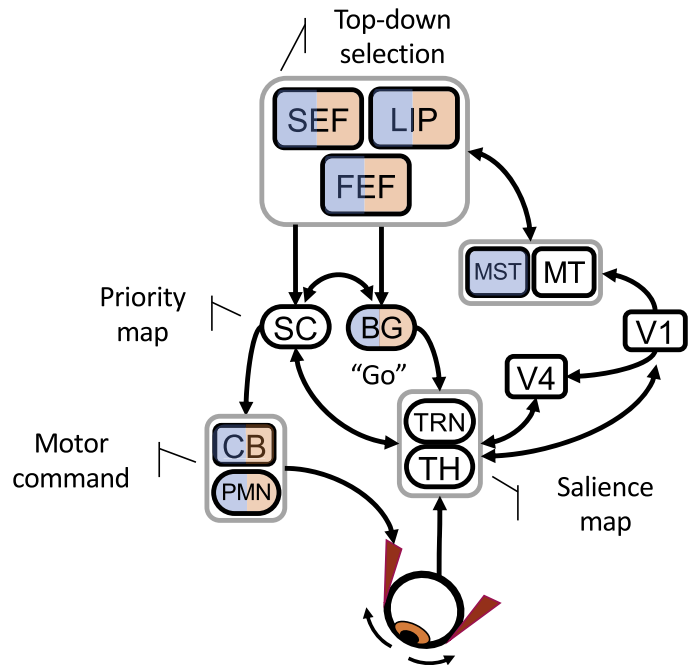


Figure 6. Outline of major cortical and subcortical pathways involved in the voluntary control of pursuit, saccadic eye movements, and visual selection, in the macaque brain. CB, cerebellum; FEF, frontal eye fields; LIP, lateral intraparietal cortex; MT, middle temporal cortex; MST, medial superior temporal cortex; PMN, premotor nuclei in the brainstem; SC, superior colliculus; SEF, supplementary eye fields; TH, thalamus; TRN, thalamic reticular nucleus; BG, basal ganglia; V1, primary visual cortex; V4, extrastriate cortical visual area. In blue (pursuit) and red (saccades) are areas or subregions that control specific eye movements. Gray boxes correspond to subcircuits. Note that we have omitted many connections. For instance, superficial layers of the SC receive a direct retinal input. Also not detailed are the numerous nuclei that comprise the thalamus, such as the lateral geniculate nucleus (LGN), the main relay of retinal information to the SC, and the pulvinar, which has reciprocal connections with several visual areas along the ventral and dorsal visual processing pathways, which made it with TRN a candidate for computing visual saliency and drive competition for neural representation along various feature maps (116). Visual areas also project to the SC.

field (SEF), frontal eye field (FEF), lateral intraparietal area (LIP, in the human the parietal eye field), and MST form a densely connected network of areas implicated in the voluntary control of saccadic and smooth pursuit eye movements (124). Saccade and pursuit related signals are segregated in subregions of SEF, FEF, and LIP and run in parallel in the cortex (125). In addition to being responsible for the voluntary control of eye movements, they participate in amplifying task-relevant sensory information. FEF can influence saccade and pursuit target selection through the SC and indeed provides a major cortical input to the structure. The SC is interconnected with the basal ganglia (caudate nucleus, CN, and substantia nigra pars reticulata, SNr). This subcircuit may be responsible for providing a go signal and adjusting response criteria (20). Another subcircuit is formed by the thalamic reticular nucleus, and the pulvinar within the thalamus. The flow of visual information between those two regions and the visual cortex have been postulated to be the embodiment of the “spotlight of attention” by Shipp (116). The pulvinar has bidirectional connections with visual areas along the ventral and dorsal visual processing stream, which makes it a suitable region for spatial selection across features

maps, a requirement to compute physical salience (116), and allowing for amplification of visual signals through a global competition, which is a competition across different spatial and feature maps. In this sketch, the SC is therefore an integrative region, in the sense that it integrates physical salience with behavioral goals to coordinate pursuit and saccadic eye movements. Its role has been defined as forming a priority map, that is, a map where activation indicates the most relevant location for behavior, rather than physical salience or any other stimulus property (117). Consistently, inactivation of the SC affects reach target selection as well as eye movements (126). A broadly similar structure was proposed to apply across vertebrate species by Knudsen (127), based on work in the avian and rodent brain. Finally, the SC represents movement priority by a spatial code in its intermediate layers, which is then translated into an appropriate motor command (calculating inverse dynamics) within a network comprising the cerebellum and premotor nuclei within the brain stem, or PMN (128, 129). The cerebellum, specifically the vermis and flocculus-paraflocculus complex, has an important role in the adjustment of motor commands for pursuit and saccades from visual errors. Lesions of the oculomotor vermis lead to hypometric saccades and slow open-loop pursuit, and an inability to adaptively change those movements based on trial-to-trial visual error feedback (130, for a review, 131). Some authors have proposed that the cerebellum has a role in the accurate planning of spatial shifts of attention, mirroring its role in adjusting saccade metrics. However, there is little unambiguous evidence that the cerebellum plays a role in visual selection independently of its oculomotor function (132). Because their role in visual selection is unclear, we are not detailing those descending pathways. Pursuit and saccade descending pathways have been reviewed in detail by Krauzlis (133).

How do cortical areas contribute to visual selection during pursuit? The pursuit-related area abutting FEF, area FEFsem or frontal pursuit area (FPA), appears to have a role in regulating the visuomotor gain of pursuit—e.g., the ability to adaptively amplify responses to motion during pursuit compared with fixation (134). After ablation of FEF, monkeys track a target by a series of forward catch-up saccades (135). Those two findings could be explained by FEFsem having a role in pursuit target selection, either by affecting motion signals in MT/MST or by influencing spatial selection in the SC. However, FEFsem inactivation may influence the visuomotor pursuit gain independently of target selection. That is, FEFsem is suggested to have a role in selecting the *response* (i.e., whether to pursue or not) but not the *target* of the eye movement (136). On the other hand, there is good evidence that activity in FEF (137, 138) and LIP (139) is related to voluntary shifts of visual attention in preparation of a saccade, as microstimulation below the movement threshold influences visual processing, presumably by shifting spatial attention toward the neuron's movement field (140, 141). Juan et al. (142) showed how visual selection signals in FEF can be selective to the visual target in an antisaccade task but have no influence on saccade trajectories, suggesting that FEF may steer visual selection while not being necessary to the coupling of visual selection and eye movements (see also 143).

At first sight, areas MT (V5 in the human) and MST seem ideal candidates for mediating the coupling of visual

attention and pursuit eye movements, since they process the visual inputs driving pursuit eye movements (144, 145). It is well established that feature (selection by motion direction) and spatial attention modulate responses multiplicatively in MT and MST (146, 147). Yet, the relationship between neural activity in MT/MST and pursuit is not straightforward. Although MT/MST activity is clearly correlated with the latency of ocular following (148), it is not predictive of target choice during pursuit (53). Furthermore, cell responses to the pursuit target are only modulated by target choice when target and distractor fall within the same receptive field (149, 150). These findings point to a target selection locus downstream of MT/MST. As we will see in the next section, the superior colliculus, which receives top-down spatial information from the FEF and visual information from MT/MST, could be well-suited for the job.

The Superior Colliculus

As we have seen above, the SC forms a priority map integrating top-down goals and physical salience. The SC also forms a priority map in the sense that its influence on eye movements is not restricted to specific movement types, but rather by specifying a motor goal that can be achieved in different ways. The SC contains a retinotopically organized and layered structure. Although superficial layers of the SC respond to visual stimuli, neurons in intermediate and deep layers have visuomotor responses. Experiments conducted by Carello and Krauzlis (151) show that visuomotor neurons are involved in the coordinated target choice for saccades and pursuit by spatial selection. Triggering saccades to moving targets by localized microstimulation in intermediate layers also generates a pursuit eye movement in the direction of the target that is selected by the saccade, suggesting that the SC could mediate the coordination between saccades and pursuit target choice.

In a first direct attempt to establish the role of the SC in both the shift of visual attention to the saccade target location and the control of saccade target selection, Kustov and Robinson (152) used microstimulation to trigger saccades during exogenous and endogenous spatial cueing. Supporting the idea that visual selection amounts to saccade target selection, saccades triggered by microstimulation deviated in the direction of an exogenously or endogenously cued location. Deviations also tracked the dynamics of attention shifts across time, with a build-up within 150 ms for exogenous cues, and circa 300 ms for endogenous cues. Therefore, at the neuron population level, attention shifts were likely combined with saccadic movement vectors elicited through microstimulation in the SC. At the single neuron level, the coupling of attention and saccadic target selection was investigated in build-up cells. Build-up cells are in intermediary layers and increase in activity before a saccade is executed. Ignashchenkova et al. (153) distinguished between three types of neurons in those layers. Visual neurons with a response to the target, motor neurons with a response to saccade preparation, and visuomotor neurons with a visual and motor response. A majority of visual and visuomotor neurons was significantly modulated by attention, whereas motor neurons were not. Further, there was a difference between visual and visuomotor neurons. Visual neurons showed a clear attentional modulation with

both endogenous and exogenous cues (i.e., larger activity for cued stimuli falling on their receptive fields), whereas the modulation with endogenous cues was weaker in visuomotor neurons. One could suggest that endogenous (central) cues require top-down control and modulate SC activity via feedback from the cortex, whereas direct bottom-up control over eye movements and attention shifts could be exerted at the level of the SC. The lack of modulation in visuomotor neurons by endogenous cues indicates that the voluntary control of attention may not necessarily implicate the generation of an eye movement program.

Although there is clear evidence of modulation of neuronal activity within the SC in response to various cues, this does not tell us about its role in modulating visual processing. Activity in the SC could have different effects on visual and nonvisual responses to cues. One possibility is that SC activity biases response choice without impacting sensory processing, as can be said of the effect of cueing on behavioral responses (6). A reanalysis of prior microstimulation studies within a signal detection framework (122), an analysis of interindividual differences in functional connectivity (fMRI) in the human (154), and correlations between SC activity and shifts in response criteria (20), suggest that the SC activity may impact target choice by shifting response criteria in favor of precued target locations, without generating a spatial bias in the global competition for sensory representation as suggested above (e.g., 116).

The view of the SC as determining target choice but not necessarily enhanced visual processing could explain the puzzling findings from Zénon and Krauzlis (123). As expected from the idea that the SC impacts vision and eye movements, they found that localized inactivation of the SC impacted the ability to discriminate the target and simultaneously biased target choice for pursuit and saccades (see also 155). Consistent with the idea that attention impacts sensory processing at the level of MT/MST, they could see an enhanced response for cued motion in those areas. However, SC inactivation had no measurable effect on the cue-related attentional modulation observed in MST and MT, meaning that visual information must have been prioritized via alternative pathways, which do not involve the amplification of firing rates (115). Sreenivasan and Sridharan (154) suggested that in the human brain, there is no need to find such alternative pathways because the SC only affects target choice. In the monkey brain, however, recent inactivation studies using a paradigm to separate shifts in criterion from shifts in sensitivity (122, 156) indicate the SC does enhance sensitivity in the task. This led to the suggestion that target representations are enhanced by excluding distractor signals (noise exclusion), rather than by enhancing the cortical representation (signal enhancement) of the target (119). By contrast, in the monkey cortex (area V4), endogenous cues increase perceptual sensitivity by signal enhancement (157). In sum, effects of SC inactivation do not simply mirror the effect of attentional cueing in the cortex, which could indicate it has a causal role in the selection of the spatial locations on which responses to stimuli and eye movements are based but not necessarily in stimulus enhancement.

The SC role in controlling target choice during pursuit initiation has also been demonstrated by inactivation studies. Inactivating the spatial receptive field of one of two potential

targets biased initial pursuit direction, suggesting SC signals are not only related to winner-take-all target selection but they also control the weighting of different motion signals. An important aspect of the paradigm was that the sensory signals originated in the lower or upper hemifield and moved toward the opposite hemifield, thereby separating spatial target selection from the movement direction (118). Those findings suggest that the SC set the target weights that determine vector averaging and subsequent winner-take-all behavior. Those weights may be determined by cortical signals modulated by attention and the intrinsic dynamics of the SC.

The superior colliculus is also heavily connected to other subcortical circuits, which could bias sensory processing and target choice. Among those are indirect pathways involving the basal ganglia, which supplement the direct pathway from FEF to SC and the pathway from MT/MST to premotor and cerebellar nuclei driving pursuit. Parallel indirect pursuit and saccade-related pathways go from FEF to SC via the CN and SNr nuclei (158). However, studies have also shown pursuit and saccade-related activity in the same neurons but showing different responses, e.g., directional preferences for visually guided saccades but not for pursuit. Microstimulation within the SNr affects pursuit, proving a causal implication of the circuit. However, unlike visuomotor activity in the SC, there is a low correlation between the SNr signal and the saccade position or pursuit velocity error, taken to suggest that the basal ganglia's role is in enabling saccades or pursuit by disinhibition of the SC (158, 159). However, other findings are consistent with the role of the SNr in target choice, as responses to a visual stimulus in the SNr can change with the probability that it will be selected as a saccade target, providing a mechanism by which the movement is gated by the disinhibition of activity in the SC, but without being directly responsible for target selection signals in the SC (159). It remains to be demonstrated that the same control principles apply for pursuit eye movements. To sum up, physiological evidence provides an increasingly differentiated picture of the role of cortical and subcortical pathways in shifting spatial attention and selecting eye movement targets. The SC appears as a key bottleneck, as its activity can be modulated by cortical top-down signals and it is able to coordinate target selection for pursuit and saccadic eye movements. It is less clear how spatial selection originates in the SC, and how it affects visual processing. This may require the exploration of the many pathways that include the SC.

■ A MODEL FOR VISUAL AND EYE MOVEMENT SELECTION

Our review of the behavioral and neurophysiological literature indicates a clear coupling between covertly shifting visual attention and selecting the target of a saccade (11), whether voluntarily executed or not (e.g., 152), leading to an enhanced visual representation of the saccade target to the exclusion of other objects. Yet, the pursuit eye movements that precede the catch-up saccades to a moving object suggest a more flexible relationship. A general model, or one that would account for tracking eye movements, would account for a coupling that is loose during the initiation of pursuit and tighter during saccadic onset, as the initiation of

pursuit is relatively unaffected by distracting spatial attention away from the target (67). In addition, the flexibility of the coupling depends on stimulus characteristics (76). We suggest that the coupling of spatial attention and eye movements can be a consequence of a heightened execution threshold in catch-up saccades and closed-loop pursuit, compared with pursuit initiation. This simple model can explain the differential role of attention for different types of eye movements and generates testable behavioral predictions, building on the notion that target selection for different types of voluntary eye movements is based on the same target signals, which may originate in the SC priority map (e.g., 151). To illustrate our argument, we will focus on pursuit initiation in the presence of a distractor. This situation provides a good test of the mechanisms at play, allowing us to contrast different eye movement directions and latencies. However, the same principles can be extended to catch-up saccades during steady-state pursuit.

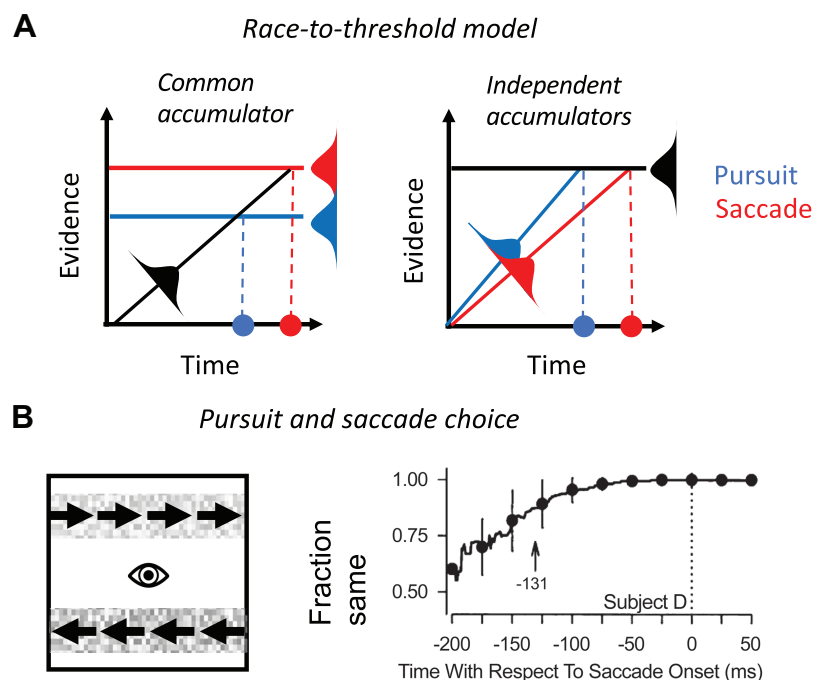
Model Components and Assumptions

Our starting point is that target selection for pursuit and saccadic eye movements are based on the same neural signals, but with pursuit being executed at lower thresholds. Figure 7A shows the predictions of two models of saccade and pursuit coordination proposed by Liston and Krauzlis (18). One model postulates a common accumulator with two different thresholds and the other model postulates two accumulators, independently accumulating evidence toward a single execution threshold. Both models can explain faster latencies for pursuit compared with saccades, but only the common accumulator model is compatible with target choice findings. Figure 7B shows an ocular tracking task in which saccade and pursuit choices can be dissociated. The observer is faced with two moving patterns moving horizontally

in opposite directions and located upwards or downwards from fixation. Their task is to track the moving pattern of changing contrast, which requires a saccade to foveate the target pattern and pursue its motion direction. The pursuit choice (pursuit direction) corresponds perfectly to the saccade choice when pursuit is measured close to the execution of the initial saccade, meaning that observers pursue the motion that is selected by the saccade (18). Therefore, pursuit and saccades rely on the same *spatial* target selection signals, except that pursuit is executed based on less evidence and with a much shorter average latency (52, 160, 161). Unlike the serial-linkage model of Gardner and Lisberger (54), which postulates winner-take-all pursuit target selection by the initial saccade, Liston and Krauzlis's (18) findings suggest a gradual increase in the agreement between spatial biases for pursuit and saccade, suggesting that coordination is not dictated by the saccade but through the reliance on the same time-varying decision signal. We can argue that the capacity limitations of visual attention can explain how different evidence thresholds set different requirements for visual selection of target representations. That is, visual selection is increasingly aligned with the eye movement target at higher execution thresholds.

We can view attention as a finite resource—e.g., resulting from the number of neurons representing the object, or resulting from mutual inhibition between neurons representing different features (162)—that enhances an object representation to the detriment of other objects in the scene, whether allocation of this resource is controlled by physical salience (contrast with the background) or the demands of the task (e.g., 5, 163). Given a limited pool of resources, increasing the evidence threshold means that a greater concentration of attentional resources devoted to processing the target representation is needed to reach that threshold.

Figure 7. A: pursuit and saccade decisions could be modeled as being based on the same accumulation of evidence, but with different execution thresholds (*left*). It could also be modeled as a decision based on different sources of evidence but reaching the same threshold. The decision to pursue would then be faster because there is faster accumulation of evidence. In this model, internal noise corrupts the decision process, allowing to predict the shape of the distribution of latencies as well as the average. **B:** in the study of Liston and Krauzlis (18) (Copyright 2003 Society for Neuroscience), observers track one of two visual patterns moving in opposite directions and located either upward or downward from the initial fixation point. The task of the observer was to track the strip which contrast changed during a short time interval (the upper strip in this example). The task requires a saccade to the strip location as well as pursuit of the strip motion. This paradigm allows to calculate the agreement between pursuit and saccadic choices as we approach the execution of the saccade. Choice agreement would mean that the pursued strip is also the fixated strip. In the illustration if we saccade downward but pursue upward there is a choice disagreement. The data (*right*) indicates perfect agreement as we approach saccade execution, providing good evidence for a single accumulator, where the same signals are responsible for target selection, but with different execution thresholds.



Therefore, one of the consequences of a lowered threshold for pursuit initiation is more flexibility in the allocation of resources to nontarget representations compared with saccade or catch-up saccade initiation.

The idea that attention is a limited resource is related to the “spotlight” and “zoom lens” metaphors of visual attention (e.g., 164). The “zoom lens” model of attention (165) postulates that the attended area (such as defined by possible target locations) or attention field (166, 167) can be adjusted depending on task demands. However, the efficiency of processing the attended information is inversely related to the size of the attention field. This is equivalent to saying that the effect of attention is to distribute a finite pool of visual processing resources. Behavioral (168, 169) and imaging evidence (166, 170, 171) support the zoom lens model, although its neural implementation remains unclear, since there are multiple stages of competition between visual features which could embody the notion of a finite visual resource. One possibility is offered by the shift in the center of receptive fields toward the focus of attention that has been observed in MT (172, 173) and V4 (174), meaning that more neurons are recruited to process the attended region (175–177).

In Fig. 8, *A* and *B*, we illustrate the relationship between the distribution of visual resources among two moving objects and the execution of different eye movement types within a race-to-threshold model in which, consistent with Liston and Krauzlis’s (18) findings, we set the pursuit threshold lower than for the initial catch up saccade. In Fig. 8*A*, we contrast evidence accumulation in a task in which one of two orthogonally moving dots is designated as the target (precued; solid lines) to a situation in which no prior information is given about which of the two motion signals is going to be the target (dotted lines; uncued condition), thereby corresponding to a stimulus-driven response. The accumulation of evidence is represented by a saturating function, representing the fact that signals do not necessarily reach execution thresholds if given more time. When the target is salient (i.e., the target is high contrast relative to the distractor; *top*) and it is precued, evidence in favor of the target (black line) accumulates much faster than for the distractor (gray line) and reaches the pursuit and saccade threshold much earlier. The cue results in a top-down bias toward the target location, which gradually suppresses the accrual of evidence at the distractor location and simultaneously enhances the accrual of evidence at the target location, consistent with the sharing of a limited visual processing resources. In this example, in which the distractor has low salience, this means that evidence in favor of the distractor’s representation never reaches the lower (pursuit) threshold. In the second scenario, when the target is not salient (Fig. 8*A*, *bottom*), a greater concentration of visual resources is needed to reach the threshold for catch-up saccade execution, since target evidence is lower than the distractor evidence to start with. This last point is illustrated in Fig. 8*B* in terms of the spatial distribution of attention, showing how the attention field may change with time, and necessarily becomes more selective to the target when its salience is low.

In the example above, stimuli differ in salience, which brings the target activity closer or farther away from a threshold, reducing or increasing the need for a top-down

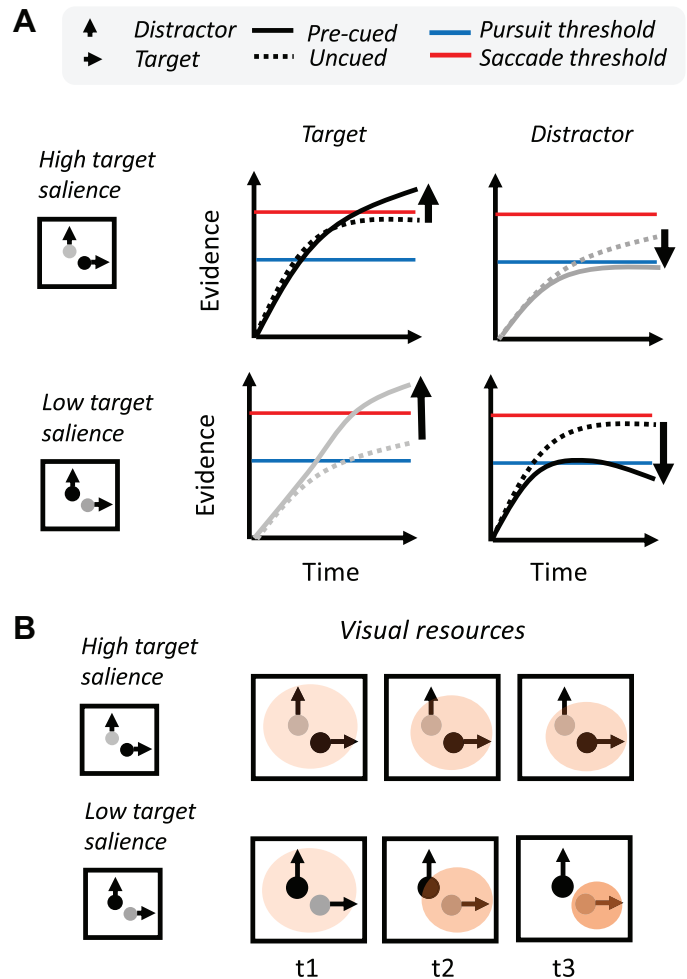


Figure 8. *A*: illustration of how visual attention can be implicated to different extents depending on the salience of a moving target. The target is always moving to the right and the distractor is always moving upward. High target salience: the execution threshold for the target can be reached without implicating much attentional resources after precueing the target, as illustrated by the small increase in evidence accumulation for the target (upward arrow) and little accompanying suppression of accumulation for the distractor (downward arrow). As a result, some attentional resources are free to process information outside the location of the target. Low-target salience: after precueing, attentional resources are required to reach the saccade execution threshold, both by increasing the evidence for the target and suppressing evidence for the distractor. *B*: hypothetical distribution of spatial attention of attention across time in low and high target salience.

bias to resolve the competition between competing motor representations. In the visual domain, a similar situation arises when looking at the interaction between top-down bias and salience. The amount of attentional modulation (inferred from the BOLD signal) that can be measured along V1 to V4 depends strongly on the salience of the stimuli (either forming a perceptual group or not), with top-down attentional modulation being greater when the competition between stimuli is not resolved in a bottom-up manner (178). The literature on saccades lends also some support to the idea that attentional requirements depend on target salience. Reflexive saccades, such as the ones forming the quick-phase of optokinetic nystagmus (OKN), show no coupling with attention (179), which could represent the extreme

case when a very salient target (in the absence of a distractor) reaches the saccade execution threshold without implicating top-down attentional control. However, one cannot exclude that the execution threshold of those saccades may be lowered (180). In summary, in those two opposing scenarios, the coupling of top-down attention and eye movement target selection depends on target salience and the execution threshold of the eye movement.

Model Predictions

The relation between the distribution of visual resources and eye movement execution could account for three main phenomena: 1) changes of the coupling of visual attention during tracking eye movements (comprising a pursuit and saccadic component), 2) averaging behavior, and 3) the coordination of saccades and pursuit.

The model accounts for how the coupling of attention and eye movements depends on movement latency, with pursuit being initiated without much involvement of attention (67), whereas selection is bound to the target during steady-state pursuit. This model also predicts that the coupling between attentional resources and pursuit or saccadic eye movements is inherently flexible, depending on target salience. This aspect is supported by previous studies (76), which showed enhanced perceptual performance in the periphery when the motion energy of the tracked target is higher than the traditional dot. Although the authors' interpretation is based on the idea that extended targets implicate different neural networks, it is also a testable prediction of the model that salient targets allow for attentional resources to be freed from the pursuit target. Salience can be modulated in different ways. A manipulation of salience independent of target size and motion energy would be able to tell apart whether the flexibility of attentional resources is primarily based on salience rather than size. For instance, a black target among white distractors compared with a black target among black distractors has the same motion energy but very different salience because the white dots pop out from the distractors.

Likewise, averaging behavior can result from the interaction between top-down attention and salience. A priority map common to pursuit and saccades, such as the one formed by the SC, sets the weights of the motion signals that are averaged and drive pursuit. Averaging occurs when the execution threshold is reached while the distractor representation is not yet suppressed (18). The validity of the model can be tested by manipulating salience and task demands. Top-down control can be manipulated by comparing precued and uncued conditions. The relative weighting then determines the direction of the pursuit response. If that is true, the effect of top-down attention (precued vs. uncued) and salience (high vs. low contrast) should be reflected in the averaging behavior. In that proposal, vector averaging indexes the allocation of visual resources to target and distractor, and therefore pursuit direction should reflect the dynamics of visual resource allocation. A dual task in which perceptual selection is assessed across time with averaging behavior could be used to test this prediction. Here, we focus on pursuit, but a similar argument could be made for saccadic averaging behavior (the global effect). For instance,

visual attention in averaging saccades is shifted to both target locations and not to the saccade end point, suggesting that saccade averaging is also an index of visual selection (181).

The model we propose is also compatible with the coordination of saccadic and pursuit eye movements by spatial selective attention. This idea was implicit in Liston and Krauzlis's proposal that there is a spatial selection mechanism common to both types of eye movements. A similar point was made by Erkelens (17), but based on a rather different line of evidence. He investigated pursuit eye movements and target choice in tracking 2D trajectories with targets that either overlapped temporally or not (gap condition). In overlap conditions, observers would often continue tracking the previous target before a saccade to the new target occurred. Further, pursuit and saccade latencies were hardly correlated. In contrast, pursuit and saccadic decisions (direction and latency) were well correlated in gap conditions. Erkelens (17) concluded that choices are coordinated by attention but that the pursuit target can remain engaged to the previous target "at the execution level." We believe this interpretation is compatible with ours, in that engagement to the previous target occurs if the new target has not yet reaching an execution threshold. In the gap condition, however, bottom-up (the target is the only moving signal) and top-down resources are engaged to the new target.

Further computational and behavioral investigations could test and refine this model. A rather simple competitive neural network model, proposed by Ferrera and Lisberger (48), can account for the dynamics of target selection driving pursuit eye movements. In the model, every motion analyzer (e.g., MT neuron) is connected via excitatory connections with neurons representing the same motion direction, and via inhibitory connections with different directions. After several iterations, the population activity transitions from a vector-average to a winner-take-all response (50). This activity explains the latency benefit when target and distractor move in the same direction (48). The possibility was entertained that attentional filters may act by shaping the weights of the connections of the competition network, which could be implemented within the pathway going from the FEF to the SC (182). The normalization model of visual attention (167) offer a computational implementation of the neural competition for representation that could generate testable predictions in the type of situation we have described and could help refine the type of neural interactions giving rise to target selection during tracking eye movements.

We have summarized here how a race to threshold model can account for the dynamics of visual selection during tracking eye movements. This simple model makes several predictions, provided with some assumptions about the way visual resources are distributed. First, pursuit should be less reliant on the allocation of attention to the target depending on the salience of the tracked stimulus, which could explain freed attentional resources during the tracking of large objects (76, 89). Second, it could explain vector averaging behavior during pursuit initiation and the subsequent winner-take-all behavior. Third, it could also explain the apparent linkage between catch-up saccades and steady-state pursuit, as a consequence of both relying on visual selection of the target.

As suggested by Basso and May (183), the SC itself may implement the normalization model of visual selection (167). Normalization assumes that the activity corresponding to two stimuli is the average of the activity elicited by each stimulus on its own and not its sum. As a consequence, a salient stimulus will be suppressed to a greater extent if the less salient stimulus needs to be selected. The inhibitory connections within the SC seem to implement normalization rather than the summation of signals. Ferrera and Lisberger (49) noted how the difference between target and distractor activity in MT/MST is too small to account for the differences in pursuit latency, especially when they appear in different hemifields. The same can be said of purely perceptual tasks, where there is little competition between hemifields (184, 185). However, those distant interactions exist at the level of the SC, further indicating the SC as a priority map for eye movements (183), which could account of the motion signals driving pursuit and catch-up saccades through spatial selection. Selection signals could originate in FEF, drive normalization along the visual cortex, and coordinate eye movements via the SC. Stimulus distance could be used to disentangle the subcortical and cortical competition driving pursuit eye movements, as there are much weaker inhibitory interactions in the cortex at longer distances (e.g., across hemifields). We can then expect perceptual tasks that rely on the cortex to dissociate from oculomotor selection.

Extension to Naturalistic Tasks

Extending a target selection model to the complex scenes involved in natural behavior requires us to go beyond pairs of dots moving within a frontoparallel plane. In Fig. 9A, we show a natural scene superimposed to the optical flow resulting from walking. In this situation, features are not neatly separated in space between target and distractor and selection is made in three dimensions, requiring pursuit vergence. Here, visual selection mechanisms are necessary for pursuit of a target in the presence of competing distractor stimuli. These mechanisms are also necessary to sustain pursuit in the presence of a moving background, as the (reafferent) background's retinal motion becomes predominant when the target is tracked (71). In the presence of equally salient objects, selective behavior relies on filtering out distractor signals. Motion in various directions abounds across the image, which is segregated into different objects and surfaces early on, based on low-level cues and top-down information, especially when low-level information is ambiguous (186). In this latter case, attention may play an important role in grouping information too, as demonstrated in the ability to pursue an integrated group of dots moving in different directions and surrounded by distractors (80, 82).

The visual system may select the target's visual features based on a variety of selection filters. The target to pursue

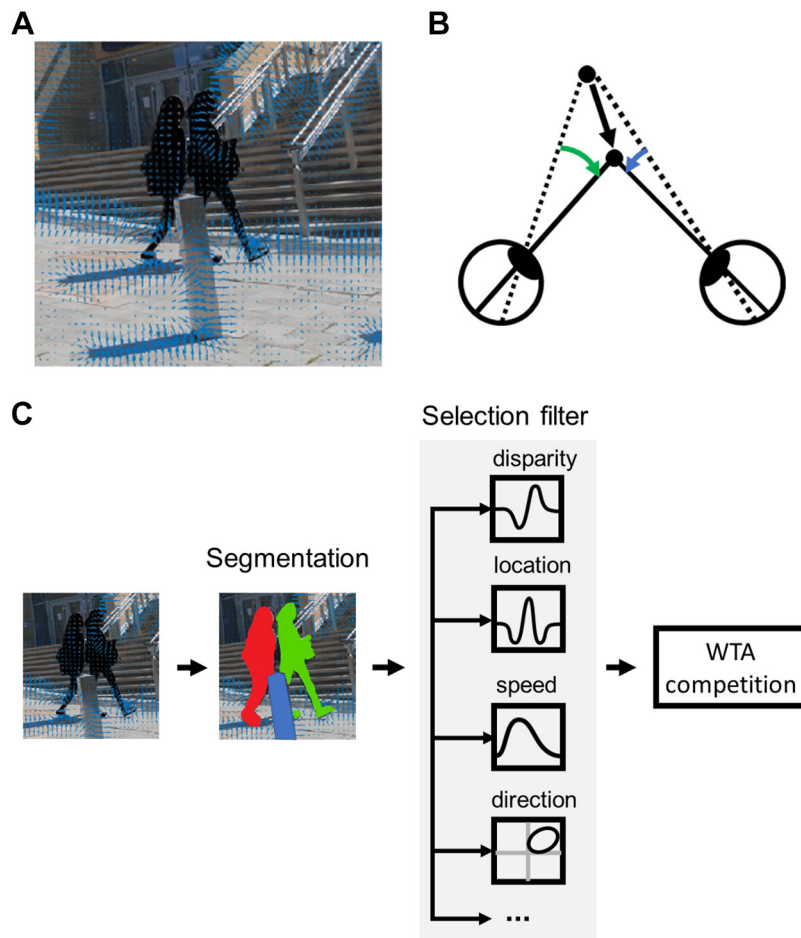


Figure 9. A: optic flow generated by walking in an urban environment. Extended objects, such as other walking people and obstacles, typically move in depth. B: pursuing targets in three dimensions (black arrow) involves coordination with the vergence system, sending conjugate (pursuit) and disconjugate (vergence) commands to the two eyes (green and blue arrows). C: a target selection mechanism is necessary to pursue the target in the presence of other equally salient motion signals. The filtering out of distractors can be guided by using a variety of top-down selection templates (filters), biasing the competition that results in winner-take-all (WTA) selection to drive tracking eye movements.

could be defined by its motion direction and speed but also by its position in the visual field, its depth, and object-related features, such as orientation, color, or shape. Those filters can bias the competition for representation and action taking place along the visual processing hierarchy, ultimately leading to selective behavior (55).

PENDING QUESTIONS

In this review, we have alluded to a few important questions relating to the coupling between attentional resources and pursuit eye movements. Central to further progress is the refinement of the mechanisms by which visual selection is achieved, allowing us to parcel out visual and motor factors. We also argue that the functional role of the coupling of visual resources to the eye movement target needs to be researched further. Beyond the function of enhancing the visual representation of the target object, the coupling may have a role in coordinating the target choice for different types of eye movement (e.g., 151).

Visual Processing, Visual Selection, and Motor Selection

Several types of dual tasks have been used to infer the need of visual attention for executing saccadic or pursuit eye movements. A caveat of those studies is that a model of how visual attention affects the secondary (nonoculomotor) task is missing. For instance, reaction times may be speeded by a change in response criterion or by speeded visual processing. Either process could be modulated by visual attention or not. Inferences about the role of attention in explaining saccadic reaction times during pursuit assume that the first stages of visual processing are unaffected by pursuit, or that vision during pursuit is equivalent to the fixation of a moving target. A further complication is that the need for visual attention may depend on the eye movement target itself. For this reason, a computational implementation of the link between visual and motor selection, from which to derive quantitative predictions, is required.

Modeling Selection Filters in Space-Time

Several issues essential to understanding the role of attention in generating pursuit eye movements have been little explored. For instance, we know little of the shape of the attentional filters used to select pursuit targets (see Fig. 9C). Psychophysical studies have shown that the effects of spatial selection can be modeled by an attentional filter made of an excitatory center and an inhibitory surround (187). The selection of motion direction for pursuit initiation may rely on similar spatiotemporal filters (or templates) combining spatial and motion information (50). However, it is not clear whether selection based on other attributes (e.g., motion, depth, shape, or color) is based on similarly shaped filters, whether those filters are flexible, and whether the same filters explain perceptual selection. Investigating those filters could also tell us about what determines the capacity to share attention between perceptual and motor targets. The variable-coupling model we put forth predicts that the amount of free attentional capacity is an emergent property of execution thresholds, with more resources being freed depending on bottom up salience, which could be reflected

in the selection filters having a flexible shape. We should note that although we focused on spatial selection to illustrate our model, spatial selection does not necessarily have a special role in target selection. The predominance of spatial attention in biasing a competition for neural representation in perception and action could be the consequence of spatial selection being the most salient feature in a specific paradigm. The same predictions may be made when considering other features (e.g., motion), for instance, in Spering and Carrasco's (188) transparent motion paradigm, in which target and distractors cannot be spatially resolved.

Our outline of the neural substrates of attention in relation to pursuit eye movements and psychophysical studies indicate that the visual system is *attuned* in many ways to performing pursuit eye movements (60, 109, 189). Endogenous and exogenous visual attention can have an effect at many levels along the visual system. Attention can also affect visual processing in a variety of ways, such as raising baseline activity, reducing noise correlations, increasing coherence for target activity across areas, enhancing the signal, reducing external noise, reshaping receptive fields, increasing response gain, shifting the effective contrast or sharpening tuning functions (for reviews, 190, 191). We have yet to understand how the smooth pursuit system exploits those mechanism to optimize pursuit and perception of the target and background. Whether there are specific attentional mechanisms supporting pursuit control remains an open question.

Small and Large Targets

As suggested recently (80, 192), the fact that the neurophysiology of pursuit eye movements may be separated into motion-correcting and position-correcting neural pathways may have implications on visual processing during pursuit. The motion-correcting pathway may involve areas similar to the ones involved in the initiation of ocular following and the slow-phase of OKN, such as the nucleus of the optic tract (193), whereas the position-correcting system may involve areas such as the SC, with a role in exogenous spatial attention and the programming of eye movements. Position and motion-correcting pathways may then overlap as the size of the target increases. It is not clear whether different attentional mechanisms are implicated in this transition or whether a single model based on the salience of the target features is enough to explain the distribution of attentional resources for small and large targets.

Visual Selection as an Oculomotor "Glue"?

The complex coordination of different oculomotor and skeletal motor systems is usually ignored in the laboratory. Much more is known about the coordination of saccades and pursuit observed with simple ramp paradigms than under natural conditions. However, attentional selection may have a functional role beyond improving perception of the target, namely, in coordinating action, as demonstrated by the excellent agreement between pursuit and saccade choices once the focus of attention is on the target (17). It is possible that attention plays a similar role in vergence eye movements and even in eye movements that are triggered

involuntarily, such as OKN (194) and ocular following, which are responses to motion over a large visual area.

The pursuit and optokinetic system have complementary roles in stabilizing the background and foreground (pursuit) image. The slow phase of OKN can have a gain close to the pursuit gain when looking at the movement field, which is often referred to as look-OKN. The high gain could be due to the addition of voluntary pursuit to the response (194–196). The slow phase of stare-OKN has a much lower gain. The slow phase of OKN may be controlled by the same system that controls smooth pursuit, which is consistent with the classical observation of Murphy et al. (197) that we may choose between slow control (or stare- and look-OKN) and smooth pursuit at will by allocating attention to the appropriate stimulus (196–198).

Vergence is another oculomotor system in which visual attention could play a coordinating role. Although pursuit is studied in the laboratory by tracking a target on a frontoparallel plane, which may approximately lie on the same horopter, we are also able to track targets that move in 3D and require a combination of conjugate (pursuit) and disconjugate eye movements (vergence), as illustrated in Fig. 9B. Neurophysiological studies suggest that a subregion of FEF encodes 3D pursuit (199, 200), forming an “intermediate representation” that could facilitate the control of pursuit in natural situations, where vergence-pursuit is required. An intriguing possibility is that the coordination of target choice in vergence and in the frontoparallel plane could involve visual selection.

Characteristics of target selection in the saccadic and pursuit system were also found in vergence, such as averaging and speed-accuracy trade-offs in selecting the target (201, 202). The effect of microstimulation on the SC also indicated encoding of position errors in 3D, indicating coordination of saccadic and vergence signals (203). In this situation, two targets have different directions in the frontoparallel plane (2D projection) while moving either toward or away from the observer. If target selection was entirely based on a 3D signal, we would predict immediate coordination, which does not seem to be the case here. We are not aware of any studies testing the possibility that target selection could be uncoordinated for pursuit and vergence using a moving target and whether, in the same way as saccades and pursuit (204), it could evolve from independent to entirely coordinated responses.

CONCLUSIONS

Several behavioral and physiological investigations have examined the role that visual attention plays in the generation of smooth pursuit eye movements. These have shown that open-loop pursuit can operate at a preattentive stage, whereas endogenous and exogenous shifts of attention away from the pursuit target affect closed-loop pursuit performance, unless the attention shift is in the same direction as the pursuit. Therefore, there is spatial but not directional flexibility in visual allocation. Additionally, during closed-loop pursuit, observers enjoy some flexibility in the allocation of visual attention based on priority instructions.

The pursuit of large objects likely involves top-down grouping mechanisms in determining the pursuit target. Although visual attention may be involved in the perceptual grouping driving pursuit, it is not clear whether we may be able to attentively track individual elements independently of the pursuit target (e.g., the dot centroid). However, extended targets may liberate visual resources by boosting the pursuit driving signal (79).

Several authors have suggested that visual attention is biased ahead of the target during steady-state pursuit. However, when perceptual performance is measured, it is found to be centered on the pursuit target location. On the other hand, the main feature of the effect of pursuit on reaction times points to suppression when probe targets are presented in the contraversive hemifield compared with those presented in the ipsiversive hemifield and compared with fixation. Intriguingly, crowding is only decreased in the contraversive hemifield. An important question for the future is to determine whether perceptual asymmetries reflect visual processes, their modulation by attention, or both.

The physiology of visual attention in relation to eye movements suggests an overlap between the brain areas responsible for voluntary shifts of attention. However, recent investigations have also uncovered separate subcortical circuits that can affect perceptual performance via different mechanisms, by suppressing competing representations, rather than enhancing target representations, as can be observed in the cortex. The SC appears to have a role in coordinating saccade and pursuit choices and in influencing the stimulus competition leading to visual selection.

Implications regarding the Premotor Theory of Attention

Research on visual attention crystalized around a few big questions, one of those being the tenets of the premotor theory of visual selection, or whether visual selection is independent from motor preparation. As proposed by other authors, the premotor theory of attention is not supported in its strictest form (9). For instance, shifting visual attention does not necessarily involve a motor program (142, 143), although generating a voluntary saccade requires the engagement of top-down visual attention. Moving on, we could set up studies to differentiate between the different cognitive and computational stages we call visual attention and how they relate to the choice of a motor target. We argue that open-loop pursuit initiation provides an example of voluntary eye movement that can be preattentive and propose that the coupling between attention and eye movements is circumstantial, depending on time, execution threshold, and the salience of the driving signal, and that it should not be understood as being mandatory.

ACKNOWLEDGMENTS

We thank Jing Cheng for his comments on part of this review.

GRANTS

This work was supported by Grant 100014_135374 from the Swiss National Science Foundation.

DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

AUTHOR CONTRIBUTIONS

D.S. and D.K. interpreted results of experiments; D.S. prepared figures; D.S. drafted manuscript; D.S. and D.K. edited and revised manuscript; D.S. and D.K. approved final version of manuscript.

REFERENCES

- Marr D. *Vision*. Cambridge, MA: The MIT Press, 1982.
- Brown B. Dynamic visual acuity, eye movements and peripheral acuity for moving targets. *Vision Res* 12: 305–321, 1972. doi:10.1016/0042-6989(72)90120-4.
- Murphy BJ. Pattern thresholds for moving and stationary gratings during smooth eye movement. *Vision Res* 18: 521–530, 1978. doi:10.1016/0042-6989(78)90196-7.
- Pashler H. *The Psychology of Attention*. Cambridge, MA: MIT Press, 1998.
- Sperling G, Melchner MJ. The attention operating characteristic: examples from visual search. *Science* 202: 315–318, 1978. doi:10.1126/science.694536.
- Luo TZ, Maunsell JHR. Attention can be subdivided into neurobiological components corresponding to distinct behavioral effects. *Proc Natl Acad Sci USA* 116: 26187–26194, 2019. doi:10.1073/pnas.1902286116.
- Hommel B, Chapman CS, Cisek P, Neyedli HF, Song J-H, Welsh TN. No one knows what attention is. *Atten Percept Psychophys* 81: 2288–2303, 2019. doi:10.3758/s13414-019-01846-w.
- Hunt AR, Reuther J, Hilchey MD, Klein RM. The relationship between spatial attention and eye movements. In: *Processes of Visuospatial Attention and Working Memory. Current Topics in Behavioral Neurosciences*, edited by Hodgson T. Cham, Switzerland: Springer, 2019, vol. 41, p. 255–278. doi:10.1007/7854_2019_95.
- Smith DT, Schenk T. The premotor theory of attention: time to move on? *Neuropsychologia* 50: 1104–1114, 2012. doi:10.1016/j.neuropsychologia.2012.01.025.
- Rizzolatti G, Riggio L, Dascola I, Umiltà C. Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychologia* 25: 31–40, 1987. doi:10.1016/0028-3932(87)90041-8.
- Deubel H, Schneider WX. Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Res* 36: 1827–1837, 1996. doi:10.1016/0042-6989(95)00294-4.
- Sheliga BM, Riggio L, Rizzolatti G. Spatial attention and eye movements. *Exp Brain Res* 105: 261–275, 1995. doi:10.1007/BF00240962.
- Kowler E. Eye movements: the past 25 years. *Vision Res* 51: 1457–1483, 2011. doi:10.1016/j.visres.2010.12.014.
- Robinson DA, Gordon JL, Gordon SE. A model of the smooth pursuit eye movement system. *Biol Cybern* 55: 43–57, 1986. doi:10.1007/BF00363977.
- Barnes GR. Cognitive processes involved in smooth pursuit eye movements. *Brain Cogn* 68: 309–326, 2008. doi:10.1016/j.bandc.2008.08.020.
- Joshua M, Lisberger SG. Reward action in the initiation of smooth pursuit eye movements. *J Neurosci* 32: 2856–2867, 2012. doi:10.1523/JNEUROSCI.4676-11.2012.
- Erkelenz CJ. Coordination of smooth pursuit and saccades. *Vision Res* 46: 163–170, 2006. doi:10.1016/j.visres.2005.06.027.
- Liston D, Krauzlis RJ. Shared response preparation for pursuit and saccadic eye movements. *J Neurosci* 23: 11305–11314, 2003. doi:10.1523/jneurosci.23-36-11305.2003.
- Green D, Swets JA. *Signal Detection Theory and Psychophysics*. Los Altos Hills, CA: Peninsula Publishing, 1966.
- Crappe TB, Lau H, Basso MA. A role for the superior colliculus in decision criteria. *Neuron* 97: 181–194.e6, 2018. doi:10.1016/j.neuron.2017.12.006.
- Eckstein MP. Probabilistic computations for attention, eye movements, and search. *Annu Rev Vis Sci* 3: 319–342, 2017. doi:10.1146/annurev-vision-102016-061220.
- Vincent BT. Bayesian accounts of covert selective attention: a tutorial review. *Atten Percept Psychophys* 77: 1013–1032, 2015. doi:10.3758/s13414-014-0830-0.
- Ratcliff R, Smith PL, Brown SD, McKoon G. Diffusion decision model: current issues and history. *Trends Cogn Sci* 20: 260–281, 2016. doi:10.1016/j.tics.2016.01.007.
- Lu ZL, Doshier BA. External noise distinguishes attention mechanisms. *Vision Res* 38: 1183–1198, 1998. doi:10.1016/S0042-6989(97)00273-3.
- Collewijn H, Tamminga EP. Human smooth and saccadic eye movements during voluntary pursuit of different target motions on different backgrounds. *J Physiol* 351: 217–250, 1984. doi:10.1113/jphysiol.1984.sp015242.
- Lisberger SG. Postsaccadic enhancement of initiation of smooth pursuit eye movements in monkeys. *J Neurophysiol* 79: 1918–1930, 1998. doi:10.1152/jn.1998.79.4.1918.
- de Brouwer S, Yuksel D, Blohm G, Missal M, Lefevre P. What triggers catch-up saccades during visual tracking? *J Neurophysiol* 87: 1646–1650, 2002. doi:10.1152/jn.00432.2001.
- Goffart L, Fleuriot J. Hic-et-nunc (here-and-now) encoding of a moving target for its saccadic foveation. *i-Perception* 3: 741–741, 2012. doi:10.1068/1f741.
- Missal M, Heinen SJ. Stopping smooth pursuit. *Philos Trans R Soc Lond B Biol Sci* 372: 20160200, 2017. doi:10.1098/rstb.2016.0200.
- Pola J, Wyatt HJ. Offset dynamics of human smooth pursuit eye movements: effects of target presence and subject attention. *Vision Res* 37: 2579–2595, 1997. doi:10.1016/s0042-6989(97)00058-8.
- Becker W, Fuchs AF. Prediction in the oculomotor system: smooth pursuit during transient disappearance of a visual target. *Exp Brain Res* 57: 562–575, 1985. doi:10.1007/BF00237843.
- Krauzlis RJ, Miles FA. Transitions between pursuit eye movements and fixation in the monkey: dependence on context. *J Neurophysiol* 76: 1622–1638, 1996. doi:10.1152/jn.1996.76.3.1622.
- Souto D, Chudasama J, Kerzel D, Johnston A. Motion integration is anisotropic during smooth pursuit eye movements. *J Neurophysiol* 121: 1787–1797, 2019. doi:10.1152/jn.00591.2018.
- Pack CC, Born RT. Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. *Nature* 409: 1040–1042, 2001. doi:10.1038/35059085.
- Masson GS, Perrinet LU. The behavioral receptive field underlying motion integration for primate tracking eye movements. *Neurosci Biobehav Rev* 36: 1–25, 2012. doi:10.1016/j.neubiorev.2011.03.009.
- Miles F. Short-latency visual stabilization mechanisms that help to compensate for translational disturbances of gaze. *Ann N Y Acad Sci* 871: 260–271, 1999. doi:10.1111/j.1749-6632.1999.tb09190.x.
- Montagnini A, Sperling M, Masson GS. Predicting 2D target velocity cannot help 2D motion integration for smooth pursuit initiation. *J Neurophysiol* 96: 3545–3550, 2006. doi:10.1152/jn.00563.2006.
- Lindner A, Ilg UJ. Initiation of smooth-pursuit eye movements to first-order and second-order motion stimuli. *Exp Brain Res* 133: 450–456, 2000. doi:10.1007/s002210000459.
- Wilmer JB, Nakayama K. Two distinct visual motion mechanisms for smooth pursuit: evidence from individual differences. *Neuron* 54: 987–1000, 2007. doi:10.1016/j.neuron.2007.06.007.
- Weichselgartner E, Sperling G. Dynamics of automatic and controlled visual attention. *Science* 238: 778–780, 1987. doi:10.1126/science.3672124.
- Cheal M, Lyon DR. Central and peripheral precuing of forced-choice discrimination. *Q J Exp Psychol A* 43: 859–880, 1991. doi:10.1080/14640749108400960.
- Horowitz TS, Holcombe AO, Wolfe JM, Arsenio HC, DiMase JS. Attentional pursuit is faster than attentional saccade. *J Vis* 4: 585–603, 2004. doi:10.1167/4.7.6.
- Müller HJ, Rabbitt PM. Reflexive and voluntary orienting of visual attention: time course of activation and resistance to interruption. *J Exp Psychol Hum Percept Perform* 15: 315–330, 1989. doi:10.1037//0096-1523.15.2.315.
- Nakayama K, Mackeben M. Sustained and transient components of focal visual attention. *Vision Res* 29: 1631–1647, 1989. doi:10.1016/0042-6989(89)90144-2.

45. **Shimozaki SS, Chen KY, Abbey CK, Eckstein MP.** The temporal dynamics of selective attention of the visual periphery as measured by classification images. *J Vis* 7: 1–20, 2007. doi:10.1167/7.12.10.
46. **Cavanagh P, Mather G.** Motion: the long and short of it. *Spat Vis* 4: 103–129, 1989. doi:10.1163/156856889x00077.
47. **Sperling G, Lu ZL.** A systems analysis of visual motion perception. In: *High-Level Motion Processing*, edited by Watanabe T, Lu ZL. Cambridge, MA: MIT Press, 2020, p. 154–183.
48. **Ferrera VP, Lisberger SG.** Attention and target selection for smooth pursuit eye movements. *J Neurosci* 15: 7472–7484, 1995. doi:10.1523/jneurosci.15-11-07472.1995.
49. **Ferrera VP, Lisberger SG.** Neuronal responses in visual areas MT and MST during smooth pursuit target selection. *J Neurophysiol* 78: 1433–1446, 1997. doi:10.1152/jn.1997.78.3.1433.
50. **Ferrera VP, Lisberger SG.** The effect of a moving distractor on the initiation of smooth-pursuit eye movements. *Vis Neurosci* 14: 323–338, 1997. doi:10.1017/s0952523800011457.
51. **Ferrera VP.** Task-dependent modulation of the sensorimotor transformation for smooth pursuit eye movements. *J Neurophysiol* 84: 2725–2738, 2000. doi:10.1152/jn.2000.84.6.2725.
52. **Krauzlis RJ, Zivotofsky AZ, Miles FA.** Target selection for pursuit and saccadic eye movements in humans. *J Cogn Neurosci* 11: 641–649, 1999. doi:10.1162/08992999563706.
53. **Lisberger SG, Ferrera VP.** Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *J Neurosci* 17: 7490–7502, 1997. doi:10.1523/jneurosci.17-19-07490.1997.
54. **Gardner JL, Lisberger SG.** Serial linkage of target selection for orienting and tracking eye movements. *Nat Neurosci* 5: 892–899, 2002. doi:10.1038/nn897.
55. **Desimone R, Duncan J.** Neural mechanisms of selective visual attention. *Annu Rev Neurosci* 18: 193–222, 1995. doi:10.1146/annurev.ne.18.030195.001205.
56. **Garbutt S, Lisberger SG.** Directional cuing of target choice in human smooth pursuit eye movements. *J Neurosci* 26: 12479–12486, 2006. doi:10.1523/JNEUROSCI.4071-06.2006.
57. **Adler SA, Bala J, Krauzlis RJ.** Primacy of spatial information in guiding target selection for pursuit and saccades. *J Vis* 2: 627–644, 2002. doi:10.1167/2.9.5.
58. **Souto D, Kerzel D.** Attentional constraints on target selection for smooth pursuit eye movements. *Vision Res* 51: 13–20, 2011. doi:10.1016/j.visres.2010.09.017.
59. **Gardner JL, Lisberger SG.** Linked target selection for saccadic and smooth pursuit eye movements. *J Neurosci* 21: 2075–2084, 2001. doi:10.1523/JNEUROSCI.21-06-02075.2001.
60. **Lisberger SG.** Visual guidance of smooth-pursuit eye movements: sensation, action, and what happens in between. *Neuron* 66: 477–491, 2010. doi:10.1016/j.neuron.2010.03.027.
61. **Klein RM.** Attention and movement. In: *Motor Control: Issues and Trends*, edited by Stelmach GE. New York: Academic Press, 1976, p. 143–173.
62. **Welch JC.** On the measurement of mental activity through muscular activity and the determination of a constant of attention. *Am J Physiol* 1: 283–306, 1898. doi:10.1152/ajplegacy.1898.1.3.283.
63. **Hutton SB, Tegally D.** The effects of dividing attention on smooth pursuit eye tracking. *Exp Brain Res* 163: 306–313, 2005. doi:10.1007/s00221-004-2171-z.
64. **Kathmann N, Hochrein A, Uwer R.** Effects of dual task demands on the accuracy of smooth pursuit eye movements. *Psychophysiology* 36: 158–163, 1999.
65. **Stubbs JL, Corrow SL, Kiang B, Panenka WJ, Barton JJS.** The effects of enhanced attention and working memory on smooth pursuit eye movement. *Exp Brain Res* 236: 485–495, 2018. doi:10.1007/s00221-017-5146-6.
66. **Kerzel D, Souto D, Ziegler NE.** Effects of attention shifts to stationary objects during steady-state smooth pursuit eye movements. *Vision Res* 48: 958–969, 2008. doi:10.1016/j.visres.2008.01.015.
67. **Souto D, Kerzel D.** Dynamics of attention during the initiation of smooth pursuit eye movements. *J Vis* 8: 1–16, 2008. doi:10.1167/8.14.3.
68. **Van Donkelaar P, Drew AS.** The allocation of attention during smooth pursuit eye movements. *Prog Brain Res* 140: 267–277, 2002. doi:10.1016/S0079-6123(02)40056-8.
69. **Van Donkelaar P.** Spatiotemporal modulation of attention during smooth pursuit eye movements. *Neuroreport* 10: 2523–2526, 1999. doi:10.1097/00001756-199908200-00016.
70. **Khurana B, Kowler E.** Shared attentional control of smooth eye movement and perception. *Vision Res* 27: 1603–1618, 1987. doi:10.1016/0042-6989(87)90168-4.
71. **Kowler E, van der Steen J, Tamminga EP, Collewijn H.** Voluntary selection of the target for smooth eye movement in the presence of superimposed, full-field stationary and moving stimuli. *Vision Res* 24: 1789–1798, 1984. doi:10.1016/0042-6989(84)90010-5.
72. **Kerzel D, Born S, Souto D.** Smooth pursuit eye movements and perception share target selection, but only some central resources. *Behav Brain Res* 201: 66–73, 2009. doi:10.1016/j.bbr.2009.01.032.
73. **Souto D, Kerzel D.** Ocular tracking responses to background motion gated by feature-based attention. *J Neurophysiol* 112: 1074–1081, 2014. doi:10.1152/jn.00810.2013.
74. **Greenlee MW, Schira MM, Kimmig H.** Coherent motion pops out during smooth pursuit. *Neuroreport* 13: 1313–1316, 2002. doi:10.1097/00001756-200207190-00020.
75. **Theeuwes J.** Feature-based attention: it is all bottom-up priming. *Philos Trans R Soc Lond B Biol Sci* 368: 20130055, 2013. doi:10.1098/rstb.2013.0055.
76. **Heinen SJ, Jin Z, Watamaniuk SN.** Flexibility of foveal attention during ocular pursuit. *J Vis* 11: 9, 2011. doi:10.1167/11.2.9.
77. **Grossberg S.** How is a moving target continuously tracked behind occluding cover? *Tech Rep CAS/CNS 96-001: 1–30*, 1996. <https://hdl.handle.net/2144/2300>
78. **Madelain L, Krauzlis RJ, Wallman J.** Spatial deployment of attention influences both saccadic and pursuit tracking. *Vision Res* 45: 2685–2703, 2005. doi:10.1016/j.visres.2005.05.009.
79. **Heinen SJ, Watamaniuk SN.** Spatial integration in human smooth pursuit. *Vision Res* 38: 3785–3794, 1998. doi:10.1016/s0042-6989(97)00422-7.
80. **Jin Z, Watamaniuk SN, Khan AZ, Potapchuk E, Heinen SJ.** Motion integration for ocular pursuit does not hinder perceptual segregation of moving objects. *J Neurosci* 34: 5835–5841, 2014. doi:10.1523/JNEUROSCI.4867-13.2014.
81. **Tyler CW.** Symmetries, structure and schemata in perceptual coding. In: *Computational and Psychophysical Mechanisms of Visual Coding*, edited by Jenkin MRM, Jenkin M, Harris L. Cambridge, UK: Cambridge University Press, 1997, p. 131–156.
82. **Fehd H, Seiffert AE.** Eye movements during multiple object tracking: where do participants look? *Cognition* 108: 201–209, 2008. doi:10.1016/j.cognition.2007.11.008.
83. **Vater C, Kredel R, Hossner E-J.** Detecting single-target changes in multiple object tracking: the case of peripheral vision. *Atten Percept Psychophys* 78: 1004–1019, 2016. doi:10.3758/s13414-016-1078-7.
84. **Jin Z, Reeves A, Watamaniuk SN, Heinen SJ.** Shared attention for smooth pursuit and saccades. *J Vis* 13: 7, 2013. doi:10.1167/13.4.7.
85. **Drew AS, van Donkelaar P.** The contribution of the human PPC to the orienting of visuospatial attention during smooth pursuit. *Exp Brain Res* 179: 65–73, 2007. doi:10.1007/s00221-006-0769-z.
86. **Jonikaitis D, Szinte M, Rolfs M, Cavanagh P.** Allocation of attention across saccades. *J Neurophysiol* 109: 1425–1434, 2013. doi:10.1152/jn.00656.2012.
87. **Duhamel JR, Bremmer F, Hamed SB, Graf W.** Spatial invariance of visual receptive fields in parietal cortex neurons. *Nature* 389: 845–848, 1997. doi:10.1038/39865.
88. **Schütz AC, Braun DI, Gegenfurtner KR.** Contrast sensitivity during the initiation of smooth pursuit eye movements. *Vision Res* 47: 2767–2777, 2007. doi:10.1016/j.visres.2007.07.006.
89. **Watamaniuk SN, Heinen SJ.** Allocation of attention during pursuit of large objects is no different than during fixation. *J Vis* 15: 9, 2015. doi:10.1167/15.9.9.[26200890]
90. **Lovejoy LP, Fowler GA, Krauzlis RJ.** Spatial allocation of attention during smooth pursuit eye movements. *Vision Res* 49: 1275–1285, 2009. doi:10.1016/j.visres.2009.01.011.
91. **Reddi BA, Carpenter RH.** The influence of urgency on decision time. *Nat Neurosci* 3: 827–830, 2000. doi:10.1038/77739.
92. **Carpenter RHS.** Contrast, probability, and saccadic latency; evidence for independence of detection and decision. *Curr Biol* 14: 1576–1580, 2004. doi:10.1016/j.cub.2004.08.058.

93. Prinzmetal W, McCool C, Park S. Attention: reaction time and accuracy reveal different mechanisms. *J Exp Psychol Gen* 134: 73–92, 2005. doi:10.1037/0096-3445.134.1.73.
94. Souto D, Born S, Kerzel D. The contribution of forward masking to saccadic inhibition of return. *Atten Percept Psychophys* 80: 1182–1192, 2018. doi:10.3758/s13414-018-1490-2.
95. Bieg H-J, Bresciani J-P, Bühlhoff HH, Chuang LL. Saccade reaction time asymmetries during task-switching in pursuit tracking. *Exp Brain Res* 230: 271–281, 2013. doi:10.1007/s00221-013-3651-9.
96. Bieg HJ, Bühlhoff HH, Chuang LL. Attentional biases during steering behavior. In: *Digital Human Modeling and Applications in Health, Safety, Ergonomics, and Risk Management. Healthcare and Safety of the Environment and Transport*, edited by Duffy VG. Berlin, Germany: Springer, 2013, p. 21–27. Lecture Notes in Computer Science vol. 8025.
97. Bieg H-J, Chuang LL, Bühlhoff HH, Bresciani J-P. Asymmetric saccade reaction times to smooth pursuit. *Exp Brain Res* 233: 2527–2538, 2015. doi:10.1007/s00221-015-4323-8.
98. Blohm G, Missal M, Lefèvre P. Processing of retinal and extraretinal signals for memory-guided saccades during smooth pursuit. *J Neurophysiol* 93: 1510–1522, 2005. doi:10.1152/jn.00543.2004.
99. Kanai R, Van Der Geest JN, Frens MA. Inhibition of saccade initiation by preceding smooth pursuit. *Exp Brain Res* 148: 300–307, 2003. doi:10.1007/s00221-002-1281-8.
100. Khan AZ, Lefèvre P, Heinen SJ, Blohm G. The default allocation of attention is broadly ahead of smooth pursuit. *J Vis* 10: 7, 2010. doi:10.1167/10.13.7.
101. Krauzlis RJ, Miles FA. Initiation of saccades during fixation or pursuit: evidence in humans for a single mechanism. *J Neurophysiol* 76: 4175–4179, 1996. doi:10.1152/jn.1996.76.6.4175.
102. Seya Y, Mori S. Spatial attention and reaction times during smooth pursuit eye movement. *Atten Percept Psychophys* 74: 493–509, 2012. doi:10.3758/s13414-011-0247-y.
103. Seya Y, Mori S. Tradeoff between manual response speed and pursuit accuracy revealed by a deadline procedure. *Exp Brain Res* 233: 1845–1854, 2015. doi:10.1007/s00221-015-4256-2.
104. Smeets JBJ, Bekkering H. Prediction of saccadic amplitude during smooth pursuit eye movements. *Hum Mov Sci* 19: 275–295, 2000. doi:10.1016/S0167-9457(00)00015-4.
105. Tanaka M, Yoshida T, Fukushima K. Latency of saccades during smooth-pursuit eye movement in man. Directional asymmetries. *Exp Brain Res* 121: 92–98, 1998. doi:10.1007/s002210050440.
106. Chukoskie L, Movshon JA. Modulation of visual signals in macaque MT and MST neurons during pursuit eye movement. *J Neurophysiol* 102: 3225–3233, 2009. doi:10.1152/jn.90692.2008.
107. Lindner A, Ilg U. Suppression of optokinetic during smooth pursuit eye movements revisited: the role of extra-retinal information. *Vision Res* 46: 761–767, 2006. doi:10.1016/j.visres.2005.09.033.
108. Malienko A, Harrar V, Khan AZ. Contrasting effects of exogenous cueing on saccades and reaches. *J Vis* 18: 4, 2018. doi:10.1167/18.9.4.
109. Schütz AC, Braun DI, Kerzel D, Gegenfurtner KR. Improved visual sensitivity during smooth pursuit eye movements. *Nat Neurosci* 11: 1211–1216, 2008. doi:10.1038/nn.2194.
110. Tong J, Patel SS, Bedell HE. Asymmetry of perceived motion smear during head and eye movements: evidence for a dichotomous neural categorization of retinal image motion. *Vision Res* 45: 1519–1524, 2005. doi:10.1016/j.visres.2004.12.004.
111. Harrison WJ, Remington RW, Mattingley JB. Visual crowding is anisotropic along the horizontal meridian during smooth pursuit. *J Vis* 14: 21, 2014. doi:10.1167/14.1.21.
112. Chen J, Valsecchi M, Gegenfurtner KR. Attention is allocated closely ahead of the target during smooth pursuit eye movements: evidence from EEG frequency tagging. *Neuropsychologia* 102: 206–216, 2017. doi:10.1016/j.neuropsychologia.2017.06.024.
113. Corbetta M, Akbudak E, Conturo TE, Snyder AZ, Ollinger JM, Drury HA, Linenweber MR, Petersen SE, Raichle ME, Van Essen DC, Shulman GL. A common network of functional areas for attention and eye movements. *Neuron* 21: 761–773, 1998. doi:10.1016/S0896-6273(00)80593-0.
114. Ohlendorf S, Kimmig H, Glauche V, Haller S. Gaze pursuit, 'attention pursuit' and their effects on cortical activations. *Eur J Neurosci* 26: 2096–2108, 2007. doi:10.1111/j.1460-9568.2007.05824.x.
115. Krauzlis RJ, Lovejoy LP, Zénon A. Superior colliculus and visual spatial attention. *Annu Rev Neurosci* 36: 165–182, 2013. doi:10.1146/annurev-neuro-062012-170249.
116. Shipp S. The brain circuitry of attention. *Trends Cogn Sci* 8: 223–230, 2004. doi:10.1016/j.tics.2004.03.004.
117. Veale R, Hafed ZM, Yoshida M. How is visual salience computed in the brain? Insights from behaviour, neurobiology and modeling. *Philos Trans R Soc Lond B Biol Sci* 372: 20160113, 2017. doi:10.1098/rstb.2016.0113.
118. Nummela SU, Krauzlis RJ. Superior colliculus inactivation alters the weighted integration of visual stimuli. *J Neurosci* 31: 8059–8066, 2011. doi:10.1523/JNEUROSCI.5480-10.2011.
119. Lovejoy LP, Krauzlis RJ. Changes in perceptual sensitivity related to spatial cues depends on subcortical activity. *Proc Natl Acad Sci USA* 114: 6122–6126, 2017. doi:10.1073/pnas.1609711114.
120. Lovejoy LP, Krauzlis RJ. Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nat Neurosci* 13: 261–266, 2010. doi:10.1038/nn.2470.
121. McPeck RM, Keller EL. Deficits in saccade target selection after inactivation of superior colliculus. *Nat Neurosci* 7: 757–763, 2004. doi:10.1038/nn1269.
122. Sridharan D, Steinmetz NA, Moore T, Knudsen EI. Does the superior colliculus control perceptual sensitivity or choice bias during attention? Evidence from a multialternative decision framework. *J Neurosci* 37: 480–511, 2017. doi:10.1523/JNEUROSCI.4505-14.2017.
123. Zénon A, Krauzlis RJ. Attention deficits without cortical neuronal deficits. *Nature* 489: 434–437, 2012. doi:10.1038/nature11497.
124. Lynch JC, Tian J-R. Cortico-cortical networks and cortico-subcortical loops for the higher control of eye movements. *Prog Brain Res* 151: 461–501, 2006. doi:10.1016/S0079-6123(05)51015-x.
125. Tian JR, Lynch JC. Corticocortical input to the smooth and saccadic eye movement subregions of the frontal eye field in Cebus monkeys. *J Neurophysiol* 76: 2754–2771, 1996. doi:10.1152/jn.1996.76.4.2754.
126. Song J-H, Rafal RD, McPeck RM. Deficits in reach target selection during inactivation of the midbrain superior colliculus. *Proc Natl Acad Sci USA* 108: E1433–E1440, 2011. doi:10.1073/pnas.1109656108.
127. Knudsen EI. Neural circuits that mediate selective attention: a comparative perspective. *Trends Neurosci* 41: 789–805, 2018. doi:10.1016/j.tins.2018.06.006.
128. Beh SC, Frohman TC, Frohman EM. Cerebellar control of eye movements. *J Neuroophthalmol* 37: 87–98, 2017. doi:10.1097/WNO.0000000000000456.
129. Robinson FR, Fuchs AF. The role of the cerebellum in voluntary eye movements. *Annu Rev Neurosci* 24: 981–1004, 2001. doi:10.1146/annurev-neuro.24.1.981.
130. Thier P, Ilg UJ. The neural basis of smooth-pursuit eye movements. *Curr Opin Neurobiol* 15: 645–652, 2005. doi:10.1016/j.conb.2005.10.013.
131. Thier P, Markanday A. Role of the vermal cerebellum in visually guided eye movements and visual motion perception. *Annu Rev Vis Sci* 5: 247–268, 2019. doi:10.1146/annurev-vision-091718-015000.
132. Haarmeier T, Thier P. The attentive cerebellum—myth or reality? *Cerebellum* 6: 177–183, 2007. doi:10.1080/14734220701286187.
133. Krauzlis RJ. Recasting the smooth pursuit eye movement system. *J Neurophysiol* 91: 591–603, 2004. doi:10.1152/jn.00801.2003.
134. Tanaka M, Lisberger SG. Role of arcuate frontal cortex of monkeys in smooth pursuit eye movements. II. Relation to vector averaging pursuit. *J Neurophysiol* 87: 2700–2714, 2002 [Erratum in *J Neurophysiol* 88: following table of contents, 2002]. doi:10.1152/jn.2002.87.6.2700.
135. Lynch JC. Frontal eye field lesions in monkeys disrupt visual pursuit. *Exp Brain Res* 68: 437–441, 1987. doi:10.1007/BF00248811.
136. Mahaffy S, Krauzlis RJ. Neural activity in the frontal pursuit area does not underlie pursuit target selection. *Vision Res* 51: 853–866, 2011. doi:10.1016/j.visres.2010.10.010.
137. Thompson KG, Hanes DP, Bichot NP, Schall JD. Perceptual and motor processing stages identified in the activity of macaque frontal eye field neurons during visual search. *J Neurophysiol* 76: 4040–4055, 1996. doi:10.1152/jn.1996.76.6.4040.
138. Thompson KG, Biscoe KL, Sato TR. Neuronal basis of covert spatial attention in the frontal eye field. *J Neurosci* 25: 9479–9487, 2005. doi:10.1523/JNEUROSCI.0741-05.2005.

139. **Bisley JW, Goldberg ME.** Neuronal activity in the lateral intraparietal area and spatial attention. *Science* 299: 81–87, 2003. doi:10.1126/science.1077395.
140. **Moore T, Fallah M.** Control of eye movements and spatial attention. *Proc Natl Acad Sci USA* 98: 1273–1276, 2001 [Erratum in *Proc Natl Acad Sci USA* 98: 4276, 2001]. doi:10.1073/pnas.021549498.
141. **Moore T, Fallah M.** Microstimulation of the frontal eye field and its effects on covert spatial attention. *J Neurophysiol* 91: 152–162, 2004. doi:10.1152/jn.00741.2002.
142. **Juan C-H, Shorter-Jacobi SM, Schall JD.** Dissociation of spatial attention and saccade preparation. *Proc Natl Acad Sci USA* 101: 15541–15544, 2004. doi:10.1073/pnas.0403507101.
143. **Juan C-H, Muggleton NG, Tzeng OJL, Hung DL, Cowey A, Walsh V.** Segregation of visual selection and saccades in human frontal eye fields. *Cereb Cortex* 18: 2410–2415, 2008. doi:10.1093/cercor/bhn001.
144. **Komatsu H, Wurtz RH.** Relation of cortical areas MT and MST to pursuit eye movements. I. Localization and visual properties of neurons. *J Neurophysiol* 60: 580–603, 1988. doi:10.1152/jn.1988.60.2.580.
145. **Newsome WT, Wurtz RH, Komatsu H.** Relation of cortical areas MT and MST to pursuit eye movements. II. Differentiation of retinal from extraretinal inputs. *J Neurophysiol* 60: 604–620, 1988. doi:10.1152/jn.1988.60.2.604.
146. **Treue S, Maunsell JH.** Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382: 539–541, 1996. doi:10.1038/382539a0.
147. **Treue S, Maunsell JH.** Effects of attention on the processing of motion in macaque middle temporal and medial superior temporal visual cortical areas. *J Neurosci* 19: 7591–7602, 1999. doi:10.1523/JNEUROSCI.19-17-07591.1999.
148. **Kawano K, Shidara M, Watanabe Y, Yamane S.** Neural activity in cortical area MST of alert monkey during ocular following responses. *J Neurophysiol* 71: 2305–2324, 1994. doi:10.1152/jn.1994.71.6.2305.
149. **Recanzone GH, Wurtz RH, Schwarz U.** Responses of MT and MST neurons to one and two moving objects in the receptive field. *J Neurophysiol* 78: 2904–2915, 1997. doi:10.1152/jn.1997.78.6.2904.
150. **Recanzone GH, Wurtz RH.** Effects of attention on MT and MST neuronal activity during pursuit initiation. *J Neurophysiol* 83: 777–790, 2000. doi:10.1152/jn.2000.83.2.777.
151. **Carello CD, Krauzlis RJ.** Manipulating intent: evidence for a causal role of the superior colliculus in target selection. *Neuron* 43: 575–583, 2004. doi:10.1016/j.neuron.2004.07.026.
152. **Kustov AA, Robinson DL.** Shared neural control of attentional shifts and eye movements. *Nature* 384: 74–77, 1996. doi:10.1038/384074a0.
153. **Ignashchenkova A, Dicke PW, Haarmeier T, Thier P.** Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nat Neurosci* 7: 56–64, 2004. doi:10.1038/nn1169.
154. **Sreenivasan V, Sridharan D.** Subcortical connectivity correlates selectively with attention's effects on spatial choice bias. *Proc Natl Acad Sci USA* 116: 19711–19716, 2019. doi:10.1073/pnas.1902704116.
155. **Nummela SU, Krauzlis RJ.** Inactivation of primate superior colliculus biases target choice for smooth pursuit, saccades, and button press responses. *J Neurophysiol* 104: 1538–1548, 2010. doi:10.1152/jn.00406.2010.
156. **Sridharan D, Steinmetz NA, Moore T, Knudsen EI.** Distinguishing bias from sensitivity effects in multialternative detection tasks. *J Vis* 14: 16, 2014. doi:10.1167/14.9.16.
157. **Luo TZ, Maunsell JHR.** Neuronal modulations in visual cortex are associated with only one of multiple components of attention. *Neuron* 86: 1182–1188, 2015. doi:10.1016/j.neuron.2015.05.007.
158. **Basso MA, Pokorny JJ, Liu P.** Activity of substantia nigra pars reticulata neurons during smooth pursuit eye movements in monkeys. *Eur J Neurosci* 22: 448–464, 2005. doi:10.1111/j.1460-9568.2005.04215.x.
159. **Basso MA, Wurtz RH.** Neuronal activity in substantia nigra pars reticulata during target selection. *J Neurosci* 22: 1883–1894, 2002. doi:10.1523/jneurosci.22-05-01883.2002.
160. **Krauzlis RJ.** The control of voluntary eye movements: new perspectives. *Neuroscientist* 11: 124–137, 2005. doi:10.1177/1073858404271196.
161. **Orban De Xivry J-J, Lefèvre P.** Saccades and pursuit: two outcomes of a single sensorimotor process. *J Physiol* 584: 11–23, 2007. doi:10.1113/jphysiol.2007.139881.
162. **Bundesen C.** A theory of visual attention. *Psychol Rev* 97: 523–547, 1990. doi:10.1037/0033-295X.97.4.523.
163. **Desimone R, Wessinger M, Thomas L, Schneider W.** Attentional control of visual perception: cortical and subcortical mechanisms. *Cold Spring Harb Symp Quant Biol* 55: 963–971, 1990. doi:10.1101/SQB.1990.055.01.090.
164. **Franconeri SL, Alvarez GA, Cavanagh P.** Flexible cognitive resources: competitive content maps for attention and memory. *Trends Cogn Sci* 17: 134–141, 2013. doi:10.1016/j.tics.2013.01.010.
165. **Eriksen CW, James JDS.** Visual attention within and around the field of focal attention: a zoom lens model. *Percept Psychophys* 40: 225–240, 1986. doi:10.3758/bf03211502.
166. **Herrmann K, Montaser-Kouhsari L, Carrasco M, Heeger DJ.** When size matters: attention affects performance by contrast or response gain. *Nat Neurosci* 13: 1554–1559, 2010. doi:10.1038/nn.2669.
167. **Reynolds JH, Heeger DJ.** The normalization model of attention. *Neuron* 61: 168–185, 2009. doi:10.1016/j.neuron.2009.01.002.
168. **Castiello U, Umiltà C.** Size of the attentional focus and efficiency of processing. *Acta Psychol (Amst)* 73: 195–209, 1990. doi:10.1016/0001-6918(90)90022-8.
169. **Downing CJ, Pinker S.** The spatial structure of visual attention. In: *Mechanisms of Attention: Attention and Performance XI*, edited by Posner MI, Marin OSM. Hillsdale, NJ: Erlbaum, 1985, p. 171–187.
170. **Datta R, Deyoe EA.** I know where you are secretly attending! The topography of human visual attention revealed with fMRI. *Vision Res* 49: 1037–1044, 2009. doi:10.1016/j.visres.2009.01.014.
171. **Muller NG, Bartelt OA, Donner TH, Villringer A, Brandt SA.** A physiological correlate of the “zoom lens” of visual attention. *J Neurosci* 23: 3561–3565, 2003. doi:10.1523/JNEUROSCI.23-09-03561.2003.
172. **Anton-Erxleben K, Stephan VM, Treue S.** Attention reshapes center-surround receptive field structure in macaque cortical area MT. *Cereb Cortex* 19: 2466–2478, 2009. doi:10.1093/cercor/bhp002.
173. **Womelsdorf T, Anton-Erxleben K, Pieper F, Treue S.** Dynamic shifts of visual receptive fields in cortical area MT by spatial attention. *Nat Neurosci* 9: 1156–1160, 2006. doi:10.1038/nn1748.
174. **Connor CE, Preddie DC, Gallant JL, Van Essen DC.** Spatial attention effects in macaque area V4. *J Neurosci* 17: 3201–3214, 1997. doi:10.1523/jneurosci.17-09-03201.1997.
175. **Anton-Erxleben K, Carrasco M.** Attentional enhancement of spatial resolution: linking behavioural and neurophysiological evidence. *Nat Rev Neurosci* 14: 188–200, 2013. doi:10.1038/nrn3443.
176. **Miconi T, VanRullen R.** A feedback model of attention explains the diverse effects of attention on neural firing rates and receptive field structure. *PLoS Comput Biol* 12: e1004770, 2016. doi:10.1371/journal.pcbi.1004770.
177. **Moore T, Zirnsak M.** Neural mechanisms of selective visual attention. *Annu Rev Psychol* 68: 47–72, 2017. doi:10.1146/annurev-psych-122414-033400.
178. **McMains S, Kastner S.** Interactions of top-down and bottom-up mechanisms in human visual cortex. *J Neurosci* 31: 587–597, 2011. doi:10.1523/JNEUROSCI.3766-10.2011.
179. **Hanning N, Deubel H.** Unlike saccades, quick phases of optokinetic nystagmus are not preceded by shifts of attention. *J Vis* 19: 53, 2019. doi:10.1167/19.10.53c.
180. **Harrison JJ, Freeman TCA, Sumner P.** Saccade-like behavior in the fast-phases of optokinetic nystagmus: an illustration of the emergence of volitional actions from automatic reflexes. *J Exp Psychol Gen* 143: 1923–1938, 2014. doi:10.1037/a0037021.
181. **Wollenberg L, Deubel H, Szinte M.** Visual attention is not deployed at the endpoint of averaging saccades. *PLoS Biol* 16: e2006548, 2018. doi:10.1371/journal.pbio.2006548.
182. **Hamker FH.** The reentry hypothesis: the putative interaction of the frontal eye field, ventrolateral prefrontal cortex, and areas V4, IT for attention and eye movement. *Cereb Cortex* 15: 431–447, 2005. doi:10.1093/cercor/bhh146.
183. **Basso MA, May PJ.** Circuits for action and cognition: a view from the superior colliculus. *Annu Rev Vis Sci* 3: 197–226, 2017. doi:10.1146/annurev-vision-102016-061234.
184. **Carlson TA, Alvarez GA, Cavanagh P.** Quadrantic deficit reveals anatomical constraints on selection. *Proc Natl Acad Sci USA* 104: 13496–13500, 2007. doi:10.1073/pnas.0702685104.
185. **Franconeri S.** The nature and status of visual resources. In: *The Oxford Handbook of Cognitive Psychology*, edited by Reisberg D.

- Oxford, UK: Oxford University Press, 2013, p 1–16. doi:[10.1093/oxfordhb/9780195376746.013.0010](https://doi.org/10.1093/oxfordhb/9780195376746.013.0010).
186. **Masson GS.** From 1D to 2D via 3D: dynamics of surface motion segmentation for ocular tracking in primates. *J Physiol Paris* 98: 35–52, 2004. doi:[10.1016/j.jphysparis.2004.03.017](https://doi.org/10.1016/j.jphysparis.2004.03.017).
187. **Hopf J-M, Boehler CN, Luck SJ, Tsotsos JK, Heinze H-J, Schoenfeld MA.** Direct neurophysiological evidence for spatial suppression surrounding the focus of attention in vision. *Proc Natl Acad Sci USA* 103: 1053–1058, 2006. doi:[10.1073/pnas.0507746103](https://doi.org/10.1073/pnas.0507746103).
188. **Spering M, Carrasco M.** Similar effects of feature-based attention on motion perception and pursuit eye movements at different levels of awareness. *J Neurosci* 32: 7594–7601, 2012. doi:[10.1523/JNEUROSCI.0355-12.2012](https://doi.org/10.1523/JNEUROSCI.0355-12.2012).
189. **Schütz AC, Braun DI, Gegenfurtner KR.** Chromatic contrast sensitivity during optokinetic nystagmus, visually enhanced vestibulo-ocular reflex, and smooth pursuit eye movements. *J Neurophysiol* 101: 2317–2327, 2009. doi:[10.1152/jn.91248.2008](https://doi.org/10.1152/jn.91248.2008).
190. **Carrasco M.** Visual attention: the past 25 years. *Vision Res* 51: 1484–1525, 2011. doi:[10.1016/j.visres.2011.04.012](https://doi.org/10.1016/j.visres.2011.04.012).
191. **Kastner S, Ungerleider LG.** Mechanisms of visual attention in the human cortex. *Annu Rev Neurosci* 23: 315–341, 2000. doi:[10.1146/annurev.neuro.23.1.315](https://doi.org/10.1146/annurev.neuro.23.1.315).
192. **Ma Z, Watamaniuk SNJ, Heinen SJ.** Illusory motion reveals velocity matching, not foveation, drives smooth pursuit of large objects. *J Vis* 17: 20, 2017. doi:[10.1167/17.12.20](https://doi.org/10.1167/17.12.20).
193. **Yakushin SB, Gizzi M, Reisine H, Raphan T, Büttner-Ennever J, Cohen B.** Functions of the nucleus of the optic tract (NOT). II. Control of ocular pursuit. *Exp Brain Res* 131: 433–447, 2000. doi:[10.1007/s002219900302](https://doi.org/10.1007/s002219900302).
194. **Mustari MJ, Ono S.** Optokinetic eye movements. In: *Encyclopedia of Neuroscience*, edited by Squire LR. Amsterdam, The Netherlands: Elsevier, 2010, p. 285–293.
195. **Ilg UJ.** Slow eye movements. *Prog Neurobiol* 53: 293–329, 1997. doi:[10.1016/s0301-0082\(97\)00039-7](https://doi.org/10.1016/s0301-0082(97)00039-7).
196. **Kanari K, Sakamoto K, Kaneko H.** Effect of visual attention on the properties of optokinetic nystagmus. *PLoS One* 12: e0175453, 2017. doi:[10.1371/journal.pone.0175453](https://doi.org/10.1371/journal.pone.0175453).
197. **Murphy BJ, Kowler E, Steinman RM.** Slow oculomotor control in the presence of moving backgrounds. *Vision Res* 15: 1263–1268, 1975. doi:[10.1016/0042-6989\(75\)90172-8](https://doi.org/10.1016/0042-6989(75)90172-8).
198. **Pola J, Wyatt HJ, Lustgarten M.** Visual fixation of a target and suppression of optokinetic nystagmus: effects of varying target feedback. *Vision Res* 35: 1079–1087, 1995. doi:[10.1016/0042-6989\(94\)00215-8](https://doi.org/10.1016/0042-6989(94)00215-8).
199. **Fukushima K, Yamanobe T, Shinmei Y, Fukushima J, Kurkin S, Peterson BW.** Coding of smooth eye movements in three-dimensional space by frontal cortex. *Nature* 419: 157–162, 2002. doi:[10.1038/nature00953](https://doi.org/10.1038/nature00953).
200. **Gamlin PD, Yoon K.** An area for vergence eye movement in primate frontal cortex. *Nature* 407: 1003–1007, 2000. doi:[10.1038/35039506](https://doi.org/10.1038/35039506).
201. **Chaturvedi V, Gisbergen JA.** Shared target selection for combined version-vergence eye movements. *J Neurophysiol* 80: 849–862, 1998. doi:[10.1152/jn.1998.80.2.849](https://doi.org/10.1152/jn.1998.80.2.849).
202. **Erkelens CJ, Collewijn H.** Control of vergence: gating among disparity inputs by voluntary target selection. *Exp Brain Res* 87: 671–678, 1991. doi:[10.1007/BF00227093](https://doi.org/10.1007/BF00227093).
203. **Chaturvedi V, van Gisbergen JA.** Perturbation of combined saccade-vergence movements by microstimulation in monkey superior colliculus. *J Neurophysiol* 81: 2279–2296, 1999. doi:[10.1152/jn.1999.81.5.2279](https://doi.org/10.1152/jn.1999.81.5.2279).
204. **Krauzlis RJ, Liston D, Carello CD.** Target selection and the superior colliculus: goals, choices and hypotheses. *Vision Res* 44: 1445–1451, 2004. doi:[10.1016/j.visres.2004.01.005](https://doi.org/10.1016/j.visres.2004.01.005).