A change in perspective:

The interaction of saccadic and pursuit eye movements
in oculomotor control and perception

Alexander Goettker* & Karl Gegenfurtner

Abteilung Allgemeine Psychologie, Justus-Liebig University Giessen, Germany

Corresponding Author: Alexander.Goettker@psychol.uni-giessen.de

Abstract

Due to the close relationship between oculomotor behavior and visual processing, eye movements have been studied in many different areas of research over the last few decades. While these studies have brought interesting insights, specialization within each research area comes at the potential cost of a narrow and isolated view of the oculomotor system. In this review, we want to expand this perspective by looking at the interactions between the two most important types of voluntary eye movements: saccades and pursuit. Recent evidence indicates multiple interactions and shared signals at the behavioral and neurophysiological level for oculomotor control and for visual perception during pursuit and saccades. Oculomotor control seems to be based on shared position- and velocity-related information, which leads to multiple behavioral interactions and synergies. The distinction between position- and velocity-related information seems to be also present at the neurophysiological level, too. In addition, visual perception seems to be based on shared efferent signals about upcoming eye positions and velocities, which are to some degree independent of the actual oculomotor response. This review suggests an interactive perspective on the oculomotor system, based mainly on different types of sensory input, and less so on separate subsystems for saccadic or pursuit eye movements.

1. Introduction

The first successful recordings of eye movement responses occurred more than 100 years ago (Dodge, 1900; Hering, 1879). Over time, eye movements became an intensely studied topic and were used in many different fields of research and applied science. Eye movements are an integral part of our visual system. Since the distribution of photoreceptors in the primate retina

30   is not uniform (Østerberg, 1935; for a recent review see Grünert & Martin, 2020), we only have

31   access to the most detailed visual information in the small foveal region at the center of the

32   visual field and spatial resolution exponentially decays toward the periphery (see Strasburger

33   et al., 2011). Thus, we have to actively select relevant objects by moving our eyes, and this way

34   eye movements offer a unique direct window into perception and cognition (see (Fooken &

35   Spering, 2020; Gegenfurtner, 2016; Kowler, 2011; Schütz, Braun, & Gegenfurtner, 2011;

36   Tatler, Hayhoe, Land & Ballard, 2011, for recent reviews).

37   Research on eye movements has often focused on two of the most common types, saccadic and

38   pursuit eye movements. These two types of movements show succinctly different dynamics.

39   Saccades are continuously used to scan the environment. They are very fast (up to ~800-1000

40   deg/s), brief jumps of the eye across the visual field with typical latencies between 150 and 200

41   ms (see Leigh & Zee, 2015). They are executed in a stereotypical manner, with tight

42   relationships between amplitude (the distance covered by the saccade), peak velocity and

43   duration, known as the 'main sequence' (Bahill, Clark, & Stark, 1975). Pursuit eye movements

44   require the perception of a moving stimulus, indicating a special relationship with velocity

45   errors (Berryhill, Chiu, & Hughes, 2006; Rashbass, 1961; Steinbach, 1976; see Lisberger,

46   2015). They are slow and smooth rotations (of up to 100 deg/s; Meyer, Lasker, & Robinson,

47   1985) of the eyes that allow precisely matching the velocities of moving objects in the

48   environment, and have a latency of 100 to 150 ms (Liston & Stone, 2014).

49   Because of these different dynamics, saccades and pursuit are classically treated as two

50   independent systems, and are usually studied independent of one another. Saccadic eye

51   movements are mainly thought to correct mismatches between current gaze position and a

52   desired gaze position (position error), while pursuit eye movements are thought to reduce

53   mismatches of target velocity and eye velocity (velocity error)[1].

54   Due to their specialization for addressing different error signals, saccades and pursuit are also

55   commonly studied in different settings. Some exemplary lines of research for saccadic eye

56   movements are (1) the investigation of which low-level stimulus characteristics attract gaze

---

[1] Please note here that while the concept of position or velocity errors is easy to grasp, we want to emphasize that the representation of such signals in the brain is still unclear. Based on the neural dynamics of the human brain, it is unlikely that such signals are coded as discrete values that would match our physical understanding of position and velocity (Goffart, Bourrelly, & Quinet, 2017; Goffart, Bourrelly, & Quinton, 2018). It seems more likely that the something like a position error could be implemented based on imbalances between the activity of the left and right superior colliculus and the eye movement is used to restore an equilibrium between their activity. (Goffart et al., 2018). Please note, that for simplicity, we will keep referring to them as position or velocity-related error signals.

(e.g. saliency, see Itti, Koch, & Niebur, 1998; Schütz et al., 2011) and predicting saccade targeting with natural images (de Haas, Iakovidis, Schwarzkopf, & Gegenfurtner, 2019; Kümmerer, Wallis, & Bethge, 2016); (2) saccadic eye movements during reading (see Engbert, Nuthmann, Richter, & Kliegl, 2005); (3) saccadic eye movements as readouts of decision making processes (e.g., Gold & Shadlen, 2007); as (4) correlates of cognitive control (Munoz & Everling, 2004) or (5) markers for diseases like Parkinson (Ouerfelli-Ethier et al., 2018); (6) changes in saccade behavior due to learning mechanisms (e.g. with saccade adaptation, Iwamoto & Kaku, 2010; McLaughlin, 1967). This is only a short selection of topics and related studies. All these studies have in common, that they used static stimuli where only position error signals are available.

In contrast, pursuit eye movements are always studied with moving stimuli, or stimuli that appear to move. Results are typically used for gaining insights into (1) motion processing (Pack & Born, 2001); (2) the transformation of visual motion signals into motor commands (Lisberger, 2015); and (3) the relationship between motion perception and oculomotor control (Spering & Montagnini, 2011; Gegenfurtner et al., 2003; Osborne et al. 2005). Since small corrective saccades usually occur during pursuit movements, their occurrence is typically minimized by using special paradigms, such as the Rashbass step-ramp paradigm (Rashbass (1961), or they are simply disregarded in the data analysis (see e.g. Klein & Ettinger, 2019).

The lines of research mentioned above have all been highly successful in elucidating properties of saccadic and pursuit eye movements. However, they cannot answer the question whether saccades and pursuit are two entirely different systems with different control circuits and specialized for different error signals, because saccades are studied in response to position errors exclusively, and pursuit in response to velocity errors only. The resulting picture of the oculomotor system is at best incomplete. In this review, we suggest that it is time to focus at eye movements in more naturalistic settings that include both saccades and pursuit and allow to measure the multitude of interactions.

Two previous review articles already demonstrated similarities and shared signals at the neurophysiological (Krauzlis, 2004) and behavioral level (Orban de Xivry and Lefevre, 2007). Krauzlis (2004) argued that "the pursuit system has a functional architecture very similar to that of the saccadic system", while Orban de Xivry and Lefevre (2007) suggested that "that saccades and pursuit are two outcomes of a single sensorimotor process". These reviews emphasized specific examples and paradigms that showed such an overlap. Here, we will build on this influential work and present recent evidence that synergetic interactions between saccades and

90   pursuit are the rule, and not the exception. We will focus on oculomotor control, but also

91   addresses other research where saccadic and pursuit eye movements were shown to interact

92   more closely than previously assumed. We propose that the distinction classically made

93   between different types of oculomotor responses (saccades vs pursuit), could be regarded as a

94   distinction in the kind of efferent or sensory information (position vs. velocity) that is available
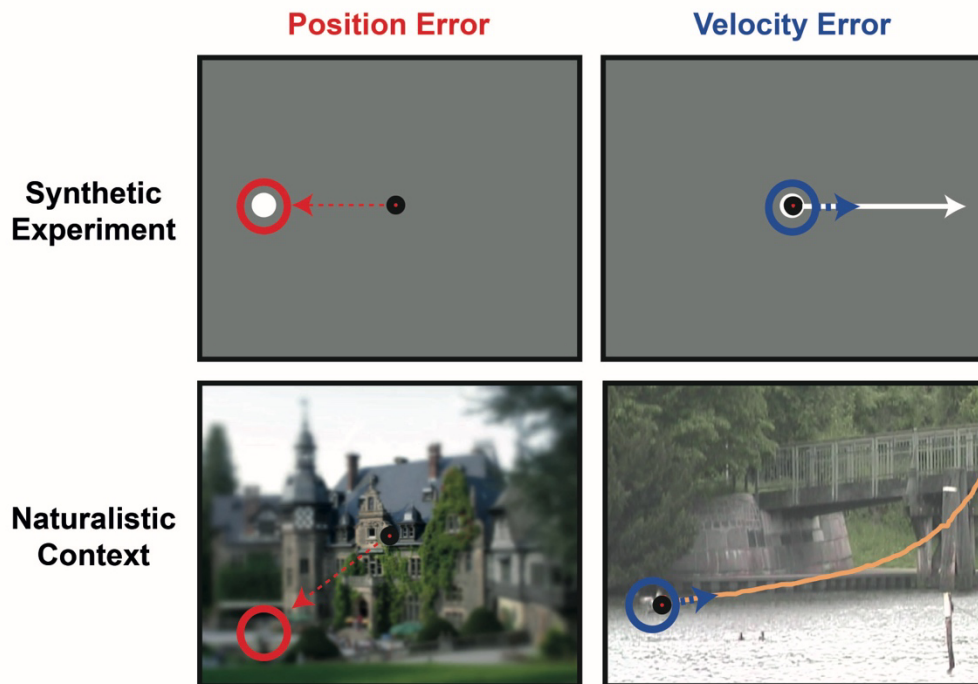
95   in a given task.

96

Figure 1. Comparison of two different perspectives on oculomotor research. A: The left panel shows typical lines of current research. The right panel shows the proposed interactive perspective on oculomotor research. Here the distinction is not based on the different type of eye movements (saccade vs. pursuit), but is based on the different type of information (position vs. velocity). **B** Depiction of typical stimuli for the occurrence of saccadic and pursuit eye movements. The black circle depicts the gaze position. The upper panels show a typical experiment under lab conditions with synthetic stimuli, while the lower panels show naturalistic contexts where the respective eye movement typically occurs. With a static image, a position error arises either by targeting the white disk or a different part of the image, which is typically corrected for by a saccadic eye movement (left panels). Note that the resolution of the naturalistic image is adjusted according to the distribution of receptors on the retina: Close to the gaze position it is high, and decays towards the periphery. The right panels show typical situations for pursuit movements. These could either be a moving dot in the lab or a flying duck following the orange trajectory. For a direct comparison of eye movements between synthetic experiments and more naturalistic conditions see Goettker, Agtzidis et al. (2020).

2. The interaction perspective

Even though saccades and pursuit are specialized for different error signals and have distinct dynamics, an interaction between them is inherently necessary. Both have their strengths in reducing one kind of error signal, but both have complementary weaknesses. Saccadic eye movements are fast and can bring the gaze quickly to any point in the visual field. But for a moving target, bringing the gaze to the position of the target is insufficient, since the target will have moved away from the new point of focus, and further saccades would be required. Each of these saccades has severe perceptual consequences, such as a reduction in visual sensitivity (Ross, Morrone, Goldberg, & Burr, 2001). Thus, it is a disadvantage to track a moving target with a sequence of saccadic eye movements. The target will move on the retina during the fixation periods, or be 'invisible' during the saccades. In contrast, pursuit eye movements keep moving targets close to the fovea without reducing visual sensitivity (Schütz, Braun, & Gegenfurtner, 2009b; Schütz, Braun, Kerzel, & Gegenfurtner, 2008), but due to their latency and limitated speed, there is an accumulation of position error. This is especially the case for unpredictably moving targets, such as a mosquito flying through a room. There is a need for additional corrective saccades to bring the target back onto the fovea (de Brouwer, Yuksel, Blohm, Missal, & Lefèvre, 2002; Coutinho, Lefèvre, & Blohm, 2021). Thus, only the combination of saccades and pursuit seems to allow optimal tracking performance.

Position and velocity errors are relevant for saccades and pursuit. Despite their specialization for one type of error signal, saccadic and pursuit eye movements can also be affected by the other type of error signal (see Orban de Xivry & Lefèvre, 2007 for a detailed overview). Multiple studies have demonstrated that saccades to moving targets are accurate and end close to the position of the target at the end of the eye movement (Ron et al., 1989; Keller & Johnson,1990; de Brouwer, Missal, Barnes, & Lefèvre, 2002; Fleuriet, Hugues, Perrinet, & Goffart, 2011; Schreiber, Missal, & Lefèvre, 2006). This is not a simple task, as there are substantial processing delays of around 100 ms in the system from the time of photons hitting the retina until this information arrives at critical oculomotor areas (see Schlag & Schlag-Rey, 2002). If saccades would aim at the position that was available at the start of the processing of information, gaze would consistently lag behind the moving target. This suggests that the control of saccadic eye movements integrates velocity-related information to estimate the correct target location at saccade end. In contrast, pursuit eye movements are initiated in response to velocity errors, but they also react to position signals. For example, pursuit trajectories can be deflected by the position of additional targets (Blohm, Missal, & Lefèvre,

144 2005) or pursuit can be accelerated when artificial position errors are introduced (Pola & Wyatt,

145 1980; Segraves & Goldberg, 1994; Buonocore et al., 2019).

146 Recent direct evidence for the contribution of both position and velocity-related information

147 for oculomotor control was presented by Goettker and colleagues (Goettker, Braun, &

148 Gegenfurtner, 2019). In their study, subjects had to track a target that stepped vertically to a

149 different position and then moved horizontally with a constant velocity. This was usually

150 achieved by an interceptive saccade followed by an immediate pursuit response. The authors

151 used luminance targets of varying contrasts, but also isoluminant chromatic stimuli, which are

152 known to attenuate speed processing (Cavanagh, Tyler, & Favreau, 1984; Lu, Lesmes, &

153 Sperling, 1999; for reviews, see Gegenfurtner & Hawken, 1996; Cropper & Wuerger, 2005).

154 They replicated previous findings (de Brouwer, Missal et al., 2002; Fleuriet et al., 2011;

155 Schreiber et al., 2006) of accurate saccadic eye movements in response to targets with

156 luminance contrasts (Figure 2A & 2B). However, for isoluminant targets, saccades

157 systematically lagged behind the targets and landed at the position the target had 100 ms before

158 saccade onset (Figure 2C). This lag fits well with the assumption that due to neuronal processing

159 delays, the last available position for saccade planning is roughly 100 ms before saccade onset

160 (de Brouwer, Missal et al., 2002). In order to bring the gaze to the target, the oculomotor system

161 seems to combine a delayed position signal with a velocity-related component. If the velocity-

162 related component is missing or impaired, saccades lands at a position that is estimated based

163 only on the delayed position signal.

164 While velocity is clearly defined physically as a change in position over time, this seems to be

165 different for brain processing, as there are dissociable effects of position and velocity

166 information. There is indeed strong evidence for at least two different processes for visual

167 motion processing: one based on changes in position over time, and one based on motion energy

168 (Braddik, 1974; Cavanagh, 1992; Lu & Sperling, 1995). The position-based mechanism seems

169 to be attenuated in the periphery and the energy-based mechanism is generally impaired by

170 isoluminant targets (Lu & Sperling, 2001; Gegenfurtner & Hawken, 1996). The study by

171 Goettker et al. (2019) presented above differentially attenuated the strength of these two motion

172 components. When the target started to move in the fovea without the initial step, saccades to

173 isoluminant targets became accurate (Figure 2D), just as pursuit movements are also known to

174 be possible for foveal isoluminant targets (Braun et al., 2008).
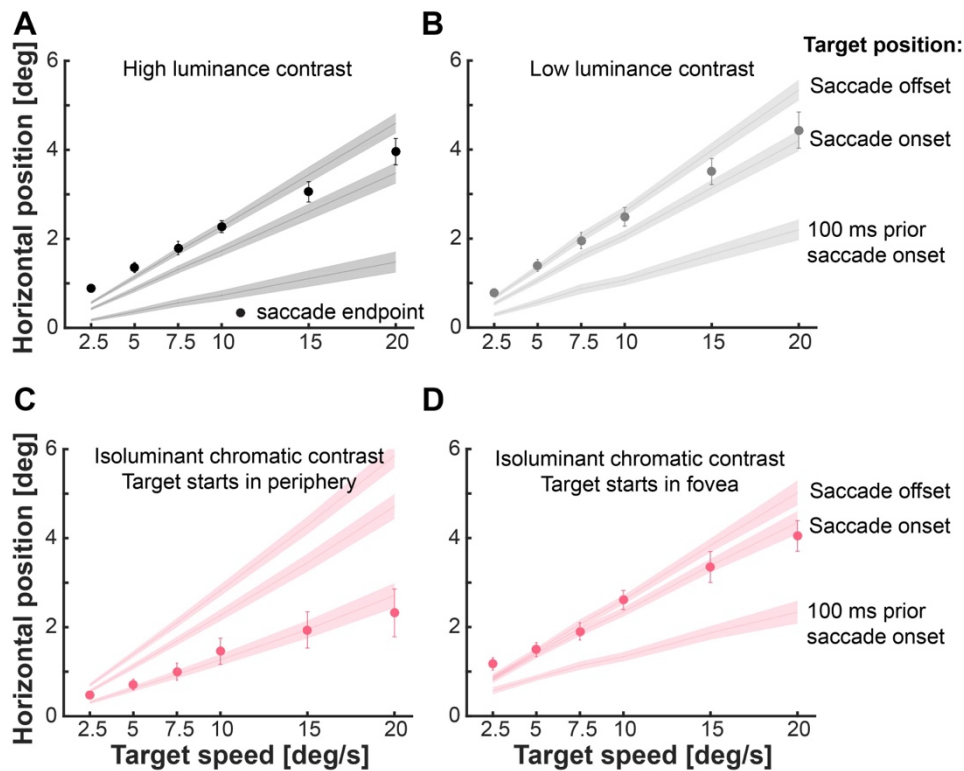
6

Figure 2. Compensation for target movements during saccades. Results from study by Goettker et al. (2019). Targets stepped 10 deg vertically and then moved horizontally at one of the different target speeds. Shown are the average horizontal positions of saccade endpoints (circles), plotted with respect to target positions at three points in time: The lowest line represents the average target position 100 ms before saccade onset, the intermediate one represents the target position at saccade onset, and the top line represents the actual target position at saccade end. (**A–B**) In the two luminance contrast conditions (A, high contrast, and B, low contrast) saccade endpoints are quite close to the actual target positions. (**C**) In the isoluminant condition, saccades landed close to the target position at 100 ms before saccade initiation when the target was moving at 10 deg in the periphery. Error bars and shaded areas symbolize the 95% CI around the mean. (**D**) When the initial step was removed, saccades to isoluminant targets became accurate again, suggesting the use of a velocity-related signals.

There is evidence that the two motion processing mechanisms are generally involved during the control of pursuit eye movements, but at different stages (Wilmer & Nakayama, 2007). During the initial open-loop phase, pursuit seems to rely on motion energy signals. After ~150 ms during the closed-loop phase, when less retinal motion of the target is available, the position-based motion signals seem to play a bigger role (see also Behling & Lisberger, 2020). This suggests that there are multiple signals that are integrated on different time scales according to availability and then are transformed into saccadic or pursuit eye movements (see Lorenceau & Cavanagh, 2020 for a perceptual example of such a weighting). An integration of signals related to changes in object positions and velocities was also proposed in an object tracking model by Kwon and colleagues (Kwon, Tadin, & Knill, 2015). The combination of these signals successfully explained different perceptual illusions regarding the motion and the position of the target, suggesting a tight coupling between the two computations.

Shared signals between saccadic and pursuit eye movements. The evidence above suggests that saccadic and pursuit eye movements are both affected by position and velocity-related error signals. The next logical question is: Are these signals shared between the systems? Goettker et al. (2019) observed that along with altered saccade endpoints, the subsequent pursuit response was also impaired with isoluminant targets. For luminance targets, the velocity of the eye scaled with target speed immediately after the saccade. Such a scaled response was not present for isoluminant targets, which strongly suggests shared signals. Along the same lines, Hainque and colleagues (2016) demonstrated that saccadic and pursuit eye movements were directed towards a new target movement at the same time. A shared underlying representation also suggested by Liston and Krauzlis (2003), who demonstrated that the direction of the initial pursuit response usually matched the direction of the upcoming saccade when selecting one of two moving targets. In trials where subjects switched to another target by employing a saccade, the pursuit movement also reversed its direction, suggesting a shared response preparation.

Further evidence for shared signals for saccadic and pursuit eye movements comes from a recent study by Watamaniuk, Badler, & Heinen, 2019. They demonstrated that saccade adaptation, which leads to a change in mapping of the target position, can also affect pursuit responses. Similar evidence for shared position-based signals comes from a study with adaptation of small catch-up saccades which occur during pursuit (Schütz & Souto, 2011). A vertical shift of the target during the saccade, not only resulted in oblique saccades, but also in increased vertical components in the pursuit response that immediately followed. These studies demonstrate that altered position signals for saccade control also affect pursuit eye movements.

Continuous control and processing. All the above findings point to shared information for saccadic and pursuit eye movement control. This leads to the next question whether there is continuous exchange of information and synergies between the two movements. Orban de Xivry and colleagues (2006) demonstrated that saccadic eye movements corrected for a decrease in pursuit velocity during target blanking, meaning that saccades directly correct for errors that arise due to pursuit variability. Such synergies can also be observed when a pursuit response after a saccade is affected by the previous saccade. Goettker et al. (2018; 2019) demonstrated an immediate adjustment of pursuit responses based on saccade landing positions. Pursuit responses during the first 150 ms after a saccade varied systematically with saccadic landing positions. Thus, the relative error at the end of a saccade immediately influenced the following pursuit response. When the saccade landed further behind the target, the pursuit response was faster (Lisi & Cavanagh, 2017; Pola & Wyatt, 1980; Segraves & Goldberg, 1994), and vice versa. At this early point in the pursuit response, new retinal information has no time

8

to become effective (see Buonocore, Skinner, & Hafed, 2019; Tavassoli & Ringach, 2009), suggesting that the initial pursuit response after the saccade is based on the predicted position error at the end of the saccade. Alternatively, it could even be based on a comparison of the target representation and a representation of the eye position during the saccade. Some visual information during the saccade is processed and can influence perception as well as eye movements following the saccade (Castet & Masson, 2000; Schweitzer, Watson, Watson, & Rolfs, 2019; Ibbotson & Cloherty, 2009; Schweitzer & Rolfs, 2020a, 2020b; Watson & Krekelberg, 2009).

The continuous processing of visual information opens up new perspectives for saccade control. There is a lot of evidence that saccades can be affected by information arriving just before execution (Schreiber et al., 2006; Schütz et al., 2012; van der Stigchel et al., 2010) and there are a few reports that information arriving during saccades can be taken into account "mid-flight" (see Gaveau et al., 2003; Kiernan et al., 2016). However, note that the studies of Gaveau et al. and Kiernan and colleagues both studied large saccades with amplitudes of more than 30 deg. Due to these large amplitudes, these saccades had a longer durations of more than 50 ms. Gaveau et al. (2003) reported that changes in saccade kinematics occurred as fast as 50 ms after changes in target positions. This matches the reports of Buonocore et al. (2019), who measured the influence of position error signals during open-loop pursuit, and also found changes in pursuit kinematics after 50 ms. This suggests that saccades might be in principle open to continuous control, and only due to their usually shorter amplitudes and durations, this does not become apparent. However, this information is highly useful in controlling eye movement behavior immediately following the saccade.

Despite all these similarities in the control of saccadic and pursuit eye movements, there are some notable differences in how incoming information is used. Recently, Bourrelly and colleagues (Bourrelly, Quinet, & Goffart, 2018a) found that inactivation of the caudal fastigial nuclei impaired saccadic eye movements to moving targets and the subsequent pursuit. The magnitude of impairments seemed to be comparable across sessions for saccadic and pursuit eye movements (see Figure 3A), but they did not observe a trial-by-trial correlation. This suggests that two separate streams of information might be used for controlling saccadic and pursuit eye movements. Alternatively, the sequential saccadic and pursuit eye movements in this paradigm might be driven by temporally separated aspects of the same evolving signal.

Differences in dynamics were indeed observed by Kwon and colleagues (2019). They investigated saccades to an aperture with a random dot field. Motion pulses ~200 ms before

266   saccade onset led to the largest deviation in saccade endpoints, whereas the responses after the

267   saccade were most sensitive to motion pulses presented ~125 ms before the saccade (see Figure

268   3B). Therefore, the absence of trial-by-trial correlations in the study by Bourrelly and

269   colleagues (2018a) could also occur as a result of different temporal integration windows of

270   shared but noisy signals. Similar differences in integration time were also observed in a decision

271   making task (Liston & Krauzlis, 2005). Their experiment revealed that oculomotor decisions

272   are presumably based on shared signals, but pursuit eye movements have a lower decision

273   threshold, and differ in their motor processing delays (see Figure 3C).
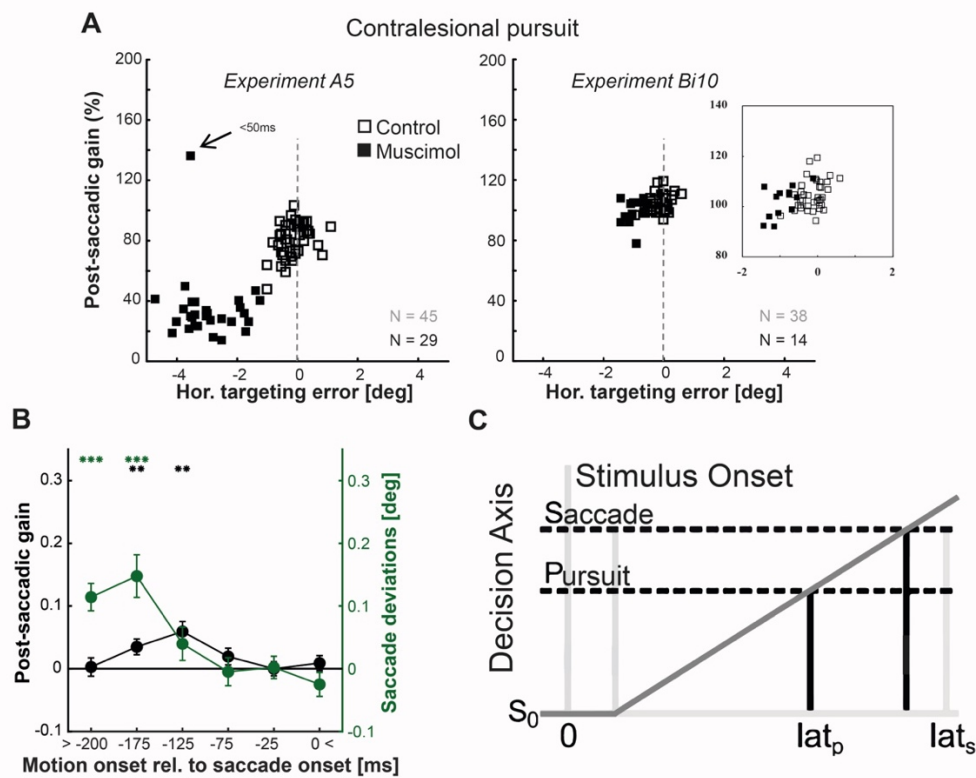

274

275   **Figure 3. Examples of differences in integration of information for saccade and pursuit control. A**
276   Modified with permission based on Bourrelly et al. (2018). Saccade dysmetria and postsaccadic pursuit
277   velocities during contralesional tracking. The horizontal (Hor.) targeting errors of saccades and
278   postsaccadic pursuit gain are shown for all trials recorded during experiments A5 and Bi10. **B** Modified
279   with permission based on Kwon et al., 2019. Presaccadic motion integration intervals for post-saccadic
280   following responses (Post-saccadic gain) and deviation in saccade endpoints in green. Post-saccadic gains
281   and saccade endpoint deviations from Experiments 2 and 3 are illustrated as a function of motion coherence
282   onset (sustained or pulsed motion stimulus) relative to saccade onset. **C** Modified with permission based
283   on Liston & Krauzlis, 2005. The graph shows a linear decision signal that rises from an initial level (S0)
284   after a common visual delay to cross two response thresholds (Pursuit and Saccade). When threshold P is
285   crossed, a pursuit response begins at latP. The saccadic system has a higher decision threshold delaying the
286   saccadic response. Saccades also have an additional motor delay, therefore saccades are only triggered at
287   latS, sometime after the decision threshold already had been reached.

288   Taken together, these results suggest that both saccadic and pursuit eye movements are driven

289   by shared representations of position- and velocity-related signals (Daye, Blohm, & Lefèvre,

290   2014; Deravet, Blohm, Xivry, & Lefèvre, 2018; Morris, Bremmer, & Krekelberg, 2016; Orban

291   de Xivry et al., 2006), but that there are different thresholds and temporal integration windows

292   that transform this input into sequences of saccadic and pursuit eye movements.

293   **Key brain areas involved in the processing of position- and motion-related information.**

294   The neural circuits involved in saccadic and pursuit eye movements have been studied in great

295   detail (see Leigh & Zee, 2015; Klein & Ettinger, 2019). While neural circuits show significant

296   overlap for the two movements (Krauzlis, 2004, 2005; Orban de Xivry & Lefèvre, 2007), they

297   are again, often considered in isolation, similar to the situation in behavioral research. For

298   example, in recent textbooks on eye movement research (e.g., Klein & Ettinger, 2019), the

299   neural circuits for saccadic and pursuit eye movements are covered in separate chapters, even

300   though almost all of the brain areas mentioned – ranging from the cerebellum to the frontal eye

301   fields – are common. The major discrepancies in these typical treatments are that (1) the

302   superior colliculus (SC), which is thought to be the one of the main areas along the position

303   stream (Gandhi & Katnani, 2011; Sparks, 1986), is typically only mentioned when discussing

304   saccadic eye movements, and (2) the middle temporal area (MT) which is thought to be one of

305   the main motion areas (Dubner & Zeki, 1971; Pack & Born, 2001) is only mentioned when

306   discussing pursuit eye movements. This description of the relevant brain areas is along the lines

307   of the specialization of saccades and pursuit, but it offers an isolated view only. Similar to the

308   results observed in studied involving behavioral interactions, there is also shared information

309   on the neural level.

310   First, it is known that pursuit eye movements are related to activity in the SC (Basso, Krauzlis,

311   & Wurtz, 2000; Krauzlis, 2005; Krauzlis, Basso, & Wurtz, 2000). Lesions of the SC lead to

312   constant position offsets, even during pursuit (Hafed, Goffart, & Krauzlis, 2008). Therefore,

313   the SC can be seen as acting as a general motor map, which indicates the position of a target

314   relative to the eye, irrespective of any specific eye movements. Saccades, pursuit and fixational

315   eye movements (Hafed & Goffart, 2020) all seem to get their position signal from the SC.

316   Second, MT is also involved in saccade planning in response to dynamic targets, as MT lesions

317   affect saccades to moving, but not to stationary stimuli (Newsome & Pare, 1988; Newsome,

318   Wurtz, Dürsteler, & Mikami, 1985). Lesions in areas related to MT, such as the nuclei of the

319   optic tract (NOT; Hoffmann, Bremmer, Thiele, & Distler, 2002; Krauzlis, 2004), or the caudal

320   fastigial nuclei (CFN; Bourrelly et al., 2018a, 2018b) produce similar effects. Lesions in those

321   areas can produce uncontrollable drifts of the eyes (Inoue, Takemura, Kawano, & Mustari,

322   2000) and impair saccades and pursuit to moving targets (Bourrelly et al., 2018a, 2018b).

323   Therefore, in analogy to the SC and position, MT and related areas seem to provide more

general motion signals, which are used in the interception moving targets. Considering signals shared by saccadic and pursuit eye movements provides crucial insights into a highly interconnected network (Krauzlis, 2004, 2005). Taken together, these results suggest that a clear distinction at the neuronal level does not necessarily arise between brain areas specialized for saccades or pursuit. Rather, the specialization seems to be for position versus motion.

3. Open questions

Changing the perspective, from studying the control of saccadic and pursuit eye movements in isolation, to an emphasis on shared signals and interactions can provide interesting insights into oculomotor control. The adoption of such an interactive framework also raises multiple new questions.

Execution of saccade or pursuit?

A critical question within a framework of shared sensory input and continuous control of oculomotor behavior concerns the decision criteria for the execution of a saccadic or pursuit eye movement as the appropriate oculomotor response. Above, we have provided evidence supporting the concept of shared information about position and velocity-related signals, but it is unclear how these two signals determine the timing and usage of saccades and pursuit. Based on current knowledge, there are several heuristics that can guide the decision.

First, if there is no velocity-related error signal, the resulting response should always be a saccade. This is seems to be an obvious statement, since there is ample evidence that pursuit eye movements require the percept of a moving target (Berryhill et al., 2006; Braun, Pracejus & Gegenfurtner, 2006; Steinbach, 1976).

Second, when there are both position- and velocity-related signals involved, the velocity signals can suppress saccades that otherwise would have been triggered given a certain position error alone (Rashbass, 1961). This has been quantified as the eye crossing time, which is the ratio of position and velocity errors (de Brouwer, Yuksel et al., 2002; Gellman & Carl, 1991). If the movement of a target reduces the position error by bringing the target closer to the fovea, saccades are inhibited. Recently, these ideas have been implemented in a mechanistic model for occurrence of saccades. In the model, saccades are triggered based on a predictive position error signal, which is computed based on position- and velocity-related signals (Coutinho et al., 2021). A saccade is triggered if enough evidence has accumulated that the predicted target position will remain outside of the fovea. The model is supported by recent behavioral data

(Nachmani et al., 2020), which demonstrate that fewer corrective saccades are triggered if the positional uncertainty of the target is increased.

Third, despite shared processing of input signals, there might be separate decision boundaries for saccadic and pursuit eye movements. Pursuit typically has lower latencies than saccadic eye movements. There is evidence that despite using the same sensory input, there is a lower decision threshold for pursuit and potentially even an additional motor delay in the preparation of saccades (Liston & Krauzlis, 2005). This lower decision threshold can lead to behavior where a pursuit response initially follows one target, but then changes direction to be in line with a different target selected by the saccade (Liston & Krauzlis, 2003; Spering, Montagnini & Gegenfurtner, 2008). These decision thresholds can also be affected by the task or other cognitive factors. Even for the same physical stimulus, saccades were triggered earlier when the goal was to manually intercept a moving target than for a perceptual velocity judgment (Goettker et al., 2019). This strategy avoids saccades close to the moment of the interception and thereby increases the reliability of visual information at that critical moment. Other predictable events, such as auditory cues, can also lead to a reduction of saccade and blink rates (Abeles, Amit, Tal-Perry, Carrasco, & Yuval-Greenberg, 2020), suggesting shifts of the decision criteria to increase task performance.

All of this information together suggests that the oculomotor system tries to balance the costs of accumulating position errors during pursuit with the costs of a saccade in terms of energy consumption (quickly accelerating and decelerating the eye) and reduction in visual sensitivity. The balance between the two is finely tuned to the requirements of a given task.

How do the eyes behave in uncertain situations?

A Bayesian framework for the integration of evidence has successfully described performance in numerous perceptual tasks (e.g., Ernst & Banks, 2002). This approach has also been adapted to explain the effect of uncertain sensory input on oculomotor behavior. For example, models of pursuit eye movements based on optimal integration of sensory input with a dynamic internal model (Bogadhi, Montagnini, & Masson, 2013; Orban de Xivry, Coppe, Blohm, & Lefèvre, 2013) correctly predict that pursuit gain is decreasing when the target is occluded. Typical undershoots observed for saccadic eye movements can be similarly explained (Lisi, Solomon, & Morgan, 2019). If uncertainty about the target position increases, saccade gains are reduced to avoid overshoots of the target. Overshoots come at the presumably high cost of corrective saccades in the direction opposite of the initial saccade. A weighted integration of information based on the reliability of the previous signals was also shown in trial-by-trial learning. This is

13

388   again affecting pursuit (Darlington, Beck, & Lisberger, 2018; Darlington, Tokiyama, &
389   Lisberger, 2017) and saccadic movements (Deravet et al., 2018) in a similar manner and seems
390   to be driven by retinal position and velocity error signals (Goettker et al., 2021).

Are distinct brain areas involved with different oculomotor behavior or different sensory information?

393   Certain brain regions have been identified that have differential responses during saccades and
394   pursuit. For example, in the FEF, subregions were related to saccadic or pursuit eye movements
395   and termed FEF_{sac} and FEF_{sem} (e.g., Yan, Cui, & Lynch, 2001), respectively. However, studies
396   identifying those differences, especially in fMRI settings (Petit, Clark, Ingeholm, & Haxby,
397   1997; Rosano et al., 2002), have used static stimuli when measuring saccadic eye movements
398   and moving stimuli when measuring pursuit. This approach does not allow dissociation of a
399   saccade from a position-related area or a pursuit from a velocity-related area. Based on the
400   evidence that saccadic and pursuit eye movements both are driven by shared position and
401   velocity-related signals, it is necessary to investigate whether these responses in these brain
402   areas actually differ based on the type of eye movement (saccade vs. pursuit), or based on the
403   relevant sensory information (position vs. velocity).

Where does information converge?

405   Based on the behavioral results of Goettker et al. (2019), there seem to be potentially
406   independent contributions of position and velocity-related signals involved in oculomotor
407   control. An interesting question then is where these signals converge to produce adequate
408   oculomotor output. Brain areas coding for both or only one of the two error signals can
409   potentially be identified based on the findings of Goettker et al. (2019), because predictive
410   processing was severely impaired for peripheral isoluminant stimuli.

411   A crucial question is, for example, whether the representation of the target position in the SC
412   lags behind the real target position, in line with the psychophysical results of Goettker et al.
413   (2019). If the SC does not have access to velocity-related signals, as suggested by Keller &
414   Johnsen (1990), it should show an equivalent response to both moving isoluminant and
415   luminance stimuli, even though eye movement behavior is drastically different. If the response
416   is similar, the SC would always deal with information from the past due to the neuronal
417   processing delays. Differences in the SC responses to moving isoluminant versus luminance
418   stimuli would indicate that the SC gets some information about target movement. This would
419   make it a candidate hub for integrating position and velocity streams. Similar logic could be

420 applied to responses in several other relevant areas throughout the brain to determine where and
421 potentially also how error signals are integrated and processed.

4. Other evidence for interactions

423 Shared information and synergies between saccadic and pursuit eye movements are not only
424 present in oculomotor control. Similar questions are studied for either saccadic or pursuit eye
425 movements. However, bringing those results together might again provide key insights into
426 overarching mechanisms.

427 **Perception around eye movements.** Why do we not notice that we constantly move our eyes,
428 despite dramatic changes to retinal input? This is a fundamental question (see e.g. Alhazen,
429 1083, cited in Binda & Morrone, 2018) that has sparked a lot of research. The main mechanism
430 proposed to discount the effect of both, saccadic and pursuit eye movements on the retinal input
431 is the use of a copy of the motor command, termed efference copy (Holst & Mittelstaedt, 1950)
432 or corollary discharge (Sperry, 1950). This efferent signal allows to distinguish between
433 movements on the retina caused by objects moving in the external world, and movements of
434 objects that are caused by eye movements (Wurtz, 2018). How perception is affected during
435 eye movements was mainly studied separately for saccades and pursuit (for review, see Schütz
436 et al., 2011 for pursuit or Binda & Morrone, 2018 for saccades).

437 When looking into this literature, there might be comparable changes in perception around
438 saccadic and pursuit eye movements. Targets flashed before saccade onsets appear to be shifted
439 in the direction of saccadic eye movements (e.g. Matin & Pearce, 1965) and similar
440 observations have also been also made during pursuit eye movements (Hansen, 1979; van Beers
441 et al. 2001; Brenner, Smeets, & van den Berg, 2001; Dowiasch, Blohm, & Bremmer, 2016;
442 Rotman, Brenner, & Smeets, 2004). Interestingly, there are also a number of factors that
443 influence the magnitude of this shift such as the availability of visual references, target
444 detectability, or the response type and the effect of these factors on mislocalization during
445 pursuit and saccades seems to be comparable (discussed in Brenner et al., 2001; Kerzel et al.,
446 2006). Related to the mislocalization of flashed targets, a more general compression of space
447 and time has been reported for saccadic eye movements (Ross, Morrone, & Burr, 1997). Flashed
448 stimuli with temporal delays of up to 200 ms and in a distance of up to 20 deg can be merged
449 together and perceived as one stimulus close to the saccade target (Morrone, Ross, & Burr,
450 2005; see Binda & Morrone, 2018). A similar spatial compression has not been observed during
451 pursuit eye movements, but temporal compression has been reported (Schütz & Morrone,
452 2010). The lack of large spatial compressions, however, might not be surprising: due to the

continuous and relatively slow eye movements that occur during pursuit, comparable time windows as for an individual saccade only led to very small displacements of the eye position. However, temporal compression could accumulate across multiple time windows and is therefore measurable.

Recently, we took a more interactive approach and studied the compensation for eye velocity when judging perceived speed for combinations of pursuit and saccadic eye movements (Goettker, Braun, Schütz, & Gegenfurtner, 2018). We found that the occurrence and direction of corrective saccades which occurred during tracking of targets systematically distorted perceived target speeds (see Figure 4B). In trials that involved corrective forward saccades, where the eye jumped in the direction of target movement to catch up with the target (see Figure 4A for an example), the target was perceived to move faster than in trials without corrective saccades ("pure pursuit"). In contrast, in trials that involved corrective backward saccades, where the eyes jumped backward to "wait" for the target, the target was perceived to move slower than in pure pursuit trials. This difference in perceived speed occurred for the same physical target movements, where the oculomotor behavior only varied due to trial-by-trial variability. During pursuit, efferent eye velocities and retinal velocity signals are thought to be combined to account for the variability in pursuit velocity while maintaining close to veridical percepts. In trials that involved corrective saccades, perceived speeds were correctly predicted *only* when including the eye velocities during saccadic epochs (Figure 4C+D). Thus, eye velocity during small corrective saccades seemed to be integrated into the efferent velocity signals that are used to compensate for pursuit eye movements. In addition, the influence of corrective saccades seems to distort the combination of extra-retinal and retinal information, and, therefore, biases the velocity reconstruction. These results strongly suggest that there is a general efferent eye velocity signal that affects the reconstruction of perception, irrespective of oculomotor responses.
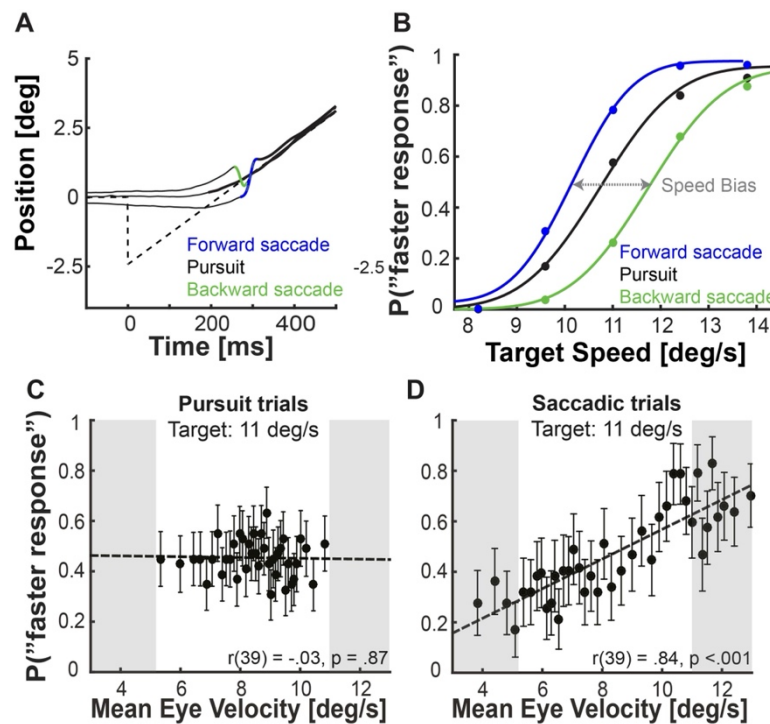
Figure 4. Influence of corrective saccades on perceived target speeds. A Different oculomotor responses to the same physical target movement illustrated with the dashed line. In one trial the oculomotor response includes a corrective forward saccade (blue), in one trial it includes a corrective backward saccade (green) and in one trial it is a pure pursuit response (black). **B** Psychometric functions for perceived speed of a single representative observer. Colors indicate the three different oculomotor responses. **C** Average mean eye velocities during pursuit trials in the first 400 ms after pursuit onset versus the probability of a "faster" response for the comparison speed of 11 deg/s. **D** Same as in **B**, but for trials with additional corrective saccades. The shaded areas represent the limits of pursuit velocities found for pure pursuit trials. Note that for saccadic trials, there was a clear relationship between average eye velocities and perceived speeds, whereas this relationship was not present in pursuit trials.

The nature and neurophysiology of efferent eye movement signals. The distinction between position- and velocity-related signals for oculomotor control might also be present in efferent information about upcoming eye movements. There is a well-established pathway that provides an efference copy of the saccadic eye movements signal, starting from the SC (Sommer & Wurtz, 2008; Sun & Goldberg, 2016) and neurons in area MST that encode eye velocity during pursuit eye movements (Ono, 2015). The pathway from the SC to the frontal eye field has been studied in great detail and causally tied to predictive remapping of receptive fields (Colby & Goldberg, 1992) and perceived visual stability (Cavanaugh, Berman, Joiner, & Wurtz, 2016; see Zimmermann & Bremmer, 2016). However, as discussed above, information from the SC, the origin of the saccade remapping pathway, is also used for pursuit control (Basso et al., 2000; Krauzlis et al., 2000) and therefore could be related to future eye position and not efference copies of saccadic eye movements.

Evidence for such a shared efferent position signal across saccadic and pursuit eye movements came from a recent study in the visual primary cortex: The firing rate of neurons in the primary

visual cortex depends not only on visual input, but is also based on gaze position (Andersen et al., 1985). Recently, Morris and Krekelberg (Morris & Krekelberg, 2019) used multi-electrode arrays to decode signals from a large population of such neurons, and used the modulation in firing rate to predict gaze positions. With this signal it was possible to accurately predict eye position during saccadic as well as pursuit eye movements with hardly any delay (see Figure 5). This resembles the neural signature of a general position efferent across eye movements which is available in close to real-time. Similar predictive eye position signals can also be found in the dorsal visual system (Morris et al., 2016; Morris, Kubischik, Hoffmann, Krekelberg, & Bremmer, 2012). The origin of these eye position signals in the primary visual cortex could be the efferent remapping pathway originating in the SC and leading to the FEF, which would suggest that the pathway described by Sommer & Wurtz (2008) could also be used to track positional changes during pursuit eye movements.
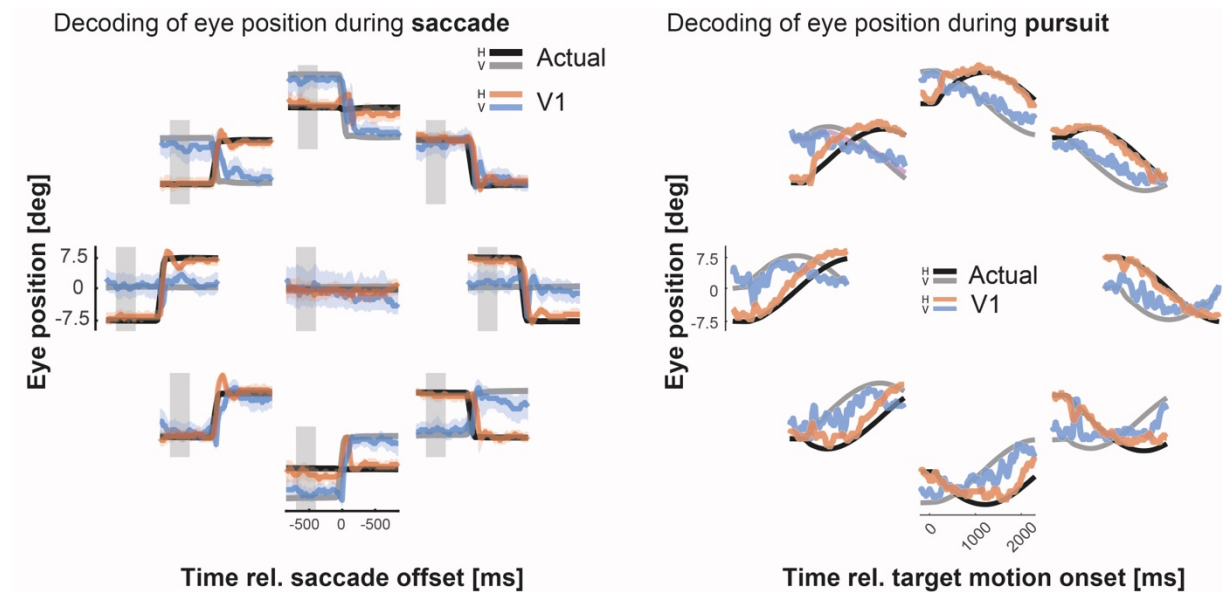

Figure 5. Decoding of eye position across saccadic and pursuit eye movements. Figures modified with permission based on Morris & Krekelberg, 2019. **Left Panel**: Decoded eye positions over time for each saccade direction (red and blue curves for horizontal and vertical position), plotted against the average eye trace (black and gray for horizontal and vertical position). Plots are arranged spatially according to the required saccade direction (no saccade was required for the central fixation position). Curves represent the median of decoded positions and shading represents variability (middle 50% of distribution) across trials. The gray shaded region represents the fixation epoch used to build the decoder. **Right panel**: Decoded eye positions over time for clockwise pursuit plotted as for saccadic eye movements.

Proprioceptive signals are another source of information about eye position. Poletti and colleagues (Poletti, Burr, & Rucci, 2013) demonstrated that during multiple saccades occurring in succession, errors in localization do not simply add up based on the expected noise of each efference copy signal. Instead, the localization errors they observed indicated that proprioceptive information might also be used and is integrated to code target positions with

18

529 respect to eye position. Such a proprioceptive signal, should also simply encode gaze position,

530 irrespective of the oculomotor response.

531 **The use of efferent information for oculomotor control and perception.** A highly debated

532 topic in neuroscience research involves the possible distinction between visual systems used

533 for perception and action control (see Rosetti et al. 2017; Goodale & Milner, 1992; 2018; Franz

534 et al, 2000). So far, we have discussed perception around eye movements, but given the early

535 interactions between saccadic and pursuit eye movements, it seems that efferent information

536 about upcoming eye movements is also involved in oculomotor control. It is therefore

537 reasonable to ask whether efferent information regarding eye movements is also shared between

538 oculomotor control and perception (Gegenfurtner, 2016; Spering & Montagnini, 2011).

539 There seem to be clear links between oculomotor behavior and perception. For example,

540 tracking a moving target with the eyes increases the accuracy with which one can predict the

541 motion direction (Spering, Schütz, Braun, & Gegenfurtner, 2011) and eye movements can be

542 used to encode the dynamics of decision processes (Fooken & Spering, 2019). The results of

543 Goettker et al. (2018) demonstrated that how we move our eyes (either with pure pursuit, or

544 with additional corrective saccades) influences how we perceive speed (see Figure 5) and also

545 how we intercept moving targets (Goettker et al., 2019). Saccadic adaptation also influences

546 perceptual localization of stimuli in the adapted space (Zimmermann & Lappe, 2016),

547 suggesting a tight coupling between oculomotor control and perception.

548 However, there are also studies that show distinct differences in these processes. Lisi and

549 Cavanagh (2015) showed that viewing a double-drift stimulus (a stimulus which contains

550 motion within a moving window) produces large shifts in perceived target locations, while

551 saccades land close to the veridical position of the stimulus. Similarly, when tracking a moving

552 target with pursuit eye movements, small perturbations in target velocity are not always

553 perceivable, although pursuit velocity is adjusted accordingly (Tavassoli & Ringach, 2010).

554 Across multiple trials, perception and oculomotor behavior also show different behavior.

555 Seeing a fast target movement increases anticipatory eye velocities in the next trial, while the

556 perceived speed of the next trial is judged to be slower (Maus, Potapchuk, Watamaniuk, &

557 Heinen, 2015). A similar pattern was observed in responses to the direction of a moving target

558 (Wu, Rothwell, Spering, & Montagnini, 2020).

559 These observations demonstrate that oculomotor control and perception are, to a large degree,

560 based on shared sensory and efferent signals, but there are cases where this information is used

561 differently: For example, context motion is subtracted from target motion for perception, but

562 the two signals are averaged for pursuit control (Spering & Gegenfurtner, 2007). Incoming

563 sensory information must be continuously translated into an adequate oculomotor response,

564 whereas the incoming information can be integrated for perceptual judgements (Goettker et al.,

565 2019). In the extreme case with multiple moving targets, the oculomotor system can only

566 produce one direct output, for example the vector average for pursuit, while we can readily

567 perceive several movements individually (see Spering & Montagnini, 2011).

568 **Allocation of attention for saccadic and pursuit eye movements.** It has been suggested that

569 attention plays a key role for remapping behavior across eye movements (Cavanagh et al., 2010;

570 Rolfs & Szinte, 2016). Attention and eye movements have been studied together for a long time

571 and there is ample evidence that they are tightly linked (Kowler et al., 1995; Hoffman &

572 Subramaniam, 1995; Deubel & Schneider, 1996; Shepherd, Findlay, & Hockey, 1986).

573 Attention shifts to targeted locations before saccadic eye movements (Rolfs, Jonikaitis, Deubel,

574 & Cavanagh, 2011). Interestingly, during pursuit attention is also located slightly ahead of the

575 eye (van Donkelaar & Drew, 2002; Khan et al., 2010; Chen, Valsecchi, & Gegenfurtner, 2017).

576 An attentional window slightly ahead of ongoing pursuit response could be equivalent to

577 presaccadic attention shifts to targeted locations. In both cases, this would amount to shifts in

578 attention to eye positions sometime in the future. These similar or potentially even shared

579 attentional mechanisms for saccadic and pursuit eye movements could be used for remapping

580 and compensation mechanisms. Therefore, studying the role of attention during combined

581 saccadic and pursuit eye movements might provide interesting insights.

582 **Biological markers for neurophysiological impairments.** One promising and exciting area

583 of research is the use of eye movement metrics as biomarkers for different psychiatric

584 (Diefendorf & Dodge, 1908; see for recent reviews Smyrnis, Amado, Krebs, & Sweeney, 2019;

585 Thakkar, Diwadkar, & Rolfs, 2017) or neurological impairments (see Leigh & Zee, 2015; Müri,

586 Cazzoli, & Nyffeler, 2019). In this approach, the quantification of simple eye movement

587 characteristics combined with the knowledge about the neurophysiological basis of the

588 oculomotor system allow the localization of impairments in the brain (see Müri et al., 2019).

589 However, not only changes in oculomotor behavior, but also the use of efferent information can

590 be directly linked to impairments. A prominent example is the impairment of efferent

591 information in schizophrenic patients, which becomes particularly visible during pursuit

592 (Holzman et al., 1977; Sereno & Holzman, 1995; Lindner, Thier, Kircher, Haarmeier, & Leube,

593 2005; Spering, Dias, Sanchez, Schütz, & Javitt, 2013). Experiments performed on patients with

594 impaired efference copy mechanisms demonstrated systematic errors in both oculomotor tasks

595 such as the double step saccade task or during predictive pursuit, as well as in perceptual tasks,

596 such as during trans-saccadic localization or motion discrimination during pursuit (see Thakkar
597 et al., 2017 for a recent overview). This suggests that in these cases, efferent mechanisms
598 involving saccadic and pursuit eye movements can be impaired. However, all of these tasks
599 were measured in separate experiments with different groups of observers. Systematic
600 investigations of potentially different impairments depending on a given task might be
601 interesting. Comparison of results from tasks related to position (e.g., saccade double-step) or
602 velocity information (motion discrimination during pursuit) could provide interesting insights
603 into the relevant processing steps or brain circuits involved with these responses.

604 5. Future directions

605 **A more integrative view of the oculomotor system.** Mirroring the trend of using more realistic
606 and natural stimuli (Goettker, Agtzidis, Braun, Dorr, & Gegenfurtner, 2020; Hayhoe, 2017;
607 Land & Hayhoe, 2001), we propose to study more naturalistic eye movement behavior. For
608 dynamic scenes, this behavior will always include a combination of saccadic and pursuit eye
609 movements. In such cases, it is possible to benefit from the immense knowledge about the two
610 classes of eye movements already gathered, and use naturalistic settings to investigate how
611 these movements work together in more detail. Instead of analyzing each type of eye movement
612 separately, or interpolating saccades when analyzing pursuit, the focus should move towards
613 the joint contributions of saccadic and pursuit eye movements and their interactions.

614 **Extend framework to other eye movements/actions.** Our review focused on saccadic and
615 pursuit eye movements and how these interact in oculomotor control and the reconstruction of
616 perception. We presented evidence that both eye movements seem to be based on shared
617 estimates of relative position and velocity errors, and could be coordinated by those signals.
618 This raises the question whether other eye movements are controlled by similar mechanism, or
619 even by the same signals. Fixational eye movements show a very similar mixture of fast discrete
620 and slow continuous movements. Microsaccades serve to reposition the gaze to preferred
621 positions within the foveola (e.g., Ko et al., 2010). The slow drift between microsaccades is
622 affected by stimulus properties such as spatial frequencies (Malevich, Bounocore, & Hafed,
623 2020). These drifting eye movements during fixation have recently been called 'micro-pursuit',
624 because they also respond to stimulus motion (Parisot et al., 2021). The combination of
625 continuous micro-pursuit and microsaccades seems to resembles a scaled-down version of the
626 interaction of saccadic and pursuit eye movements and could be controlled within a similar
627 framework. The combination of drift and small saccadic eye movements seems to be optimized

to enhance visual acuity (Intoy & Rucci 2020; Rucci et al. 2007; Rucci et al., 2018; Zhang et al. 2020).

Another type of movement that shows similarities to the proposed saccade and pursuit control model are interceptive reaching movements. Interception endpoints can be predicted by a combination of position and velocity errors (Brenner & Smeets, 2011, 2017; de La Malla, Smeets, & Brenner, 2018), with independent contributions of position and velocity-related information (Smeets & Brenner, 1995). Changes in perceived velocities produced by how we move our eyes does indeed transfer to errors in interception behavior (Goettker, Brenner et al., 2019). The continuous control of arm movements, which allows for the online control of reaches (Gaveau et al., 2014; Prablanc, Desmurget, & Gréa, 2003), could also provide a useful model for eye movements . For example, the optimal control frame work (Scott, 2012) has been related to the sophisticated mechanisms of online control, and could be adapted to oculomotor behavior as well (Crevecoeur & Kording, 2017; John et al., 2021).

Integration of top-down factors. The main focus of this review was how oculomotor behavior is driven by sensory signals. However, it is known that eye movement behavior is not only based on incoming sensory information, but also depends on cognitive processing (see Figure 6). One factor that can influence target selection and response vigor to the same sensory signal is the associated reward (e.g., Choi et al., 2014; see Shadmehr et al., 2019; Wolf & Lappe, 2021). Along similar lines, different tasks can lead to drastically different fixation patterns (Yarbus, 1967). The particular task can also lead to differences in the use of incoming information or changes to the decision thresholds for triggering a saccade (Hoppe & Rothkopf, 2016; Goettker et al., 2019b). In addition, anticipatory eye movements are based on the prediction of future events (see Kowler et al., 2019) or future relevance (Diaz et al., 2013; Sullivan et al. 2021). How these top-down factors are integrated and interact with the incoming sensory information will be critical to understand naturalistic eye movement behavior.

6. "Two outcomes of a single sensorimotor system"

The overall goal of this review was to gain new insights into the oculomotor system by proposing a change in perspective. We specifically considered interactions and shared information between saccadic and pursuit eye movements, which is in contrast to the still prevailing view to treat them in isolation. The results we presented demonstrate synergies and shared information at multiple levels, from oculomotor control to perception around both eye movements, reinforcing the conclusion Orban de Xivry & Lefèvre (2007) had arrived at: Saccades and pursuit seem to be "two outputs of a single sensorimotor process" (see Figure 6).

There are multiple interactions between saccadic and pursuit eye movements, and they seem to be driven by shared position- and velocity-related information. Shared information seems to be the rule and not the exception, suggesting that the distinction classically made between saccadic and pursuit eye movements should rather be made based on the available sensory information (position versus velocity). We go one step further and propose that efferent information used for accurate perception during the time of eye movements is organized in a similar manner. The proposed system can be summarized as follows:

Saccadic and pursuit eye movements are part of a single sensorimotor system, which is based on separate, continuous streams of position and velocity-related information. Within this framework, compensation for eye movements is also based on efferent information about upcoming eye positions and eye velocities, allowing to discount for retinal effects of any combination of saccadic and pursuit eye movements. Based on this proposed model of shared representation of eye position and velocity, dynamic interactions and synergies between the two movements allow for optimal tracking performance, while at the same time maintaining perceptual stability.
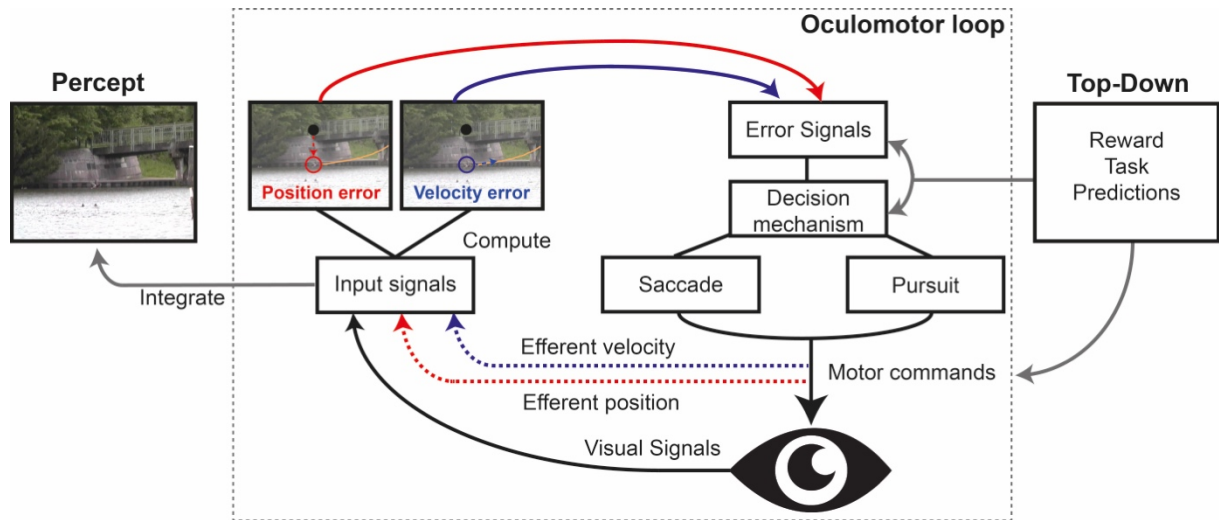

Figure 6. Interactive framework. In the oculomotor loop, position and velocity-related errors are computed given the visual input and efferent signals. Both error signals are used to decide whether the following movement should be a saccadic or pursuit eye movement. Depending on the combination of error signals, either saccadic or pursuit eye movements are executed. The motor commands are used for efferent information about changes in eye position and velocity. The oculomotor loop can is visually driven and can be affected by top-down signals (see Future Directions). The efferent signals are also used to compensate for the influence of eye movements on the retinal input and create a valid percept by integrating this information over time.

References

Abeles, D., Amit, R., Tal-Perry, N., Carrasco, M., & Yuval-Greenberg, S. (2020). Oculomotor inhibition precedes temporally expected auditory targets. Nature Communications, 11(1), 3524.

Andersen, R. A., Essick, G. K., & Siegel, R. M. (1985). Encoding of spatial location by posterior parietal neurons. Science, 230(4724), 456-458.

Bahill, A. T., Clark, M. R., & Stark, L. (1975). The main sequence, a tool for studying human eye movements. Mathematical biosciences, 24(3-4), 191–204.

Basso, M. A., Krauzlis, R. J., & Wurtz, R. H. (2000). Activation and Inactivation of Rostral Superior Colliculus Neurons During Smooth-Pursuit Eye Movements in Monkeys. Journal of Neurophysiology, 84(2), 892–908.

Behling, S., & Lisberger, S. G. (2020). Different mechanisms for modulation of the initiation and steady-state of smooth pursuit eye movements. Journal of Neurophysiology, 123(3), 1265–1276.

Berryhill, M. E., Chiu, T., & Hughes, H. C. (2006). Smooth pursuit of nonvisual motion. Journal of Neurophysiology, 96(1), 461–465.

Binda, P., & Morrone, M. C. (2018). Vision during saccadic eye movements. Annual review of vision science, 4, 193–213.

Blohm, G., Missal, M., & Lefèvre, P. (2005). Direct evidence for a position input to the smooth pursuit system. Journal of Neurophysiology, 94(1), 712–721.

Bogadhi, A. R., Montagnini, A., & Masson, G. S. (2013). Dynamic interaction between retinal and extraretinal signals in motion integration for smooth pursuit. Journal of Vision, 13(13), 5.

Bourrelly, C., Quinet, J., & Goffart, L. (2018a). Pursuit disorder and saccade dysmetria after caudal fastigial inactivation in the monkey. Journal of Neurophysiology, 120(4), 1640–1654.

Bourrelly, C., Quinet, J., & Goffart, L. (2018b). The caudal fastigial nucleus and the steering of saccades toward a moving visual target. Journal of Neurophysiology, 120(2), 421–438.

Braddik, O. (1974). A short-range process in apparent motion. Vision Research, 14(7), 519–527.

Braun, D. I., Mennie, N., Rasche, C., Schütz, A. C., Hawken, M. J., & Gegenfurtner, K. R. (2008). Smooth pursuit eye movements to isoluminant targets. Journal of Neurophysiology, 100(3), 1287–1300.

Braun, D.I., Pracejus, L. & Gegenfurtner, K.R. (2006) Motion aftereffect elicits smooth pursuit eye movements. *Journal of Vision*, 6, 671-684.

Brenner, E., & Smeets, J. B. J. (2011). Continuous visual control of interception. Human Movement Science, 30(3), 475–494.

Brenner, E., & Smeets, J. B. J. (2017). Accumulating visual information for action. Progress in Brain Research, 236, 75–95.

Brenner, E., Smeets, J. B. J., & van den Berg, A. V. (2001). Smooth eye movements and spatial localisation. Vision Research, 41(17), 2253–2259.

Buonocore, A., Skinner, J., & Hafed, Z. M. (2019). Eye Position Error Influence over "Open-Loop" Smooth Pursuit Initiation. Journal of Neuroscience, 39(14), 2709–2721.

Castet, E., & Masson, G. S. (2000). Motion perception during saccadic eye movements. Nature neuroscience, 3(2), 177–183.

732   Cavanagh, P., Tyler, C. W., & Favreau, O. E. (1984). Perceived velocity of moving chromatic
733   gratings. JOSA A, 1(8), 893-899.
734   Cavanagh, P. (1992). Attention-based motion perception. Science, 257(5076), 1563–1565.
735   Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of
736   attention pointers. Trends in cognitive sciences, 14(4), 147-153.
737   Cavanaugh, J., Berman, R. A., Joiner, W. M., & Wurtz, R. H. (2016). Saccadic Corollary Discharge
738   Underlies Stable Visual Perception. The Journal of Neuroscience : the Official Journal of the
739   Society for Neuroscience, 36(1), 31–42.
740   Chen, J., Valsecchi, M., & Gegenfurtner, K. R. (2017). Attention is allocated closely ahead of the
741   target during smooth pursuit eye movements: Evidence from EEG frequency tagging.
742   Neuropsychologia, 102, 206–216.
743   Choi, J. E., Vaswani, P. A., & Shadmehr, R. (2014). Vigor of movements and the cost of time in
744   decision making. *Journal of neuroscience*, *34*(4), 1212-1223.
745   Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal
746   cortex by intended eye movements. Science, 255(5040), 90-92.
747   Coutinho, J. D., Lefèvre, P., & Blohm, G. (2021). Confidence in predicted position error explains
748   saccadic decisions during pursuit. Journal of Neurophysiology, 125(3), 748-767.
749   Crevecoeur, F., & Kording, K. P. (2017). Saccadic suppression as a perceptual consequence of
750   efficient sensorimotor estimation. Elife, 6, e25073.
751   Cropper, S. J., & Wuerger, S. M. (2005). The perception of motion in chromatic stimuli. Behavioral and
752   Cognitive Neuroscience Reviews, 4(3), 192-217.
753   Darlington, T. R., Beck, J. M., & Lisberger, S. G. (2018). Neural implementation of Bayesian
754   inference in a sensorimotor behavior. Nature Neuroscience, 21(10), 1442–1451.
755   Darlington, T. R., Tokiyama, S., & Lisberger, S. G. (2017). Control of the strength of visual-motor
756   transmission as the mechanism of rapid adaptation of priors for Bayesian inference in smooth
757   pursuit eye movements. Journal of Neurophysiology, 118(2), 1173–1189.
758   Daye, P. M., Blohm, G., & Lefèvre, P. (2014). Catch-up saccades in head-unrestrained conditions
759   reveal that saccade amplitude is corrected using an internal model of target movement. Journal of
760   Vision, 14(1).
761   de Brouwer, S., Missal, M., Barnes, G., & Lefèvre, P. (2002). Quantitative analysis of catch-up
762   saccades during sustained pursuit. Journal of Neurophysiology, 87(4), 1772–1780.
763   de Brouwer, S., Yuksel, D., Blohm, G., Missal, M., & Lefèvre, P. (2002). What triggers catch-up
764   saccades during visual tracking? Journal of Neurophysiology, 87(3), 1646–1650.
765   de Haas, B., Iakovidis, A. L., Schwarzkopf, D. S., & Gegenfurtner, K. R. (2019). Individual
766   differences in visual salience vary along semantic dimensions. Proceedings of the National
767   Academy of Sciences, 116(24), 11687–11692.
768   Deravet, N., Blohm, G., Xivry, J.-J. O. de, & Lefèvre, P. (2018). Weighted integration of short-term
769   memory and sensory signals in the oculomotor system. Journal of Vision, 18(5), 16.
770   Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for
771   a common attentional mechanism. Vision Research, 36(12), 1827–1838.
772   de La Malla, C. , Smeets, J. B. J., & Brenner, E. (2018). Errors in interception can be predicted from
773   errors in perception. Cortex, 98, 49–59.
774   Diaz, G., Cooper, J., Rothkopf, C., & Hayhoe, M. (2013). Saccades to future ball location reveal
775   memory-based prediction in a virtual-reality interception task. *Journal of vision*, *13*(1), 20-20.
776   Diefendorf, A. R., & Dodge, R. (1908). An experimental study of the ocular reactions of the insane
777   from photographic records. Brain, 31(3), 451-489.
778   Dodge, R. (1900). Visual perception during eye movement. Psychological Review, 7(5), 454.
779   Dowiasch, S., Blohm, G., & Bremmer, F. (2016). Neural correlate of spatial (mis-) localization during
780   smooth eye movements. European Journal of Neuroscience, 44(2), 1846–1855.
781   Dubner, R., & Zeki, S. M. (1971). Response properties and receptive fields of cells in an anatomically
782   defined region of the superior temporal sulcus in the monkey. Brain research, 35(2), 528–532.
783   Engbert, R., Nuthmann, A., Richter, E. M., & Kliegl, R. (2005). SWIFT: A dynamical model of
784   saccade generation during reading. Psychological Review, 112(4), 777.
785   Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically
786   optimal fashion. Nature, 415(6870), 429-433.

787 Fleuriet, J., Hugues, S., Perrinet, L., & Goffart, L. (2011). Saccadic foveation of a moving visual target
788   in the rhesus monkey. Journal of Neurophysiology, 105(2), 883–895.
789 Fooken, J., & Spering, M. (2019). Decoding go/no-go decisions from eye movements. Journal of
790   vision, 19(2), 5.
791 Fooken, J., & Spering, M. (2020). Eye movements as a readout of sensorimotor decision processes.
792   Journal of Neurophysiology, 123(4), 1439–1447.
793 Franz, V. H., Gegenfurtner, K. R., Buelthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No
794   evidence for a dissociation between perception and action. Psychological Science, 11(1), 20-25.
795 Gandhi, N. J., & Katnani, H. A. (2011). Motor functions of the superior colliculus. Annual Review of
796   Neuroscience, 34, 205–231.
797 Gaveau, V., Martin, O., Prablanc, C., Pélisson, D., Urquizar, C., & Desmurget, M. (2003). On-line
798   modification of saccadic eye movements by retinal signals. Neuroreport, 14(6), 875–878.
799 Gaveau, V., Pisella, L., Priot, A.-E., Fukui, T., Rossetti, Y., Pélisson, D., & Prablanc, C. (2014).
800   Automatic online control of motor adjustments in reaching and grasping. Neuropsychologia, 55,
801   25–40.
802 Gegenfurtner, K. R. (2016). The interaction between vision and eye movements. Perception, 45(12),
803   1333–1357.
804 Gegenfurtner, K. R., & Hawken, M. J. (1996). Perceived velocity of luminance, chromatic and non-
805   Fourier stimuli: Influence of contrast and temporal frequency. Vision Research, 36(9), 1281–1290.
806 Gegenfurtner, K. R., Xing, D., Scott, B. H., & Hawken, M. J. (2003). A comparison of pursuit eye
807   movement and perceptual performance in speed discrimination. Journal of Vision, 3(11), 19-19.
808 Gellman, R. S., & Carl, JR (1991). Motion processing for saccadic eye movements in humans.
809   Experimental Brain Research, 84(3), 660–667.
810 Goettker, A. (2021). Retinal error signals and fluctuations in eye velocity influence oculomotor
811   behavior in subsequent trials. *Journal of Vision*, *21*(5), 28-28.
812 Goettker, A., Agtzidis, I., Braun, D. I., Dorr, M., & Gegenfurtner, K. R. (2020). From Gaussian blobs
813   to naturalistic videos: Comparison of oculomotor behavior across different stimulus complexities.
814   Journal of vision, 20(8), 26.
815 Goettker, A., Braun, D. I., & Gegenfurtner, K. R. (2019). Dynamic combination of position and
816   motion information when tracking moving targets. Journal of vision, 19(7), 2.
817 Goettker, A., Braun, D. I., Schütz, A. C., & Gegenfurtner, K. R. (2018). Execution of saccadic eye
818   movements affects speed perception. Proceedings of the National Academy of Sciences, 115(9),
819   2240–2245.
820 Goettker, A., Brenner, E., Gegenfurtner, K. R., & La Malla, C. de (2019). Corrective saccades
821   influence velocity judgments and interception. Scientific reports, 9(1), 5395.
822 Goffart, L., Bourrelly, C., & Quinet, J. (2017). Synchronizing the tracking eye movements with the
823   motion of a visual target: Basic neural processes. In Progress in brain research (pp. 243–268).
824   Elsevier.
825 Goffart, L., Bourrelly, C., & Quinton, J.-C. (2018). Neurophysiology of visually guided eye
826   movements: Critical review and alternative viewpoint. Journal of Neurophysiology, 120(6), 3234–
827   3245.
828 Gold, J. I., & Shadlen, M. N. (2007). The neural basis of decision making. Annual review of
829   neuroscience, 30.
830 Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. Trends in
831   neurosciences, 15(1), 20-25.
832 Goodale, M. A., & Milner, A. D. (2018). Two visual pathways—Where have they taken us and where
833   will they lead in future?. Cortex: A Journal Devoted to the Study of the Nervous System and
834   Behavior.
835 Grünert, U., & Martin, P. R. (2020). Cell types and cell circuits in human and non-human primate
836   retina. Progress in retinal and eye research, 100844.
837 Hafed, Z. M., & Goffart, L. (2020). Gaze direction as equilibrium: More evidence from spatial and
838   temporal aspects of small-saccade triggering in the rhesus macaque monkey. Journal of
839   Neurophysiology, 123(1), 308–322.
840 Hafed, Z. M., Goffart, L., & Krauzlis, R. J. (2008). Superior colliculus inactivation causes stable
841   offsets in eye position during tracking. Journal of Neuroscience, 28(32), 8124–8137.

Hansen, R. M. (1979). Spatial localization during pursuit eye movements. Vision Research 19(11), 1213–1221

Hainque, E., Apartis, E., & Daye, P. M. (2016). Switching between two targets with non-constant velocity profiles reveals shared internal model of target motion. European Journal of Neuroscience, 44(8), 2622–2634.

Hayhoe, M. M. (2017). Vision and action. Annual review of vision science, 3, 389–413.

Hering, E. (1879). Über Muskelgeräusche des Auges. Sitzungsber. d. der Wiener Akad. der Wiss. Mathem.-naturw. Klasse., 79, 137.

Hoffmann, K.-P., Bremmer, F., Thiele, A., & Distler, C. (2002). Directional asymmetry of neurons in cortical areas MT and MST projecting to the NOT-DTN in macaques. Journal of Neurophysiology, 87(4), 2113–2123.

Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. Perception & psychophysics, 57(6), 787-795.

Holst, E. von, & Mittelstaedt, H. (1950). Das reafferenzprinzip. Naturwissenschaften, 37(20), 464–476.

Holzman, P. S., Kringlen, E., Levy, D. L., Proctor, L. R., Haberman, S. J., & Yasillo, N. J. (1977). Abnormal-pursuit eye movements in schizophrenia: Evidence for a genetic indicator. Archives of General Psychiatry, 34(7), 802-805.

Hoppe, D., & Rothkopf, C. A. (2016). Learning rational temporal eye movement strategies. *Proceedings of the National Academy of Sciences*, *113*(29), 8332-8337.

Ibbotson, M. R., & Cloherty, S. L. (2009). Visual perception: Saccadic omission--suppression or temporal masking? Current Biology : CB, 19(12), R493-6.

Inoue, Y., Takemura, A., Kawano, K., & Mustari, M. J. (2000). Role of the pretectal nucleus of the optic tract in short-latency ocular following responses in monkeys. Experimental Brain Research, 131(3), 269–281.

Intoy, J., & Rucci, M. (2020). Finely tuned eye movements enhance visual acuity. Nature communications, 11(1), 1–11.

Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. IEEE Transactions on pattern analysis and machine intelligence, 20(11), 1254–1259.

Iwamoto, Y., & Kaku, Y. (2010). Saccade adaptation as a model of learning in voluntary movements. Experimental Brain Research, 204(2), 145–162.

John, A., Aleluia, C., Van Opstal, A. J., & Bernardino, A. (2021). Modelling 3D saccade generation by feedforward optimal control. *PLOS Computational Biology*, *17*(5), e1008975.

Keller, E., & Johnsen, S. S. (1990). Velocity prediction in corrective saccades during smooth-pursuit eye movements in monkey. Experimental Brain Research, 80(3), 525–531.

Kerzel, D., Aivar, M. P., Ziegler, N. E., & Brenner, E. (2006). Mislocalization of flashes during smooth pursuit hardly depends on the lighting conditions. Vision Research, 46(6-7), 1145-1154.

Khan, A. Z., Lefèvre, P., Heinen, S. J., & Blohm, G. (2010). The default allocation of attention is broadly ahead of smooth pursuit. Journal of Vision, 10(13), 7-7.

Kiernan, D., Manson, G., Heath, M., Tremblay, L., & Welsh, T. N. (2016). Corrections in saccade endpoints scale to the amplitude of target displacements in a double-step paradigm. Neuroscience letters, 611, 46–50.

Klein, C., & Ettinger, U. (2019). Eye Movement Research: An Introduction to Its Scientific Foundations and Applications: Springer Nature.

Ko, H. K., Poletti, M., & Rucci, M. (2010). Microsaccades precisely relocate gaze in a high visual acuity task. Nature neuroscience, 13(12), 1549-1553.

Kowler, E. (2011). Eye movements: The past 25 years. Vision Research, 51(13), 1457–1483.

Kowler, E., Rubinstein, J. F., Santos, E. M., & Wang, J. (2019). Predictive smooth pursuit eye movements. *Annual review of vision science*, *5*, 223-246.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. Vision research, 35(13), 1897-1916.

Krauzlis, R. J. (2004). Recasting the smooth pursuit eye movement system. Journal of Neurophysiology, 91(2), 591–603.

Krauzlis, R. J. (2005). The control of voluntary eye movements: New perspectives. The Neuroscientist, 11(2), 124–137.

Krauzlis, R. J., Basso, M. A., & Wurtz, R. H. (2000). Discharge properties of neurons in the rostral superior colliculus of the monkey during smooth-pursuit eye movements. Journal of Neurophysiology, 84(2), 876–891.

Kümmerer, M., Wallis, T. S. A., & Bethge, M. (2016). DeepGaze II: Reading fixations from deep features trained on object recognition. arXiv preprint arXiv:1610.01563.

Kwon, O.-S., Tadin, D., & Knill, D. C. (2015). Unifying account of visual motion and position perception. Proceedings of the National Academy of Sciences, 112(26), 8142–8147.

Kwon, S., Rolfs, M., & Mitchell, J. F. (2019). Presaccadic motion integration drives a predictive postsaccadic following response. Journal of vision, 19(11), 12.

Land, M. F., & Hayhoe, M. (2001). In what ways do eye movements contribute to everyday activities? Vision Research, 41(25-26), 3559–3565.

Leigh, R. J., & Zee, D. S. (2015). The neurology of eye movements: OUP USA.

Lindner, A., Thier, P., Kircher, T. T. J., Haarmeier, T., & Leube, D. T. (2005). Disorders of agency in schizophrenia correlate with an inability to compensate for the sensory consequences of actions. Current Biology, 15(12), 1119–1124.

Lisberger, S. G. (2015). Visual guidance of smooth pursuit eye movements. Annual review of vision science, 1, 447–468.

Lisi, M., & Cavanagh, P. (2015). Dissociation between the perceptual and saccadic localization of moving objects. Current Biology, 25(19), 2535–2540.

Lisi, M., & Cavanagh, P. (2017). Cooperative interactions between saccadic and pursuit planning when targeting a moving object. Journal of vision, 17(10), 1278.

Lisi, M., Solomon, J. A., & Morgan, M. J. (2019). Gain control of saccadic eye movements is probabilistic. Proceedings of the National Academy of Sciences of the United States of America, 116(32), 16137–16142.

Liston, D., & Krauzlis, R. J. (2003). Shared response preparation for pursuit and saccadic eye movements. Journal of Neuroscience, 23(36), 11305–11314.

Liston, D., & Krauzlis, R. J. (2005). Shared decision signal explains performance and timing of pursuit and saccadic eye movements. Journal of vision, 5(9), 3.

Liston, D. B., & Stone, L. S. (2014). Oculometric assessment of dynamic visual processing. Journal of vision, 14(14), 12.

Lorenceau, J., & Cavanagh, P. (2020). Jumpy and Jerky: When Peripheral Vision Faces Reverse-Phi. i-Perception, 11(5), 2041669520939107.

Lu, Z. L., & Sperling, G. (1995). Attention-generated apparent motion. *Nature*, *377*(6546), 237-239.

Lu, Z.-L., Lesmes, L. A., & Sperling, G. (1999). Perceptual motion standstill in rapidly moving chromatic displays. Proceedings of the National Academy of Sciences, 96(26), 15374–15379.

Malevich, T., Bouonocore, A., & Hafed, Z. M. (2020). Rapid stimulus-driven modulation of slow ocular position drifts. Elife, 9.

Matin, L., & Pearce, D. G. (1965). Visual perception of direction for stimuli flashed during voluntary saccadic eye movements. Science, 148(3676), 1485–1488.

Maus, G. W., Potapchuk, E., Watamaniuk, S. N. J., & Heinen, S. J. (2015). Different time scales of motion integration for anticipatory smooth pursuit and perceptual adaptation. Journal of vision, 15(2), 16.

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. Perception & Psychophysics, 2(8), 359–362.

Meyer, C. H., Lasker, A. G., & Robinson, D. A. (1985). The upper limit of human smooth pursuit velocity. Vision Research, 25(4), 561–563.

Morris, A. P., Bremmer, F., & Krekelberg, B. (2016). The dorsal visual system predicts future and remembers past eye position. Frontiers in systems neuroscience, 10, 9.

Morris, A. P., & Krekelberg, B. (2019). A stable visual world in primate primary visual cortex. Current Biology, 29(9), 1471-1480. e6.

Morris, A. P., Kubischik, M., Hoffmann, K.-P., Krekelberg, B., & Bremmer, F. (2012). Dynamics of eye-position signals in the dorsal visual system. Current Biology, 22(3), 173–179.

Morrone, M. C., Ross, J., & Burr, D. (2005). Saccadic eye movements cause compression of time as well as space. Nature neuroscience, 8(7), 950–954.

Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. Nature Reviews Neuroscience, 5(3), 218–228.

Müri, R., Cazzoli, D., & Nyffeler, T. (2019). Eye Movements in Neurology. In Eye Movement Research (pp. 749–774). Springer.

Nachmani, O., Coutinho, J., Khan, A. Z., Lefèvre, P., & Blohm, G. (2020). Predicted Position Error Triggers Catch-Up Saccades during Sustained Smooth Pursuit. ENeuro, 7(1).

Newsome, W. T., & Pare, E. B. (1988). A selective impairment of motion perception following lesions of the middle temporal visual area (MT). Journal of Neuroscience,, 8(6), 2201–2211.

Newsome, W. T., Wurtz, R. H., Dürsteler, M. R., & Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. Journal of Neuroscience, 5(3), 825–840.

Ono, S. (2015). The neuronal basis of on-line visual control in smooth pursuit eye movements. Vision Research, 110(Pt B), 257–264.

Orban de Xivry, J.-J., Bennett, S. J., Lefèvre, P., & Barnes, G. R. (2006). Evidence for synergy between saccades and smooth pursuit during transient target disappearance. Journal of Neurophysiology, 95(1), 418–427.

Orban de Xivry, J.-J., Coppe, S., Blohm, G., & Lefèvre, P. (2013). Kalman filtering naturally accounts for visually guided and predictive smooth pursuit dynamics. The Journal of Neuroscience : the Official Journal of the Society for Neuroscience, 33(44), 17301–17313.

Orban de Xivry, J.-J., & Lefèvre, P. (2007). Saccades and pursuit: Two outcomes of a single sensorimotor process. The Journal of Physiology, 584(Pt 1), 11–23.

Osborne, L. C., Lisberger, S. G., & Bialek, W. (2005). A sensory source for motor variation. Nature, 437(7057), 412-416.

Østerberg, S. (1935). Topography of the layer of rods and cones in the human retina. Acta opthal. suppi.,6,11-97.

Ouerfelli-Ethier, J., Elsaeid, B., Desgroseilliers, J., Munoz, D. P., Blohm, G., & Khan, A. Z. (2018). Anti-saccades predict cognitive functions in older adults and patients with Parkinson's disease. PloS one, 13(11).

Pack, C. C., & Born, R. T. (2001). Temporal dynamics of a neural solution to the aperture problem in visual area MT of macaque brain. Nature, 409(6823), 1040–1042.

Parisot, K., Zozor, S., Guérin-Dugué, A., Phlypo, R., & Chauvin, A. (2021). Micro-pursuit: A class of fixational eye movements correlating with smooth, predictable, small-scale target trajectories. Journal of Vision, 21(1), 9-9.

Petit, L., Clark, V. P., Ingeholm, J., & Haxby, J. V. (1997). Dissociation of saccade-related and pursuit-related activation in human frontal eye fields as revealed by fMRI. Journal of Neurophysiology, 77(6), 3386–3390.

Pola, J., & Wyatt, H. J. (1980). Target position and velocity: The stimuli for smooth pursuit eye movements. Vision Research, 20(6), 523–534.

Poletti, M., Burr, D. C., & Rucci, M. (2013). Optimal multimodal integration in spatial localization. Journal of Neuroscience, 33(35), 14259–14268.

Prablanc, C., Desmurget, M., & Gréa, H. (2003). Neural control of on-line guidance of hand reaching movements. Progress in brain research, 142, 155–170.

Rashbass, C. (1961). The relationship between saccadic and smooth tracking eye movements. The Journal of Physiology, 159, 326–338.

Ron, S., Vieville, T., & Droulez, J. (1989). Target velocity based prediction in saccadic vector programming. Vision Research, 29(9), 1103–1114.

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. Nature Neuroscience, 14(2), 252–256.

Rolfs, M., & Szinte, M. (2016). Remapping attention pointers: Linking physiology and behavior. Trends in cognitive sciences, 20(6), 399–401.

Rosano, C., Krisky, C. M., Welling, J. S., Eddy, W. F., Luna, B., Thulborn, K. R., & Sweeney, J. A. (2002). Pursuit and saccadic eye movement subregions in human frontal eye field: A high-resolution fMRI investigation. Cerebral Cortex, 12(2), 107–115.

Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. Nature, 386(6625), 598–601.

Ross, J., Morrone, M. C., Goldberg, M. E., & Burr, D. C. (2001). Changes in visual perception at the time of saccades. Trends in neurosciences, 24(2), 113–121.

1008 Rossetti, Y., Pisella, L., & McIntosh, R. D. (2017). Rise and fall of the two visual systems theory. Annals
1009   of physical and rehabilitation medicine, 60(3), 130-140.
1010 Rotman, G., Brenner, E., & Smeets, J. B. J. (2004). Quickly tapping targets that are flashed during
1011   smooth pursuit reveals perceptual mislocalisations. Experimental Brain Research, 156(4), 409–414.
1012 Rucci, M., Ahissar, E., & Burr, D. (2018). Temporal coding of visual space. Trends in cognitive
1013   sciences, 22(10), 883–895.
1014 Rucci, M., Iovin, R., Poletti, M., & Santini, F. (2007). Miniature eye movements enhance fine spatial
1015   detail. Nature, 447(7146), 852–855.
1016 Schlag, J., & Schlag-Rey, M. (2002). Through the eye, slowly: Delays and localization errors in the
1017   visual system. Nature Reviews Neuroscience, 3(3), 191.
1018 Schreiber, C., Missal, M., & Lefèvre, P. (2006). Asynchrony between position and motion signals in
1019   the saccadic system. Journal of Neurophysiology, 95(2), 960–969.
1020 Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2009a). Improved visual sensitivity during smooth
1021   pursuit eye movements: Temporal and spatial characteristics. Visual neuroscience, 26(3), 329.
1022 Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2009b). Object recognition during foveating eye
1023   movements. Vision Research, 49(18), 2241–2253.
1024 Schütz, A. C., & Souto, D. (2011). Adaptation of catch-up saccades during the initiation of smooth
1025   pursuit eye movements. *Experimental brain research*, *209*(4), 537-549.
1026 Schütz, A. C., Braun, D. I., & Gegenfurtner, K. R. (2011). Eye movements and perception: A selective
1027   review. Journal of Vision, 11(5).
1028 Schütz, A. C., & Morrone, M. C. (2010). Compression of time during smooth pursuit eye movements.
1029   Vision Research, 50(24), 2702–2713.
1030 Schütz, A. C., Trommershäuser, J., & Gegenfurtner, K. R. (2012). Dynamic integration of information
1031   about salience and value for saccadic eye movements. Proceedings of the National Academy of
1032   Sciences, *109*(19), 7547-7552.
1033 Schweitzer, R., & Rolfs, M. (2020a). Intra-saccadic motion streaks as cues to linking object locations
1034   across saccades. Journal of vision, 20(4), 17.
1035 Schweitzer, R., & Rolfs, M. (2020b). Intra-saccadic motion streaks jump-start gaze correction.
1036   bioRxiv.
1037 Schweitzer, R., Watson, T., Watson, J., & Rolfs, M. (2019). The joy of retinal painting: A build-it-
1038   yourself device for intrasaccadic presentations. Perception, 48(10), 1020–1025.
1039 Sereno, A. B., & Holzman, P. S. (1995). Antisaccades and smooth pursuit eye movements in
1040   schizophrenia. Biological psychiatry, 37(6), 394-401.
1041 Scott, S. H. (2012). The computational and neural basis of voluntary motor control and planning.
1042   Trends in cognitive sciences, 16(11), 541–549.
1043 Segraves, M. A., & Goldberg, M. E. (1994). Effect of stimulus position and velocity upon the
1044   maintenance of smooth pursuit eye velocity. Vision Research, 34(18), 2477–2482.
1045 Shadmehr, R., Reppert, T. R., Summerside, E. M., Yoon, T., & Ahmed, A. A. (2019). Movement
1046   vigor as a reflection of subjective economic utility. Trends in neurosciences, 42(5), 323-336.
1047 Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye movements and
1048   spatial attention. The Quarterly Journal of Experimental Psychology, 38(3), 475–491.
1049 Smeets, J. B. J., & Brenner, E. (1995). Perception and action are based on the same visual information:
1050   Distinction between position and velocity. Journal of Experimental Psychology: Human Perception
1051   and Performance, 21(1), 19–31.
1052 Smyrnis, N., Amado, I., Krebs, M.-O., & Sweeney, J. A. (2019). Eye Movements in Psychiatry. In
1053   Eye Movement Research (pp. 703–748). Springer.
1054 Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits for the internal monitoring of movements.
1055   Annu. Rev. Neurosci., 31, 317–338.
1056 Sparks, D. L. (1986). Translation of sensory signals into commands for control of saccadic eye
1057   movements: Role of primate superior colliculus. Physiological reviews, 66(1), 118–171.
1058 Spering, M., & Gegenfurtner, K. R. (2007). Contrast and assimilation in motion perception and
1059   smooth pursuit eye movements. Journal of Neurophysiology, 98(3), 1355-1363.
1060 Spering, M., Dias, E. C., Sanchez, J. L., Schütz, A. C., & Javitt, D. C. (2013). Efference copy failure
1061   during smooth pursuit eye movements in schizophrenia. Journal of Neuroscience, 33(29), 11779–
1062   11787.

1063 Spering, M., & Montagnini, A. (2011). Do we track what we see? Common versus independent
1064   processing for motion perception and smooth pursuit eye movements: A review. Vision Research,
1065   51(8), 836–852.

1066 Spering, M., Montagnini, A., & Gegenfurtner, K. R. (2008). Competition between color and
1067   luminance for target selection in smooth pursuit and saccadic eye movements. Journal of Vision,
1068   8(15), 16-16.

1069 Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual
1070   inversion. Journal of comparative and physiological psychology, 43(6), 482.

1071 Steinbach, M. J. (1976). Pursuing the perceptual rather than the retinal stimulus. Vision Research,
1072   16(12), 1371–1376.

1073 Strasburger, H., Rentschler, I., & Jüttner, M. (2011). Peripheral vision and pattern recognition: A
1074   review. Journal of vision, 11(5), 13-13.

1075 Sullivan, B., Ludwig, C. J., Damen, D., Mayol-Cuevas, W., & Gilchrist, I. D. (2021). Look-ahead
1076   fixations during visuomotor behavior: Evidence from assembling a camping tent. Journal of
1077   vision, 21(3), 13-13.

1078 Sun, L. D., & Goldberg, M. E. (2016). Corollary discharge and oculomotor proprioception: Cortical
1079   mechanisms for spatially accurate vision. Annual review of vision science, 2, 61–84.

1080 Tavassoli, A., & Ringach, D. L. (2009). Dynamics of smooth pursuit maintenance. Journal of
1081   Neurophysiology, 102(1), 110–118.

1082 Tavassoli, A., & Ringach, D. L. (2010). When your eyes see more than you do. Current Biology,
1083   20(3), R93-R94.

1084 Tatler, B. W., Hayhoe, M. M., Land, M. F., & Ballard, D. H. (2011). Eye guidance in natural vision:
1085   Reinterpreting salience. Journal of vision, 11(5), 5-5.

1086 Thakkar, K. N., Diwadkar, V. A., & Rolfs, M. (2017). Oculomotor prediction: A window into the
1087   psychotic mind. Trends in cognitive sciences, 21(5), 344–356.

1088 Van Beers, R. J., Wolpert, D. M., & Haggard, P. (2001). Sensorimotor integration compensates for
1089   visual localization errors during smooth pursuit eye movements. Journal of Neurophysiology, 85(5),
1090   1914-1922.

1091 Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they
1092   tell us. Neuroscience & biobehavioral reviews, 30(5), 666-679.

1093 Van Donkelaar, P., & Drew, A. S. (2002). The allocation of attention during smooth pursuit eye
1094   movements. Progress in brain research, 140, 267-277.

1095 Watamaniuk, S., Badler, J. B., & Heinen, S. J. (2019). Saccade adaptation alters smooth pursuit
1096   velocity of small, but not large objects. Journal of vision, 19(10), 252b.

1097 Watson, T. L., & Krekelberg, B. (2009). The relationship between saccadic suppression and perceptual
1098   stability. Current Biology, 19(12), 1040–1043.

1099 Wilmer, J. B., & Nakayama, K. (2007). Two distinct visual motion mechanisms for smooth pursuit:
1100   Evidence from individual differences. Neuron, 54(6), 987–1000.

1101 Wolf, C., & Lappe, M. (2021). Vision as oculomotor reward: cognitive contributions to the dynamic
1102   control of saccadic eye movements. Cognitive Neurodynamics, 1-22.

1103 Wu, X., Rothwell, A. C., Spering, M., & Montagnini, A. (2020). Expectations about motion direction
1104   affect perception and anticipatory smooth pursuit differently. bioRxiv.

1105 Wurtz, R. H. (2018). Corollary Discharge Contributions to Perceptual Continuity Across Saccades.
1106   Annual review of vision science, 4(1), 215–237.

1107 Yan, Y.-J., Cui, D.-M., & Lynch, J. C. (2001). Overlap of saccadic and pursuit eye movement systems
1108   in the brain stem reticular formation. Journal of Neurophysiology, 86(6), 3056–3060.

1109 Yarbus, A. L. (1967). Eye movements during perception of complex objects. In *Eye movements and
1110   vision* (pp. 171-211). Springer, Boston, MA.

1111 Zhang, T., Tian, X., & Hafed, Z. (2020). Triggering microsaccades by foveal motor error is sufficient
1112   to modulate peripheral visual sensitivity: Neural and perceptual evidence. Journal of vision, 20(11),
1113   1246.

1114 Zimmermann, E., & Bremmer, F. (2016). Visual Neuroscience: The Puzzle of Perceptual Stability.
1115   Current Biology : CB, 26(5), R199-201.

1116 Zimmermann, E., & Lappe, M. (2016). Visual space constructed by saccade motor maps. Frontiers in
1117   human neuroscience, 10, 225.

1118