



Execution of saccadic eye movements affects speed perception

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Due to the foveal organization of our visual system we have to constantly move our eyes to gain precise information about our environment. Doing so massively alters the retinal input. This is problematic for the perception of moving objects, because physical motion and retinal motion become decoupled and the brain has to discount the eye movements to recover the speed of moving objects. Two different types of eye movements, pursuit and saccades, are combined for tracking. We investigated how the way we track moving targets can affect the perceived target speed. We found that the execution of corrective saccades during pursuit initiation modifies how fast the target is perceived compared with pure pursuit. When participants executed a forward (catch-up) saccade they perceived the target to be moving faster. When they executed a backward saccade they perceived the target to be moving more slowly. Variations in pursuit velocity without corrective saccades did not affect perceptual judgments. We present a model for these effects, assuming that the eye velocity signal for small corrective saccades gets integrated with the retinal velocity signal during pursuit. In our model, the execution of corrective saccades modulates the integration of these two signals by giving less weight to the retinal information around the time of corrective saccades.

visual perception | eye movements | smooth pursuit | saccades | motion perception

The analysis of visual motion plays an important role in successful interactions with our environment. It has multiple functions related to perception and action, such as planning and monitoring goal-directed movements or the analysis of self-motion for stabilizing posture and gait (1–3). Most importantly, it is used to determine the velocity of moving objects of interest, so that they can be tracked with our gaze to keep them in foveal view (4–7). To achieve efficient tracking of such targets the oculomotor system needs to minimize velocity and position errors that are inflicted by noise and internal processing delays (8, 9). Animals with foveated eyes use two different types of eye movements to keep their gaze close to a moving target: high-speed, discrete saccades and low-speed, continuous smooth pursuit. For a long time the saccadic and pursuit eye movement system have been thought to be completely independent, but recently interactions and overlap have been found at the anatomical and functional level (10, 11). The saccadic system mainly corrects for position errors, the distance between the eye axis and the location of static or expected target locations. However, for moving targets the motion of the target also influences saccade planning (12–15). The pursuit system mainly responds to retinal target motion, but it can also be affected by position information (16–18). Because of inherent visual processing delays as well as a limited eye velocity and acceleration range the pursuit system depends on the corrections by the saccadic system to prevent large position errors when targets begin to move or change their trajectories. Thus, to effectively track a target the oculomotor system uses a mixture of tightly interacting saccadic and pursuit eye movements.

Tracking eye movements vastly improve the visual perception of a moving target by keeping its image more or less stationary in the fovea and thus reducing blur (e.g., ref. 19). They also increase the accuracy of predictions about the future path of

motion in collision and interception tasks (20, 21). They do come at the cost of dramatically changing the retinal input, though. Each time we move our eyes to track a target, retinal image motion and physical motion become decoupled. While the projection of the moving target is held nearly stationary on or close to the fovea during pursuit, the image of any static background is moved across the retina in the opposite direction. Thus, for the percept of a stable world and for valid velocity estimates of moving objects the visual system has to account for retinal motion induced by eye movements (22). Access to information about upcoming eye movements, the corollary discharge (efference copy), allows the visual system to distinguish between motion of objects in the world and motion caused by eye movements and to actively compensate for the latter (23–26).

To reconstruct the velocity of a moving target during pursuit and to account for the variability in eye velocity our visual system seems to use a combination of the extraretinal eye velocity signal and the sensed retinal motion signals (22). Nevertheless, there are some well-known illusions that demonstrate that this compensation is not perfect. In the Filehne illusion, briefly flashed stationary objects appear to move in the direction opposite to pursuit (27). In the Aubert-Fleischl phenomenon pursued targets appear to be moving more slowly than during fixation (28). The execution of saccades also comes at a cost. Around the time of saccadic eye movements visual sensitivity is greatly reduced (29, 30), spatial positions are perceptually shifted toward the saccade target (31),

Significance

Intensive research has focused on the question of how the visual system distinguishes between and accounts for retinal motion caused by eye movements or by physical object movements to maintain a stable world. So far, interactions between saccades and smooth pursuit movements during tracking responses and their specific effects on visual perception were mainly studied in isolation. We investigated the effect of corrective saccades on speed perception during pursuit initiation and found that the direction of corrective saccades influenced whether the observer perceived the tracked moving targets to be moving faster or more slowly than in pure pursuit trials. This small loss in perceptual accuracy is probably outweighed by the improvement in tracking through the rapid reduction in both position and velocity errors.

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and empty visual space is compressed (32). Thus, object tracking with a combination of smooth pursuit and saccadic eye movements presents a challenging task for our visual system.

Using a speed discrimination task we tested whether differences in tracking responses to targets moving at the same physical speed affect the perception of target speed. We show that the execution of corrective saccades during the initiation of smooth pursuit affects the perceived speed of moving targets in a specific way: Compared with pure pursuit responses tracked targets appear to be moving faster after forward saccades, while targets appear to be moving more slowly after backward saccades. We propose a model where small corrective saccades, typically around 1° in size, are integrated into the extraretinal eye velocity signals that are used for the perceptual speed estimates and for the control of the future eye velocity. This confusion between saccades and pursuit leads to a perceptual illusion that washes out over time, but also to an immediate adjustment of the pursuit velocity that helps to achieve better postsaccadic tracking.

Results

Our observers had to discriminate the speed of horizontally moving targets they pursued. Stimuli were devised so that targets moving at the same physical speed could lead to different oculomotor responses: pure smooth pursuit or pursuit combined with a forward or a backward saccade. We used a modified version of the Rashbass paradigm (33). Rashbass demonstrated that for a step-ramp movement, where the initial displacement (step) was in the opposite direction of the continuing linear target movement (ramp), certain combinations of step sizes and ramp speeds elicited pure pursuit responses without any initial saccades. More recently it was shown that the eye crossing time (EX), the time the target needs to cross its former position before the step, is the determining factor for the occurrence of a corrective saccade (34, 35). As shown in Fig. 1, medium EXs of around 200 ms most likely lead to a pure pursuit response. Shorter durations have a higher probability of eliciting a corrective saccade in the direction of the target movement (forward saccade), while longer ones frequently cause a corrective saccade in the opposite direction (backward saccade). We changed the size of the target step according to the upcoming ramp speeds (8.2, 9.6, 11, 12.4, or 13.8°/s) of the target to generate variations in the EX. This way, we could manipulate the specific oculomotor behavior during trials (i.e., pure pursuit or pursuit combined with forward or backward saccades to stimuli of the same physical speed). The speed discrimination task after each

pursued trial included a memorized standard stimulus with a standard speed of 11°/s, shown in the beginning and randomly before 10% of the trials. Participants were asked to follow the target as precisely as possible with their eyes and then to compare the speed in each trial to the memorized standard speed (see refs. 36 and 37 for a similar method). To ensure that we could elicit varying oculomotor responses for each participant we ran a pilot session with multiple EXs (Fig. S1). For each observer we determined six EXs scattered around the center of the saccade-free “smooth zone” (35) so that even the shortest and longest ones produced a mixture of pure pursuit responses and pursuit responses with corrective saccades. This way we could directly compare for each observer the perceived speed of targets moving with the same physical speed but being tracked with different oculomotor responses in the speed discrimination task (Fig. 1).

Saccades Affect Speed Perception. To investigate whether perceptual judgments are affected by different oculomotor responses we compared speed judgments for trials with pure pursuit to those containing a forward or a backward corrective saccade. We calculated separate psychometric functions for the three different oculomotor responses to quantify possible differences in perceived target speed (Fig. 2A). This allowed us to measure a possible perceptual bias as a shift of the point of subjective equality (PSE) of the psychometric functions and differences in the ability to discriminate different target speeds as the just-noticeable difference (JND). We found a saccade-specific speed bias: Targets were perceived as moving faster in trials containing forward (catch-up) saccades compared with trials containing backward saccades. Targets tracked with a pure pursuit response were perceived to move at a close-to-veridical intermediate speed (Fig. 2B). The statistical analysis revealed that the oculomotor behavior had a significant effect on the perceived target speed [$F(2,56) = 76.379$, $P < 0.001$]. When comparing individual PSEs with post hoc t tests we found significant differences between all three oculomotor behaviors (all P values < 0.001). There was no difference between the JNDs of the psychometric functions for the three different oculomotor responses [$F(2,56) = 0.322$, $P = 0.726$]. Average JNDs were 1.30°/s for pursuit with forward saccade trials, 1.36°/s for pure pursuit trials, and 1.30°/s for pursuit with backward saccade trials.

These results raise the question of whether the observed speed bias was influenced by the different oculomotor behaviors used for tracking or by the different EXs of the step-ramp stimuli. To answer this question we compared the perceived target speeds for

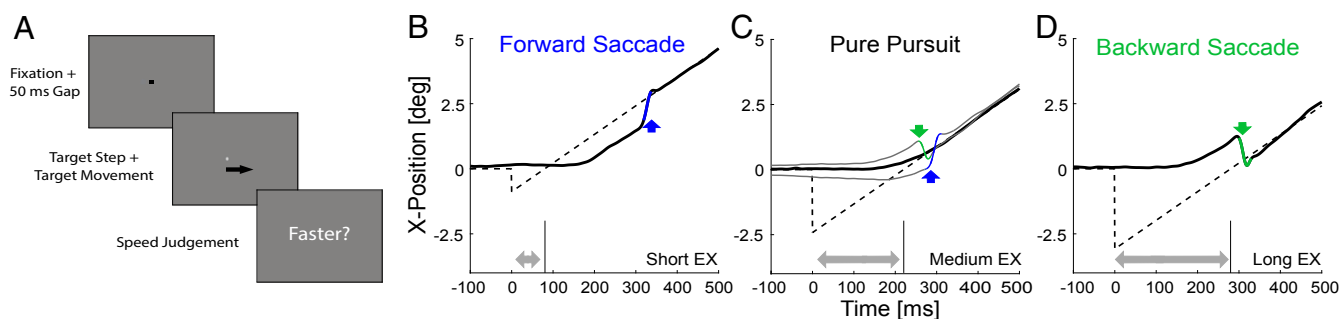


Fig. 1. Experimental paradigm and example trials for the different conditions. (A) Participants fixated on a small black square in the center of the screen. After a 50-ms gap, a white generalized Gaussian appeared at an eccentric location and immediately moved horizontally across the uniform gray screen at one of five different speeds (8.2, 9.6, 11, 12.4, and 13.8°/s) for a varying time (for further details see *Methods*). After each trial the target speed had to be compared with the memorized standard speed of 11°/s. (B) Stimulus (dashed line) and eye position (solid curve) as a function of time. Double arrows and vertical gray lines indicate the EX, the time the target needed after the step to cross the screen center. The blue part of the curve illustrates a forward saccade, as was often observed with short EXs. (C) Medium EXs around 200 ms produced mainly pure pursuit but could also elicit forward (blue) or backward (green) corrective saccades, indicated by the gray traces. (D) The green part of the curve illustrates a backward saccade, as was often observed with long EXs. Corrective saccades occurred under all three conditions, which allowed us to directly compare the effects of the oculomotor responses at the same EX.

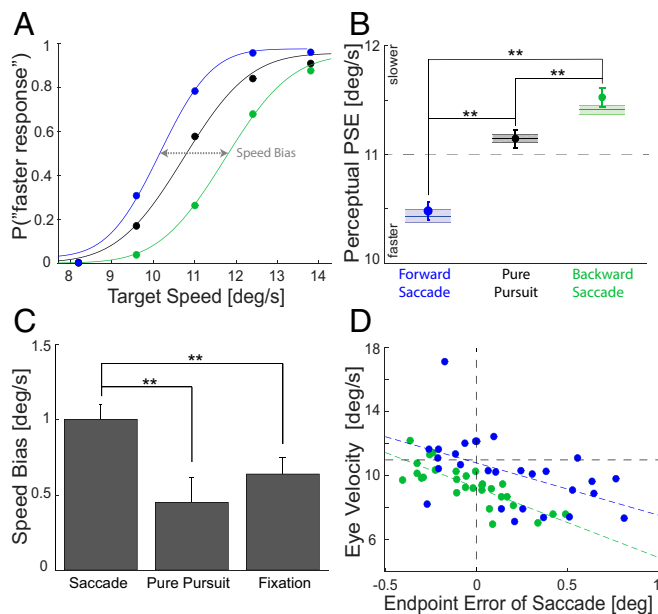


Fig. 2. Effects of different oculomotor responses on perceived speed and eye velocity. (A) Psychometric functions of a single representative observer. Colors indicate the three different oculomotor responses (blue, pursuit with a forward saccade; black, pure pursuit responses; and green, pursuit with a backward saccade). (B) Dots show the average PSE across participants. Error bars indicate the SEM, ** indicates significance at the 1% level. The horizontal lines show the prediction of the model presented below, the shaded area the SE of the model. The dashed horizontal line indicates the standard speed of 11°/s. (C) Average speed bias across participants based on different available extraretinal information. The speed bias is a measurement of the difference between the PSEs of trials with forward and backward saccades or physically comparable trials with pure pursuit responses or during fixation. (D) Relationship between position error and pursuit velocity after forward (blue) and backward (green) saccades. Each data point depicts the average across target speeds and across saccades with comparable latencies for one participant. Colored dashed lines indicate linear regressions fitted separately to the data of forward and backward saccades. Negative endpoint errors indicate saccadic endpoints behind the moving target. The dashed black lines indicate zero position error and the standard speed of 11°/s for comparison.

trials with short and long EXs for extraretinal signals specified by (i) pursuit with corrective saccades, (ii) pure pursuit, or (iii) during fixation at the center of the screen (Fig. 2C). We define the speed bias as the PSE difference between the short and the long EXs, calculated for all trials under the respective extraretinal conditions. A positive speed bias indicated that trials with short EXs were perceived faster. We found that the difference in perceived speed between trials with forward and backward saccades was larger than the difference between the speed judgments for the same physical conditions when observers responded with pure pursuit or when they fixated. Note, however, that there was a residual speed bias under these conditions. This was the case even in the gap condition, when the pursuit target was not initially presented at the screen center, to prevent a motion signal in the direction of the step. The residual effect might be driven by a response bias of our observers. Even though we randomized movement duration, targets starting further on one side (longer EX times) would on average move to less-eccentric final positions. An additional analysis (Fig. S2) showed that the effect of corrective saccades remained when the exact same types of trials were selected from the medium EXs and used to estimate perceived speed under the different oculomotor conditions. In principle, the observed changes of speed perception could also be caused by variations of an initial sensory estimate of motion, which could then lead to differences in oculomotor behavior. However, the

average eye velocity across participants during the open-loop phase of pursuit (0–100 ms after pursuit onset) was not different for the different oculomotor responses [$F(2,54) = 1.276$, $P = 0.288$; no main effect of oculomotor behavior in ANOVA with factors oculomotor behavior and target speed]. We are therefore confident that the speed bias is not linked to variations in initial sensory estimates but driven by the occurrence and direction of corrective saccades.

Interactions Between Pursuit and Corrective Saccades. Our results raise the question of whether the execution of corrective saccade not only affects perceived speed but also the postsaccadic pursuit velocity. We compared the pursuit velocity during a 60-ms time interval preceding the onset and following the offset of corrective saccades. For each participant we used trials with saccadic latencies between 250–300 ms only, so that the time between pursuit and saccade onset was fairly constant. In analogy to the perceptual results, we found a significant difference in pursuit velocity after corrective saccades, depending on their direction [$t(27) = 3.270$, $P = 0.003$; see Fig. 2D]: Pursuit was faster after forward saccades (10.2°/s) compared with pursuit after backward saccades (9.4°/s). In line with the results concerning the open-loop eye velocity reported above, we found no differences in pursuit velocity [$t(27) = 1.42$, $P = 0.168$] before the onset of forward saccades (pursuit velocity = 6.34°/s) or backward saccades (pursuit velocity = 6.02°/s). Position errors before both types of corrective saccades were also comparable in size, although their directions differed [−0.85° for forward saccades and 0.79° for backward saccades; $t(27) = 0.65$, $P = 0.524$]. Pursuit velocity was also correlated with the saccadic landing position [forward saccades: $r(28) = -0.51$, $P = 0.006$; backward saccades: $r(29) = -0.81$, $P < 0.001$]. If the saccade amplitude was too short and the saccade landed behind the moving target post-saccadic pursuit was faster; if the saccade landed in front of the moving target postsaccadic pursuit was slower (Fig. 2D). These results suggest that corrective saccade parameters were used to adjust the ongoing pursuit response and that both the saccade and pursuit system interact closely to improve tracking responses. The quick adaptation of pursuit velocity based on the direction of the corrective saccade resembles the effect observed above for the differences in perceived speed.

Integration of Corrective Saccades into the Eye Velocity Signal.

During ongoing pursuit the perceived speed of the target depends mainly on extraretinal information, the eye velocity signal, and the residual retinal velocity of the target image, the retinal slip. If the eye is perfectly following the target the retinal slip is zero. In general, the target speed is given by the sum of these two signals during pursuit. Corrective saccades seem to disturb this fine balance, because the measurement and processing of retinal information becomes distorted around the time of saccades (39). Also, the eye movement signals for saccades and pursuit might be controlled by at least partly different circuitry. The question therefore arises of how the extraretinal eye velocity signal and the retinal velocity signal are computed and processed during corrective saccades. The simplest answer would be that the eye velocity signal during the small corrective saccades is treated in the same manner as during pursuit movements. If this is the case, forward saccades should lead to larger eye velocity signals, because forward saccades move the eyes in the same direction as the ongoing pursuit. Analogously, backward saccades should lead to lower eye velocity signals, because they move the eyes in the direction opposite of pursuit.

To compute the correlation between the average eye velocity and psychophysical judgments of the target speed we aligned all trials so that a positive value indicates eye velocity in the direction of the target movement. This way, negative eye velocities during backward saccades lead to a lower average eye velocity. Then, we divided all trials across all observers into bins according to eye velocity and calculated the proportions of a “faster” response in

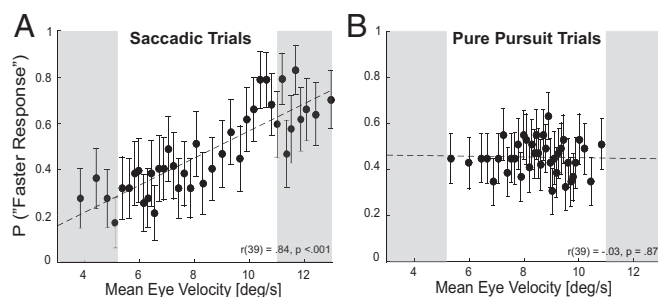


Fig. 3. Relationship between eye velocity and perceived target speed for saccadic and pursuit trials. (A) Average mean eye velocity of saccadic trials during the first 400 ms after pursuit onset versus the probability of a “faster” response at the standard target speed (11°/s). Data were collapsed across all observers and sorted based on the average eye velocity. The 1.25% fastest and slowest trials were excluded and all other trials were split into 39 bins each containing 2.5% of all trials. The eye velocity is substantially lower than the target speed, because it takes a while for the eye to accelerate. Error bars depict the SD estimated by bootstrapping random samples of the trials in each bin. (B) Average mean eye velocity in pure pursuit trials and the probability of “faster” responses. The shaded areas represent the limits of pursuit velocity found for pure pursuit trials.

each bin (Fig. 3). There was a significant relationship between average eye velocity and perceived speed of the target for trials with corrective saccades [$r(39) = 0.84, P < 0.001$]. This was not the case for pure pursuit trials [$r(39) = -0.03, P = 0.87$] or for the fixation condition [$r(39) = 0.14, P = 0.38$]. The correlation for the saccadic trials was significant at all target speeds. The correlation was driven by the saccadic epochs with high eye speeds: When we interpolated the eye velocity between the beginning and the end of each saccade to exclude the high-speed epochs the correlation between the average eye velocity and speed perception was absent for the same trials [$r(39) = -0.11, P = 0.49$]. Together, these results demonstrate that the perceived target speed scales with the average eye velocity for trials containing corrective saccades. The corrective saccades potentially contribute to the eye velocity estimate, but this does not suffice to explain our data. There needs to be an additional mechanism attenuating the contribution of the retinal slip signal, as otherwise the variations in eye velocity could again be compensated for.

Further experiments support the idea that corrective saccades get integrated into the extraretinal eye velocity signal for pursuit. The influence of corrective saccades on speed perception becomes smaller as trial duration increases (*SI Results* and Fig. S3), presumably because their relative contribution to the overall signal decreases with increasing trial length. We also found that observers were not aware of their small corrective saccades with peak velocities of around 60°/s, which can in principle still be covered by pursuit (*SI Results* and Fig. S4). When we presented targets with the same horizontal step-ramp movements but added a vertical offset of 8° to increase the size of the initial saccade these larger saccades had no effect on the speed perception. Presumably this was the case because their peak velocities were outside of the pursuit velocity range (*SI Results* and Fig. S5).

Perceived Speed During Pursuit-Saccade Interaction. We combined the three basic findings of our experimental work into a computational model designed to explain the changes of perceived target speed caused by corrective saccades during pursuit initiation. (i) The extraretinal eye velocity signal for pursuit includes motor commands for small corrective saccades. (ii) Corrective saccades affect the combination of extraretinal and retinal information. (iii) Larger saccades do not affect the extraretinal eye velocity signal (Fig. S5). A flowchart of our model is presented in Fig. 4 and a more detailed description is given in *Supporting Information*. In line with standard models of speed perception

during pursuit (22, 23), our model uses a combination of the extraretinal eye velocity signal and the retinal slip signal to produce an estimate of target motion. We extended this standard model with saccadic eye movements. We assume that during the execution of saccades the relative weight of the retinal slip signal becomes smaller. During pursuit, we set the weighting between retinal and extraretinal signals to 50:50. During saccades, it changes to $50 - \Delta_w : 50 + \Delta_w$ with a Gaussian time course from the start to the end of the saccade. In our model this higher weight for the extraretinal eye velocity signal leads to higher speed estimates for trials with forward saccades and slower estimates for trials with backward saccades. Since the effect of saccades on perceived speed was absent for large saccades (Fig. S5) we considered epochs with retinal speeds above 40°/s as irrelevant for the estimation of target speed. We initially estimated this upper limit as a parameter, but it turned out to be fairly constant across observers and close to the speed of 40°/s, above which the firing of neurons in the middle temporal area (MT) is massively attenuated (38). To approximate the variability of the psychophysical judgments we added noise to the model’s final speed estimates. The noise magnitude was directly estimated from the empirical psychometric functions. The input to the model is the eye velocity and the retinal slip over the course of each trial. Both values are weighted and combined, given that the retinal slip is below 40°/s, and that the model’s output speed is integrated over the whole trial for a perceptual speed estimate. A “faster” judgment is given by the model whenever the integrated eye velocity is larger than the standard speed value (*Modeling*).

Fig. 2B shows that the model reproduces the observed effect of corrective saccades on perceived target speed, the different PSE values, quite well for the whole group of observers. We only used one free parameter per observer, Δ_w , the magnitude of the weight change. This parameter can be interpreted as the strength of the attenuation of the retinal slip signal during saccades. Its average value is 0.23 ± 0.16 , indicating that the weight of the retinal slip is reduced to around 25% and thus biased the combined estimate toward the eye velocity signal. The model is also able to explain some individual differences between the participants (Fig. S6A), [$r(89) = 0.85, P < 0.001$]. Predicted and observed PSEs are correlated for forward saccades [$r(29) = 0.65, P < 0.001$], for pursuit [$r(30) = 0.76, P < 0.001$], and for backward saccades [$r(30) = 0.72, P < 0.001$]. The model can also reproduce the observed correlation of eye velocity and perceived target speed for the pursuit trials with corrective saccades, as well as the lack of such a correlation for the pure pursuit trials (Fig. S6 B and C).

Discussion

We found a close relationship between the occurrence and direction of corrective saccades during pursuit of moving targets and subsequent speed judgments. Target speed was overestimated in trials with forward saccades compared with trials with backward saccades, while pure pursuit led to intermediate perceived speeds. We also found a correlation between the average eye velocity during each trial and the perceptual judgment, but only for trials with corrective saccades. These results suggest that the eye velocity signal of corrective saccades is integrated into the speed estimate of the tracked target. Our modeling efforts suggest that around the time of corrective saccades the strength of the retinal motion signal is reduced relative to the extraretinal signal about eye motion. The effect of the corrective saccades on perceived target speed can tell us three important things about the combination of retinal and extraretinal signals to reconstruct target speed (Fig. 4).

First, the extraretinal signal about the upcoming eye velocity seems to include not only motor commands for pursuit but also at least those for small corrective saccades. When we interpolated the speed of the eye during the corrective saccade the relationship with the perceptual responses disappeared. It is

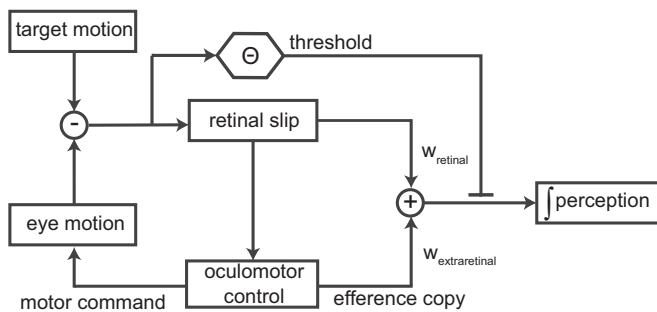


Fig. 4. Flowchart model for speed perception during pursuit-saccade interaction. Our model has two main signals, the retinal slip and the extraretinal eye velocity, which are combined and integrated for the perception of the target speed. The weights of both components are dynamically modulated around the time of corrective saccades, when the retinal slip signal gets unreliable and its weight is reduced. Additional factors important for oculomotor control like position errors, predictive signals, and gain control (see refs. 4 and 10) are not shown. The retinal slip and the efference copy (eye velocity signal) are used for target speed estimation. Their weighted sum is not used for perceptual judgments whenever the retinal speed exceeds a certain threshold Θ .

somewhat puzzling where this signal might arise in the nervous system, because current models have treated the efference copies for saccades and pursuit as completely separate processes. However, the anatomical and functional pathways for the control of pursuit and saccades are largely overlapping, and at some point the outputs of both signals need to be combined to drive the eye muscles. At this point we are not able to resolve this question with our current psychophysical data.

Second, the observed effects indicate that small corrective saccades attenuate the retinal motion signal. Otherwise this signal could again be used to compensate for the variability in the eye velocity caused by the saccade, and the perceived target speed would be unaffected. However, for the same average eye velocities as during pursuit eye movements (central areas in Fig. 3) there is a close correlation between eye velocity and the perceived target speed for the saccadic trials. Therefore, the compensation mechanism does not seem to function properly during saccades. This change in weighting could be caused by an increase in the noise of the retinal slip estimate, by a reduction of the strength of the signal through active saccadic suppression, or by a combination of both factors. Many studies have shown that active and passive processes attenuate visual sensitivity during saccadic eye movements (refs. 39 and 40, but see ref. 41), making the retinal motion signal less reliable. Therefore, the information about the eye velocity should gain more weight in the estimation process, at least in a Bayesian framework (e.g., ref. 22). Alternative mechanisms are possible, for example compressive nonlinearities of the retinal slip signal during saccades. We chose our current approach because dynamic weighting of eye velocity and retinal velocity has been used by others to model pursuit control (42, 43) and saccadic suppression (44). Furthermore, recent evidence was obtained that the activity of neurons in the smooth eye movement subregion of the frontal eye field (FEFsem) and the medial superior temporal area (MST) is modulated by different contributions of retinal and extraretinal information over the time course of pursuit (45). Our model shows that the differential weighting can also explain the observed perceptual effects for the different tracking responses. In the case of pursuit with a corrective saccade the weight of the retinal motion is reduced and because of the higher influence of the eye velocity signal the integrated perceptual estimate of target speed is larger for forward saccades and smaller for backward saccades compared with trials without saccades.

Third, the influence of saccades is limited to small corrective saccades during tracking responses. In the control experiment with an additional vertical offset (Fig. S5) we confirmed that larger initial saccades are not integrated into the target speed estimate. For the process of reconstructing the target speed based on the available signals this implies some kind of threshold mechanism which is able to distinguish larger from small corrective saccades and to prevent the integration of their eye velocity signals into the target speed estimate. As mentioned above one of the determining factors to distinguish between pursuit and saccades is the movement speed. The small corrective saccades in our experiment were still roughly in the speed range covered by pursuit movements. Recordings of neurons in area MT, which is a candidate for the neural substrate for the detection of retinal slip during pursuit (46), revealed that for retinal speeds above 40°/s the responses of MT neurons massively decreased (38). Mechanisms like this provide a potential neuronal basis for such a proposed threshold.

At first the influence of small corrective saccades on perceived speed appears to be a disadvantage, because it leads to inaccuracies in perception. However, the notable change in the internal speed estimate through this extra boost of the eye velocity signal might actually constitute an adaptive response during tracking, resulting in appropriate adjustments of pursuit velocity. We found that the pursuit velocity was increased or decreased dynamically based on the saccade direction (Fig. 2D). While large saccades are mainly made to reposition the eyes to a different part of the visual field, corrective saccades during pursuit may serve as a dynamic error signal: Forward saccades are needed when the pursuit velocity is too slow, and therefore it would be a useful strategy to increase the internal target speed estimate, while backward saccades are needed when the pursuit velocity is too high. This is exactly what we observed. In general, postsaccadic pursuit velocity seems to be finely tuned by the two kinds of corrective saccades, because they also take the position error after landing into account (47). For saccades landing behind the target pursuit velocity was higher than when the eyes were ahead of the target. Despite some transient perceptual inaccuracies the integration of the eye velocity of the corrective saccades might serve a functional role to improve tracking accuracy.

Conclusion

The effects of pursuit eye movements on motion perception are quite well studied (e.g., refs. 22 and 23), but the significant relationship between the occurrence and direction of corrective saccades during pursuit initiation and their effects on perceived speed comes as a surprise. Targets moving at the same physical target speed when tracked with a forward corrective saccade were more likely to be perceived as faster compared with targets tracked with a backward saccade. Since the effect scaled with the combined eye velocity of pursuit and corrective saccades, the most straightforward explanation of our results is that the eye velocity of corrective saccades is integrated into the signal used as the target speed estimate. Together with a different weighting of information about retinal motion during corrective saccades, this leads to an overall bias in the target speed estimate. While the bias introduced by corrective saccades is probably of little consequence for perception over longer time intervals, it has the functional benefit of a rapid adjustment of the pursuit velocity after corrective saccades, resulting in improved tracking performance. Overall, the sensorimotor system seems to be using a whole variety of dynamic adjustments within the sensorimotor loop to accurately keep track of moving targets (48–50).

Methods

General Paradigm. The observer started each trial by pressing the space bar (Fig. S1). We collected data for two different step-ramp versions. In the regular step-ramp experiment ($n = 13$ observers) the target initially appeared at the screen center and stepped to the left or right after a random fixation period (750–1,500 ms) before the ramp movement started. In the gap version ($n =$

17 observers), we first presented a central fixation target, a small black square, which disappeared 50 ms before the pursuit target appeared at an eccentric location. We used the gap paradigm to control for a possible influence of the apparent motion caused by the target step. In both cases the pursuit target appeared eccentrically and moved toward the center of the screen and onward for varying amounts of time. Because the results of both experiments were the same we combined the data. The target stimulus was a white generalized Gaussian distribution (*SI Methods*). In the fixation control the small black square stayed on till the end of the trial. The critical variable of our experiment was the EX, which was determined by the target speed and step size in each trial. This way we could induce different oculomotor behaviors to targets moving at the same ramp speed. We used six EXs individually determined for each participant based on a pilot session (Fig. S1).

Speed Discrimination Task. The memorized standard stimulus was presented five consecutive times at the beginning of each block so that the participants could memorize its speed. Throughout the experiment the standard stimulus was presented again randomly before 10% of the trials. The standard stimulus always moved with the speed of 11°/s and had an EX of 200 ms, a typical value used before (see, e.g., ref. 15). The standard stimulus kept moving across the screen until it reached an eccentricity of 15° and disappeared. To make sure that the end position of the stimulus could not serve as an indicator of the target speed we presented the stimuli for either 600 or 1,000 ms with an additional randomly assigned jitter of -50, 0, or 50 ms in the step paradigm or for a random interval sampled from a uniform random distribution between 600 and 1,000 ms in the gap paradigm. Five randomly interleaved target speeds were used (8.2, 9.6, 11, 12.4, and 13.8°/s). Motion was horizontal in

two directions, left or right. Overall participants took part in 720 trials for the speed discrimination task and 360 trials in the fixation control task. The pilot session took roughly 45 min, the speed discrimination task roughly 2 h, and the fixation condition 1 h. Participants usually came on four separate days and took part in the different experiments for 1 h with breaks in between. All participants gave informed consent before the experiment (Declaration of Helsinki) to take part in the experiment. All procedures were approved by the local ethics committee (Giessen University LEK 2013-0018). The data presented in this article are freely available at zenodo.org (doi: 10.5281/zenodo.1073168).

Setup and Visual Stimuli. Participants sat at a desk in an illuminated room facing a monitor (Display ++, LCD; Cambridge Research Systems Ltd), as illustrated in Fig. 1A. Their heads were stabilized on a chin and forehead rest to minimize head movements. The distance between eyes and screen was 90 cm and the eye positions corresponded approximately to the center of the screen. We recorded from the left eye of each subject with a desk-mounted eye tracker with a temporal frequency of 1,000 Hz (EyeLink 1,000 Plus; SR Research). Experiments were controlled by MATLAB, using the Psychtoolbox (51).

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