

Individual differences link sensory processing and motor control

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Abstract

Research on saccadic and pursuit eye movements already made great contributions to our understanding of sensory processing and human behavior. However, studies often have focused on average behavior of only one specific type of eye movement in a specific task. By leveraging individual differences of 50 observers across a unique combination of different tasks, we demonstrate that critical links and variations in the control of oculomotor behavior are missed by focusing on average behavior across participants of isolated eye movements. We observed that saccade and pursuit behavior across tasks are correlated, but only when tested with matched sensory information: accuracy of saccades to moving targets is correlated with pursuit gain, but not accuracy of saccades to stationary targets. Within the same task, the coordination of saccadic and pursuit eye movements is tailored to the strengths of the individual: observers with more accurate saccades to moving targets use them more frequently to catch-up with moving targets. Our findings demonstrate that individual variations in sensorimotor behavior are more than just measurement noise and questions previous results and interpretations based on the comparison of saccadic and pursuit eye movements with different sensory input.

Introduction

Due to the foveal-centric organization of our visual system, eye movements are an essential part of perception and are studied across a wide range of different research areas (for overviews, see ¹⁻⁵). Humans mainly use a combination of fast saccadic and slow pursuit eye movements to keep targets of interest within foveal vision. Because these two types of eye movements operate in distinct speed ranges, they have been considered as fully independent. This has also led to them being studied separately with paradigms that maximize the differences. Most lines of saccadic research are conducted with static visual input. For example, isolated saccades are studied when looking at simple stationary dots ⁶⁻⁸, during reading of static text (e.g. ^{9,10}) or gaze distributions are used to predict where observers fixate in static images (e.g. ¹¹⁻¹³). In contrast, pursuit eye movement research makes almost exclusive use of dynamic, moving stimuli. For example, pursuit is mostly studied with moving dots to understand how the brain transforms visual input into a continuous motor output ⁴ or to study the link between motion perception and pursuit behavior ¹⁴. Such pursuit studies often rely on a specific paradigm, the step-ramp paradigm ¹⁵, to reduce the need for the naturally occurring catch-up saccades. The focus on different paradigms also leads to different control signals: for static targets, the main signal driving the eye movement is position-related (the mismatch between eye and target position) and for dynamic targets, the main signal is velocity-related (the mismatch between eye and target velocities). While this previous work has provided important insights, it is neglecting two important issues.

First, during natural behavior saccadic and pursuit always occur together to allow for optimal tracking. Interactions and shared information between saccade and pursuit have been shown for complex natural movements in highly dynamic situations ¹⁶⁻¹⁸, but also with simpler paradigms under full experimental control ¹⁹⁻²³, for reviews see ^{24,25}). It has also been shown that the neurophysiological structures involved in the control of saccades and pursuit are not as independent as initially thought, but exhibit a large overlap ^{5,26}. In line with this overlap, converging evidence demonstrates that both saccades and pursuit are used and able to correct for both position- and velocity-related signals ²⁴: Saccades to moving targets successfully integrate velocity-information ^{23,27} and pursuit is affected by target position ²⁸⁻³¹. Due to this confound inherent in commonly used paradigms, it is impossible to dissociate whether differences in the control of saccadic and pursuit eye movements are based on the oculomotor response or whether they are based on differences in the related sensory signals. This is also relevant for comparing brain responses for saccades to static targets with pursuit to moving targets, which has been a common tool for mapping out oculomotor brain circuits ³²⁻³⁴.

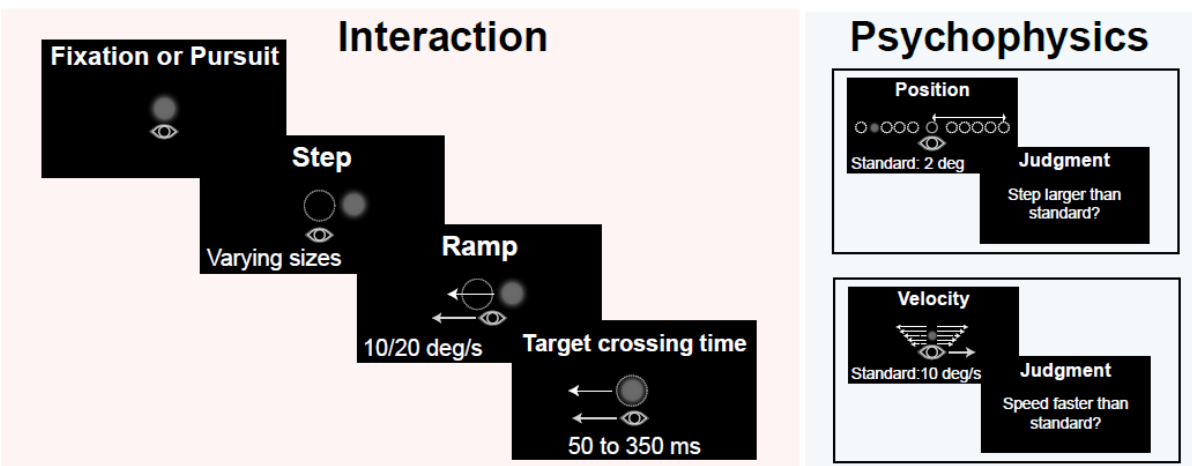
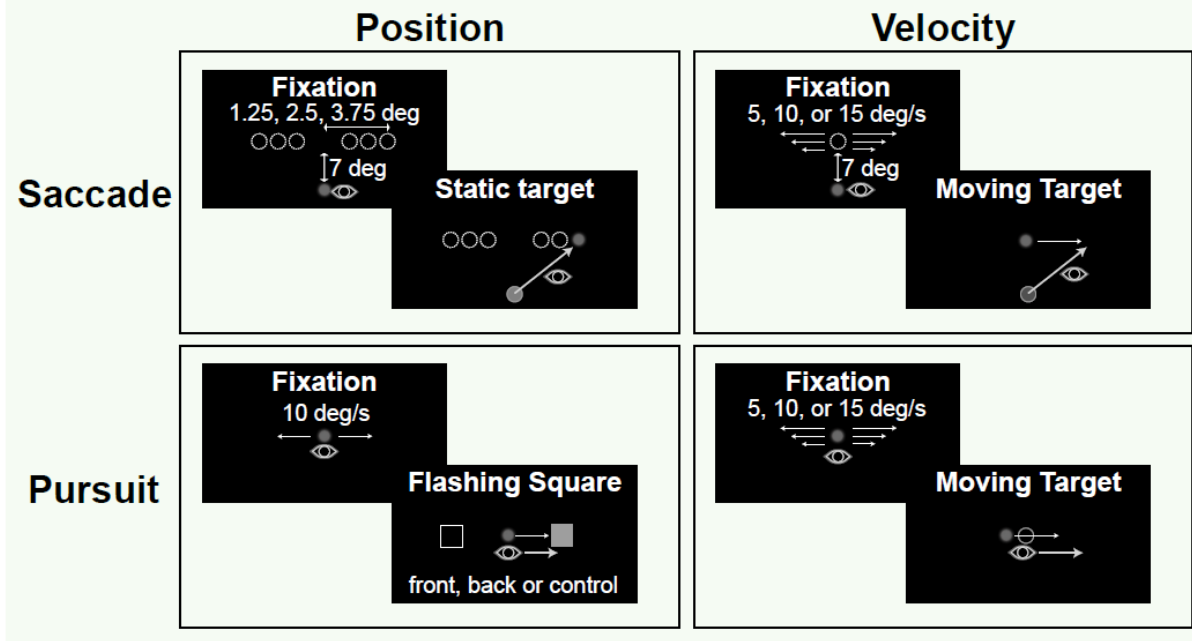
Second, the vast majority of eye movement studies focuses on the behavior of the average across many observers and variance between observers is often treated as noise. However,

massive Individual differences have been shown for the control of both saccadic^{35–39} and pursuit eye movements^{40–42}, and in how saccadic and pursuit eye movements are combined to track a moving target. The same stimulus that is tracked with smooth pursuit by one observer, is tracked by a combination of saccadic and pursuit eye movements by another observer^{43,44}. These interindividual differences in oculomotor behavior are strong and stable, so that even ideas of an ‘oculomotor signature’ or ‘oculomotor fingerprint’ have been proposed^{36,45–47}. The focus on average behavior might miss out on a substantial amount of interesting information.

We address both of these two issues by investigating individual differences in saccades, pursuit, and saccade-pursuit interactions together. However, we not only measure individual variability, but leverage the individual differences to gain insight into the structure of sensory processing and oculomotor control (⁴⁸, see for reviews of more examples in vision science^{49,50}). We compared oculomotor performance across observers at two levels: First, we resolved the confound of stationary and moving stimuli in eye movement research with a unique combination of tasks (see Figure 1), where, for the same observers, we carefully balance sensory information (position, velocity) and eye movement (saccade, pursuit). For example, we compared the accuracy of saccades to stationary targets with pursuit gain, and contrasted this to the correlation between the accuracy of saccades to moving targets and pursuit gain. Second, within the same task with matched sensory information, we studied how saccadic and pursuit eye movements are coordinated by different individuals with different abilities in performing isolated saccades and pursuit. For example, will an observer who is making accurate saccadic eye movements use them more frequently when tracking a moving target?

Our results show that behavior of observers for isolated saccadic and pursuit eye movements is correlated, but only across tasks where sensory information is matched (e.g., saccades and pursuit to moving targets). Thus, performance across tasks mainly seems to vary based on whether position or velocity information is relevant, and less so on whether a saccade or pursuit is executed. Within the same task, we observed that the coordination of saccadic and pursuit eye movements is tailored to the individual strengths of observers. Observers with more accurate pursuit eye movements rely more on pursuit to track a moving target, whereas observers with more accurate saccades to moving targets trigger saccades more frequently. We discuss how these results lead to a more integrative view of the oculomotor system and demonstrate the importance of considering individual differences in behavior. They are crucial for the re-interpretation of now classic results, comparing the control of saccadic eye movements and pursuit eye movements with either static or moving stimuli.

Isolated Movements



98

99 **Figure 1. Overview of experiments.** Please note that the dimensions, contrast of the stimuli, and the
 100 representation of the eye position (gray eye) were adjusted for illustrative purposes. Experiments were
 101 conducted with a low contrast Gaussian blob in front of a gray background and observers were
 102 supposed to look at the targets. Each observer completed all tasks. **Top.** Depiction of the additional
 103 experiments each observer performed. The experiments were separated based on the relevant sensory
 104 information (either position or velocity) and the type of task (saccade, pursuit). In short, observers
 105 needed to either make comparable saccades to static or moving targets, pursue a target where
 106 additional position cues were flashed or just pursue a moving target. **Bottom Left.** Paradigms for
 107 measuring saccade-pursuit interactions. Depending on the task, observers were fixating or already
 108 pursuing a moving target (in this case there was already an initial target step with a following movement,
 109 not illustrated here). In both paradigms, the critical timepoint was the target step with the following
 110 change in target velocity (either from 0 to 10 deg/s for fixation or from 10 to 20 deg/s for pursuit). By
 111 changing the target step, the time until the target crossed the position it had before the target step varied
 112 between 50 to 350 ms of target crossing time. **Bottom Right.** Psychophysical tasks for position- or
 113 velocity-related information. Observers needed to make perceptual judgements about the size of a target
 114 step or speed of a moving target and compare it to a memorized standard velocity.

115

116 **Results**

117 **Relevant sensory information links behavior across different tasks**

118 A large group of observers (N=50) completed a battery of four oculomotor tasks (see Figure 1,
119 top). To address the typical confound of saccadic eye movements being studied with static
120 stimuli and pursuit eye movements with moving stimuli, we balanced the relevant sensory
121 information (position- or velocity-related signals) across eye movements in our tasks (see
122 Methods for detailed description of the tasks). Saccades performance was measured to static
123 and moving targets. Participants initially fixated at the bottom of the screen and then a target
124 was shown on the vertical midline of the screen, which was either also horizontally displaced
125 and stationary or appeared in the center and then moved to the left or right with different
126 velocities. Pursuit responses were investigated to targets moving at different velocities, as well
127 as to positional cues flashed during tracking ²⁸. To estimate the position-related influence on
128 pursuit, participants were tracking a moving target and changes in eye velocity were observed
129 dependent on whether the positional cue was flashed either in front or behind the target
130 movement. Leveraging the individual differences in oculomotor behavior across the individual
131 tasks allows us then to assess the relevance of the performed oculomotor behavior (saccade
132 or pursuit) and the relevant sensory information (position- or velocity-related).

133 An illustration of the results of the individual tasks can be seen in Figure 2. The top row shows
134 the average saccade endpoints for each observer relative to the target position. Saccades to
135 static and moving targets were quite accurate, with average errors usually below 1 degree,
136 indicating a successful integration of position- and velocity-related information for saccadic eye
137 movements. Nevertheless, note that there is substantial variability in the average error across
138 observers (see Figure 2, top row). Since the initial vertical position step was identical for
139 saccades to stationary and moving targets (see Figure 1), we extracted the horizontal saccade
140 target error as a reflection of accuracy for saccades to stationary or moving targets. For the
141 pursuit-position task, we observed that the average eye velocity across observers depended
142 on the position of the cue. Pursuit was faster when the cue appeared ahead and slower when
143 it was behind the target, indicating that also the pursuit response is correcting for positional
144 errors. To estimate the positional influence on pursuit eye movements, we computed the
145 difference in eye velocity between the condition where the positional cue was in the front vs in
146 the back. For the pursuit-velocity task, observers had to track target movements with different
147 velocities - the average eye velocity in response to these target movements is shown in Figure
148 2. As a measurement for pursuit performance, we extracted average pursuit gain across the
149 different velocities (see Figure 2, bottom row).

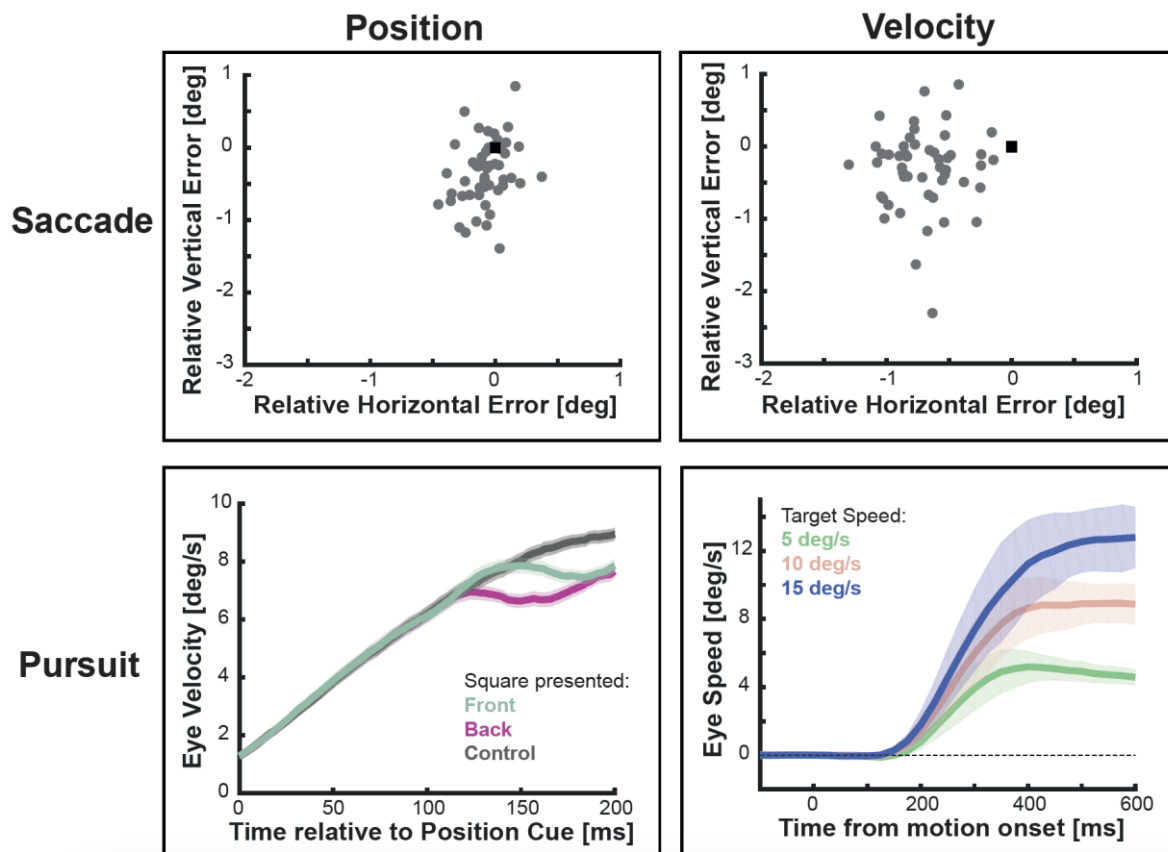


Figure 2. Overview over data from other experiments. Top row. Average relative saccade endpoint for each observer for stationary (left) and moving (right) targets. All endpoints are aligned, such that the target is at 0,0 (black square). Dots depict individual observers. **Bottom row.** On the left side, the average eye velocity across observers aligned to the time the additional position cue was presented. The green color represents the condition where the cue was presented in front, the pink color the condition where the cue was presented in the back. The gray condition shows the control condition where no cue was presented. On the right, the average eye velocity across observers is shown for different target velocities in the pursuit-velocity experiment. Eye velocity was aligned to motion onset. Shaded areas represent the standard error of the mean.

Based on the individual differences in eye movement behavior, we can now calculate the critical correlations (Figure 3). First, we looked at the relationship between the tasks typically used to study saccadic and pursuit eye movements: saccade accuracy to a static target and pursuit gain in response to moving targets. We observed no significant correlation between performance in the two tasks ($r(47) = -.09$, $p = .523$), which could point to the often assumed separate systems for saccadic and pursuit eye movements. However, due to our balanced combination of tasks, we can also look at the relationships between saccade and pursuit performance when the relevant sensory information is matched. There was a significant correlation between saccadic and pursuit behavior when comparing pursuit gain and saccade error to moving targets ($r(47) = -.38$, $p = .008$), as well as for the position influence on pursuit and saccade error to stationary targets ($r(48) = .29$, $p = .041$). This suggests that the absence of a correlation for the typically studied tasks is mostly related to the different sensory

information. The importance of controlling for sensory information is also supported by the correlation of the position influence during pursuit with saccade accuracy to static targets, while the correlation is absent when correlated with saccade accuracy to moving targets ($r(48) = .04$, $p = .804$).

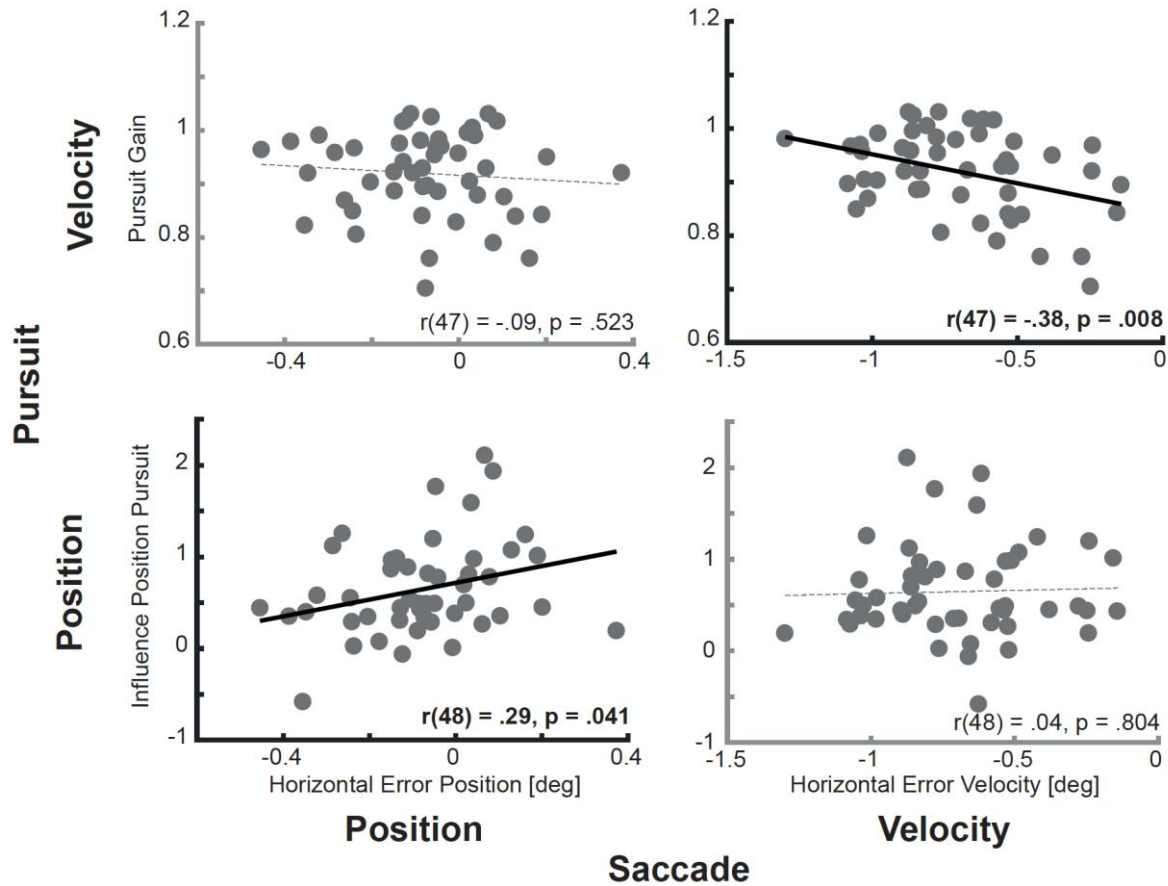


Figure 3. Link across eye movements. Four correlations are shown, grouped based on the respective oculomotor response (saccade vs pursuit) and relevant sensory information (position vs velocity). The metrics selected are pursuit gain in the pursuit velocity experiment, the difference in velocity when the positional cue was presented in front or back in the pursuit position experiment, the horizontal saccade error for targets moving horizontally, and the horizontal saccade error for static targets. Each point represents one observer, and significant correlations are indicated with a solid black regression line.

Together, these results show that assuming independent and separate systems while only comparing saccades to static targets with pursuit to moving targets is missing critical links in the control of saccadic and pursuit eye movements^{24,25}. For position information, a larger influence of position error on pursuit eye movements goes along with a smaller undershoot of saccadic eye movements to stationary targets. For velocity information, lower pursuit gain is related to more accurate saccades to moving targets. We will address this correlation in more detail below, when focusing on the coordination of saccadic and pursuit eye movements for the same task, as it seems counterintuitive at first sight: when there is shared relevant sensory

information, one might expect a positive link, e.g., higher pursuit gain and more accurate saccades to moving targets.

We can now use our large dataset to obtain an estimate of the relative contribution of the relevant sensory signal and motor response across tasks. In simple terms: Does saccade performance differ depending on the task or are there observers who are generally better in making saccades?

Contributions of sensory information and motor behavior across different tasks

To estimate the contributions of sensory information for variations in oculomotor behavior across tasks, we compared the correlations for the same motor responses (either saccade or pursuit) when related to the same sensory information and once across metrics when related to different sensory information (see Figure 4 and Methods for more details). If the executed oculomotor response is the relevant factor (e.g., someone is generally good at making saccades), we would not expect a large difference between the correlations. As a baseline, we observed highly significant correlations between the same oculomotor responses (see Figure 4 left) when the metric was related to the same sensory response (saccade: $r(48) = .85$, $p < .001$; pursuit: $r(47) = .54$, $p < .001$). This shows that individual differences in oculomotor behavior across tasks are highly reliable. For comparison, we correlated performance for the same oculomotor behavior, but with different relevant sensory information. In this case, the correlations were reduced by about half (saccade: $r(48) = .44$, $p = .001$; pursuit: $r(47) = .25$, $p = .080$). To estimate the contribution of the relevant sensory information for saccadic and pursuit eye movements across tasks, we computed the proportion of the explained variance when different sensory-information was used in comparison to the explained variance in the baseline with the same sensory information (see Figure 4 right). Sensory information explained roughly three quarters of the total explainable variance (Saccade: 73%, Pursuit: 78%), leaving one quarter of explainable variance for the oculomotor response.

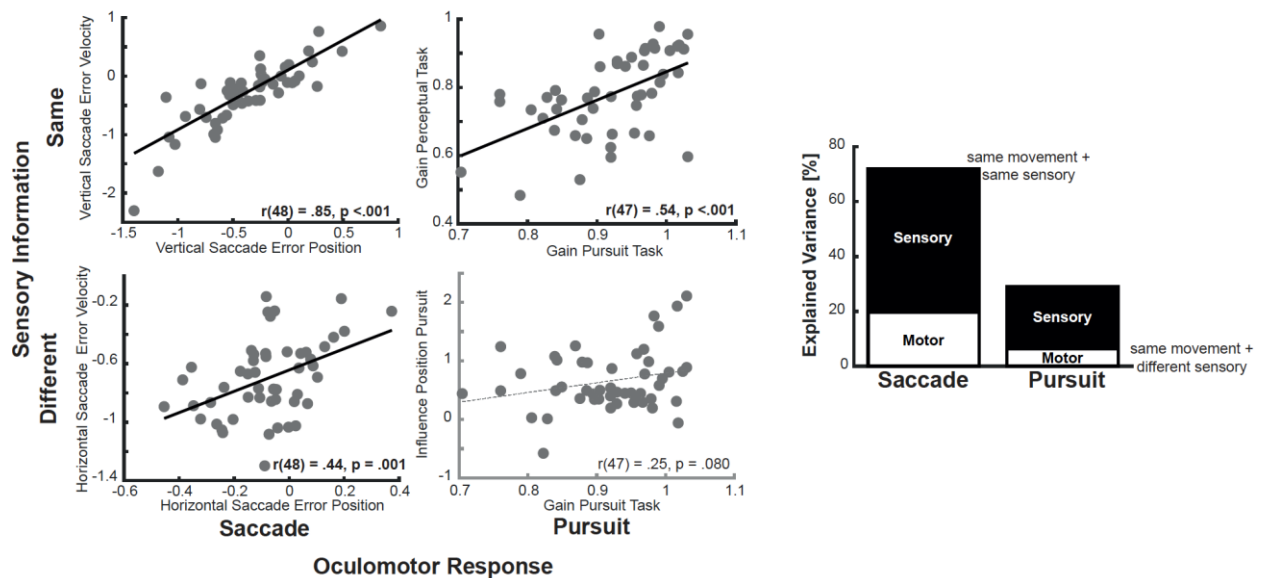


Figure 4. Sensory vs Motor variability. Left. Correlations for pursuit and saccadic eye movements when either the same or different sensory information was relevant. Metrics used are pursuit gain for the pursuit velocity and perception velocity task, the positional influence on pursuit, vertical saccade error for the stationary targets or horizontally moving targets and horizontal error to stationary and horizontally moving targets. Presentation of the data is similar to the top panel. Each point is one observer, with significant correlations indicated by a solid black regression line. Right. The sources of explained variance estimated by the different correlations. Height of the bar shows the explained variance by the same oculomotor response + same sensory information. The white part of the bar is the explained variance by the same oculomotor response, different sensory information correlations. Therefore, the difference should be a coarse estimate of the contribution of relevant sensory information.

We validated our assumption of the critical role of sensory information using a data-driven approach by performing a principal component analysis on the extracted metrics for the isolated eye movement measures (see Methods for more details). We observed that, across all 10 metrics extracted for the isolated eye movement tasks, four factors obtained an Eigenwert above 1 and could together explain 75% of the variance (see Table 1). If the control of saccades and pursuit was independent systems one could expect that the variables should be grouped by the executed eye movement. However, the first factor was related to eye movement performance for moving targets (pursuit gain, pursuit latency and horizontal saccade error to moving targets), combining saccadic and pursuit metrics for the same sensory information. This pattern repeated for the other factors: The second factor was specifically related to saccadic eye movements to stationary targets, whereas the third factor again represented a mixture of saccadic and pursuit metrics related to positional cues with the horizontal saccade error to a position target, the position influence on pursuit, as well as pursuit acceleration. The fourth factor was related to saccade latency.

Table 1. PCA results. Factor loadings for metrics extracted for the isolated eye movement experiments on the first four principal components. Shading reflects the strength of the evidence. Light Gray, weights above 0.2, darker gray dominant variables.

Metric	PC1	PC2	PC3	PC4
Pursuit Gain	-0.861	-0.035	0.191	-0.175
Pursuit Latency	0.797	-0.121	-0.062	-0.006
Saccade HorError Velocity Task	0.641	0.096	0.354	0.006
Saccade VerError Velocity Task	-0.035	0.952	0.041	0.022
Saccade VerError Position Task	-0.004	0.935	0.068	-0.181
Pursuit Position Influence	-0.275	0.007	0.786	0.208
Pursuit Acceleration	0.025	-0.037	0.785	-0.179
Saccade HorError Position Task	0.313	0.354	0.625	0.006
Sacc Latency Velocity Task	0.014	-0.152	0.006	0.894
Sacc Latency Position Task	0.117	0.010	-0.013	0.893
Eigenwert	2.320	2.085	1.675	1.401
Proportion var.	0.198	0.196	0.180	0.174
Cumulative	0.198	0.393	0.573	0.746

Together, these results converge on the fact that variations in oculomotor behavior across different tasks are mainly driven by the relevant sensory information. We did not observe evidence for the often-present assumption of separate systems for the control of saccadic and pursuit eye movements. Such a distinction would have shown in high correlations between tasks where the same eye movement was measured independent of the respective task. Instead, we observed that saccadic and pursuit behavior was correlated with matched sensory information and that the relevant sensory information modulated the strength of the relationship between different saccadic or pursuit measurements across tasks. This suggests that a high-level distinction across tasks should not be based on the executed eye movements, but should be based on the relevant sensory information.

Variability in the coordination of saccadic and pursuit eye movements

The variations in isolated saccadic and pursuit eye movements across tasks revealed the importance of the relevant sensory information. However, saccadic and pursuit eye movements often occur together in the same tasks. Therefore, we asked how saccadic and pursuit eye movements are coordinated when the same sensory information is relevant. For this, we studied the coordination of saccadic and pursuit eye movements when tracking moving targets (see Figure 1 Bottom Left).

We operationalized saccade-pursuit interactions as the combination of position and velocity errors that are related to triggering a corrective saccade during pursuit (see Figure 5A; ^{22,51}). The combination of both error signals can be summarized as the target crossing time (the time the target needs given its current position and velocity to cross the current eye position). Across different target crossing times, it is possible to fit a “smooth zone” for each observer (see Figure 5B; four observers were excluded from the analysis due to unreliable fits - see Methods for

details), which contains trials with a lower probability of corrective saccades⁴³. At the center
 of the smooth zone is the combination of position- and velocity-error that led to the minimum
 number of corrective saccades. The smooth zone was measured during fixation or out of
 steady-state pursuit, due to potentially faster pursuit dynamics and different relevant
 information while already pursuing a target^{48,52}. Similar to the investigation of isolated eye
 movements, we found substantial variability in the center of the smooth zone across observers
 (see Figure 5C). It ranged between target crossing times of 150 to 400 ms across observers.
 This means that the same combination of errors could be tracked exclusively with pursuit by
 some observers, while other observers would mainly exhibit corrective saccades.

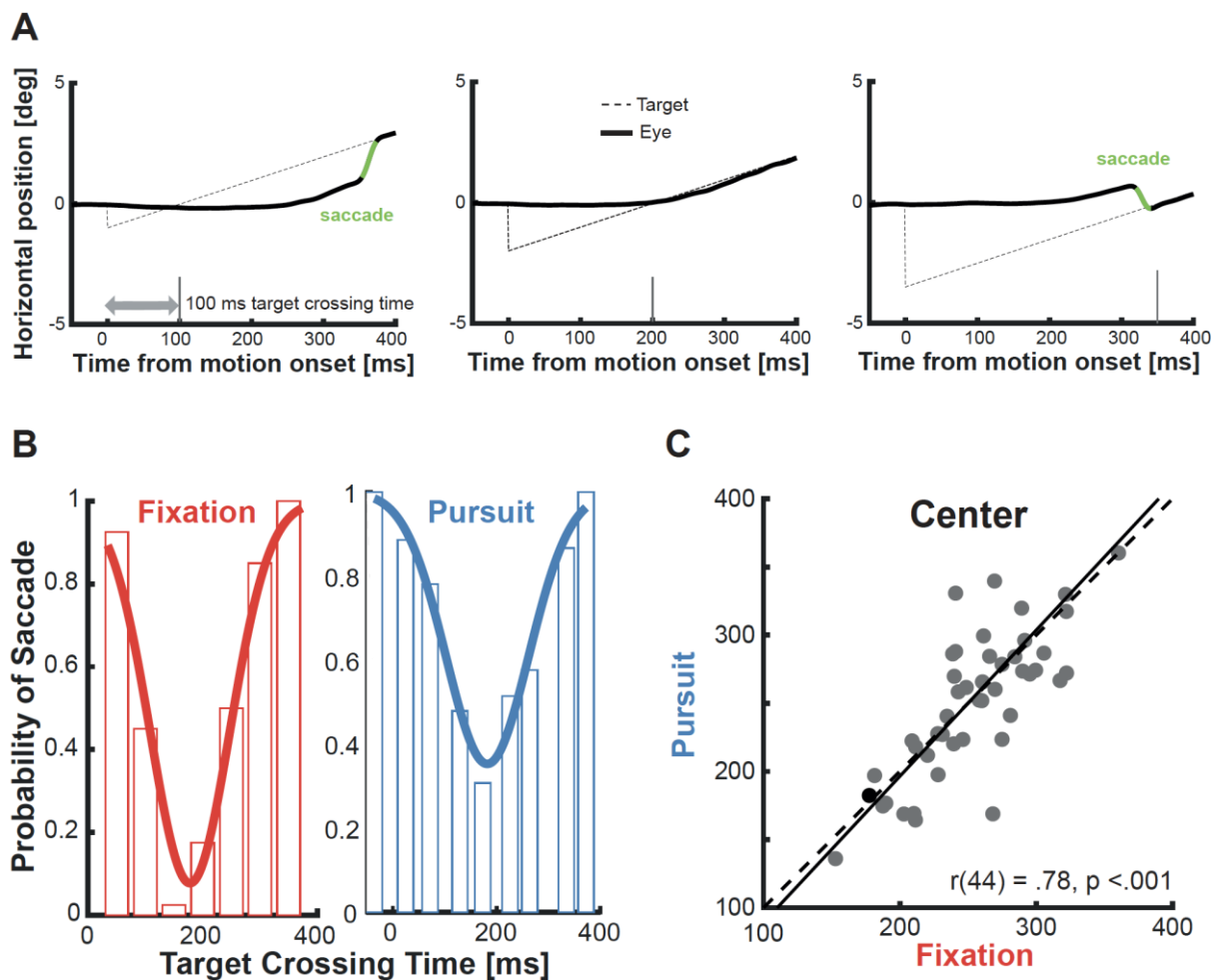


Figure 5. Saccade-Pursuit Interactions. **A.** Examples for trials in the fixation condition with different target crossing times. Plotted is the horizontal target (dashed) and horizontal eye (solid line) position over time. Target crossing time increases from left to right (from 100 to 350 ms). Please note that only in the left and right panels is there an additional corrective saccade (green line) in the initial following response, whereas no saccade is present in the example trial with a target crossing time of 200 ms. **B.** Examples showing the “smooth zone” - our measurement of saccade pursuit interactions for fixation (left) and steady-state pursuit (right). Bars show the probability of a corrective saccade during the initial following response across different target crossing times. Please note here that the analysis was performed based on corrected target crossing times, so as to account for the consistent lag behind the target in the pursuit condition. We fitted an inverse Gaussian to the data, and extracted three parameters: the minimum, the mean (center of the function), as well as the width of the zone (see Methods for more details). **C.** Comparison of the center of the smooth zone between fixation and steady-

state pursuit. There is large variability in the center. The black dot represents the data for the representative observer shown in B.

We observed that the center of the smooth zone was comparable when measured for fixation or during steady-state ($t(45) = 0.92$, $p = .362$) and the similarity was accompanied by a high correlation between the two estimates (with $r(44) = .78$, $p = <.001$). This suggests similar mechanisms for triggering corrective saccades during fixation and pursuit (see Badler et al., 2019), which combine position- and velocity-related signals independent of potential differences in dynamics^{48,52}. There were also some significant differences. The probability of saccades at the center of the smooth zone was higher during steady-state pursuit ($M = 0.21$ for fixation vs $M = 0.29$ for steady state, $t(45) = 3.49$, $p = .001$), and the smooth zone got wider during steady-state ($M = 88.65$ ms for fixation vs $M = 102.98$ ms for steady state, $t(45) = 2.66$, $p = .011$). Together, these results can be explained in the context of a recent model⁵⁴: A noisier sensory signal during pursuit⁵⁵ in combination with a fixed threshold for triggering saccades leads to a larger variability in target crossing times that elicit a corrective saccade⁵⁶, which matches the observed increase of the minimum and width of the smooth zone during steady-state pursuit.

Tracking behavior is tailored to the respective strengths of the observer

To link the results of the oculomotor tasks with the parameters of the smooth zone, we computed correlations between the performance in the other oculomotor and two additional psychophysics tasks (see Method for more details) and the center of the smooth zone, separately for the fixation, as well as the steady-state pursuit condition (see Figure 6 for a selection of correlations). For the fixation condition, we observed significant correlations between the center of the smooth zone and pursuit latency ($r(44) = .35$, $p = .02$), the horizontal saccade error for the velocity task ($r(44) = .57$, $p <.001$) and pursuit gain ($r(44) = -.58$, $p <.001$). For the links to the smooth zone in the steady-state pursuit condition, we observed the same pattern of results: The center of the zone correlated significantly with pursuit latency ($r(44) = .49$, $p < .001$), the horizontal saccade error ($r(44) = .55$, $p < .001$), and pursuit gain ($r(44) = -.56$, $p <.001$). The other metrics did not show a significant correlation.

These results suggest that within the same task, observers tailored the coordination of saccadic and pursuit eye movements to their respective strengths. On the one hand, participants with good pursuit performance (lower pursuit latency and higher pursuit gain) showed an earlier center of the smooth zone. Thus, they relied on pursuit to quickly catch up to the target without additional corrective saccades. On the other hand, observers with accurate corrective saccades to moving targets showed later centers of the smooth zone, thus they relied on them more frequently to catch up with targets moving away from the eye. Conversely, they use them less frequently when target needs more time to cross the fixation (long target crossing times). Thus, how participants coordinated saccadic and pursuit eye

movements reflected the performance of the isolated movements. Please note that the results cannot be interpreted as observers with generally good and accurate eye movements (e.g., high pursuit gain and high saccadic accuracy) having earlier centers of the smooth zone, since there was a negative correlation between saccadic accuracy and pursuit gain for moving targets (see Figure 3). The coordination is also again specialized based on the relevant sensory information, as the accuracy of saccades to stationary targets did not correlate with the center of the smooth zone. These results rather speak for a fine-tuned specialization and optimization of tracking performance within a task based on the individual strengths of each observer, when saccadic and pursuit eye movements need to be coordinated.

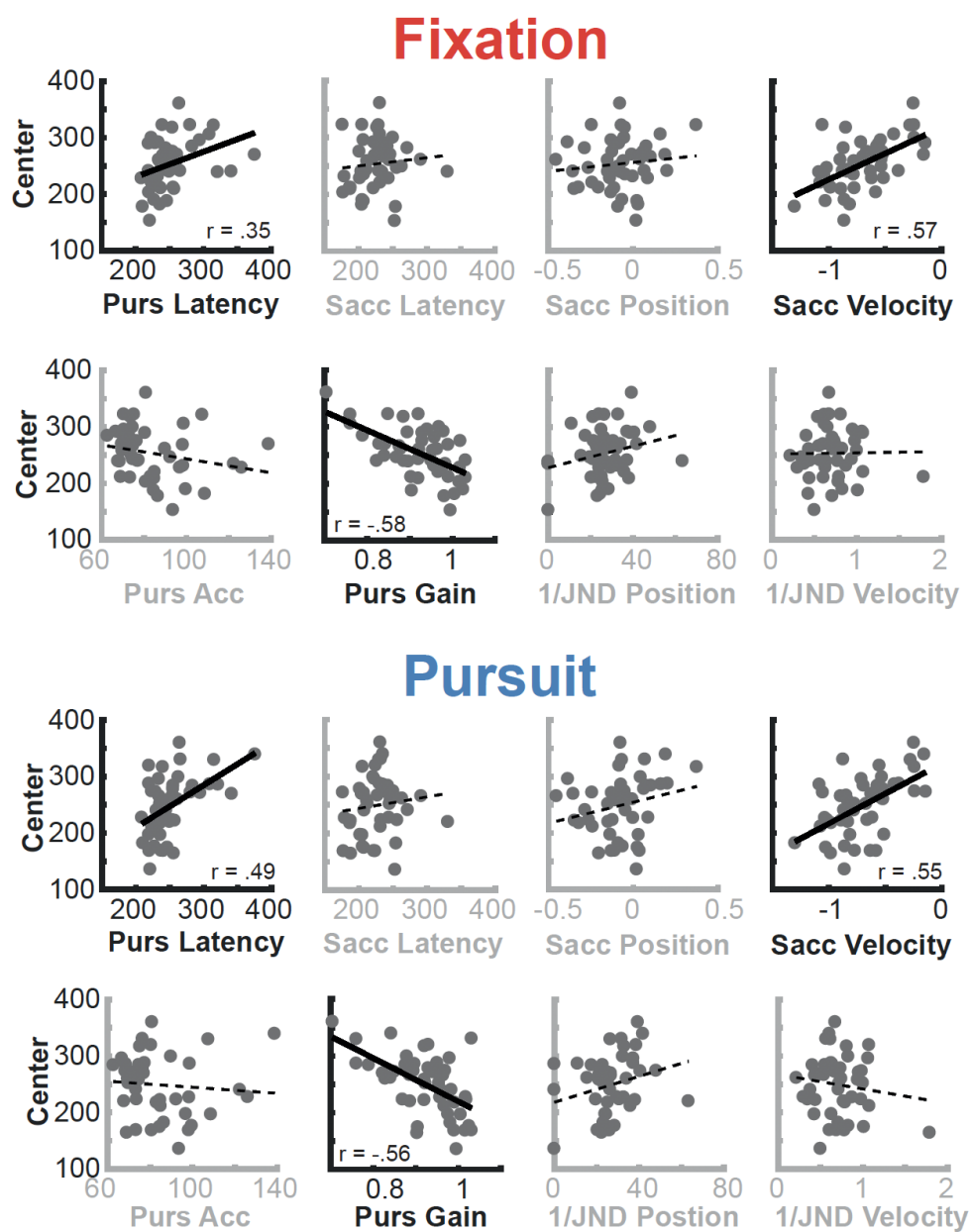


Figure 6. Link between metrics and smooth zone. Top. Shown are correlations between the center of the smooth zone for the fixation experiment estimated based on corrected target crossing times and

different metrics extracted from the other experiments. Each data point reflects the data from one observer. Lines reflect a linear regression fitted to the data; the line is solid if the correlation reached significance. **Bottom.** Same as on the top, but this time with the center of the smooth zone for the steady-state pursuit experiment.

Discussion

Due to their importance for visual perception, eye movements are often considered to be a 'window into the mind' ^{2,57–60}. One of the big advantages of studying eye movements is that they can serve as objective, implicit and continuous measurements of sensory ⁴ and decision processes ⁶¹, and their neurophysiological underpinnings seem to be quite well understood ⁶². However, studies often have focused on average behavior for one specific type of eye movement in one specific task. Our findings demonstrate that this approach misses out on critical links and variations in the control of oculomotor behavior. When comparing saccadic and pursuit eye movements across different tasks, we could show that individual variability across different tasks is mainly related to the relevant sensory information (position vs velocity) and less on the relevant eye movement (saccade vs pursuit). This questions the presumed distinction of different processing streams for saccadic and pursuit eye movements ^{1,62,63}.

By now, multiple studies have shown strong interactions and shared information between saccadic and pursuit eye movements at the behavioral ^{24,25} and neurophysiological level ^{5,26}. Our unique dataset allowed us to take this line of work one step further by using individual differences to investigate relationships between different oculomotor tasks. A critical assumption behind that approach is that these differences are systematic and reliable. Previous research has shown that saccadic and pursuit eye movements have a good re-test reliability ^{40,45,64}, are stable with respect to fixation preferences in images ^{35,36} or effects of a structured background ⁴¹. The stable correlations between tasks conform and extend previous work ^{65,66}, strongly suggesting that variations of oculomotor behavior reflect a trait of the observer ^{45–47}.

The study of Bargary and colleagues ⁴⁵ had measured a set of different oculomotor tasks across observers and suggested that a major contributor to oculomotor behavior might be related to the type of task and not necessary to the eye movements themselves. We extend their work by adding the crucial conditions of saccades to moving targets and pursuit in response to position-related cues. This unique combination of tasks allowed us to firmly link the individual differences across these tasks. Saccadic and pursuit performance are uncorrelated when the relevant sensory information is different. However, when relevant sensory information is matched, performance of saccadic and pursuit eye movements are correlated (Figure 3). A data-driven approach supported the separation of tasks based on the relevant sensory-information (see Table 1).

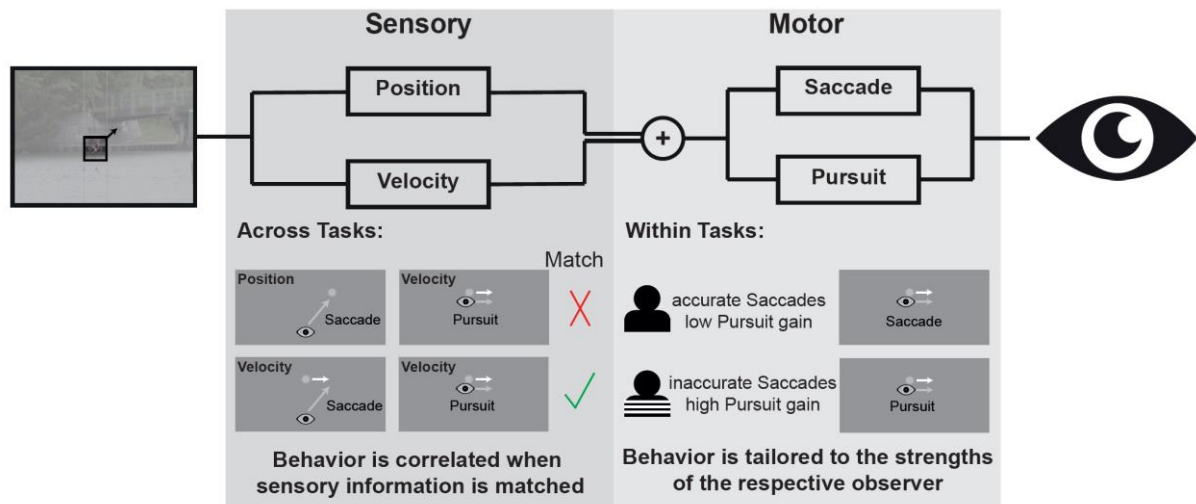


Figure 7. Integrative oculomotor framework. The velocity and position of a potential eye movement target are analyzed. Both information streams are then used to trigger a combination of saccadic and pursuit eye movements to bring the eye towards the target. Across different tasks, saccadic and pursuit eye movement behavior is correlated when the sensory information is matched (e.g., for a saccade to a moving target and pursuit of a moving object, but not for a saccade to a stationary target and pursuit of a moving object). Within the same task, the decision when to trigger a saccadic or pursuit eye movements is based on the individual strengths of a respective observer. An observer with accurate saccades to moving targets is more likely to use a saccade to catch up with a moving target. Another observer with more accurate pursuit, is more likely to use a pure pursuit response for the same trial.

Our findings have far reaching consequences. In most previous studies, the paradigms used for saccadic or pursuit eye movements differ fundamentally with respect to the relevant sensory information (position-related information for saccades and velocity-related information for pursuit). Neuroimaging studies often have used these comparisons to dissociate areas in the brain responsive to saccadic or pursuit eye movements^{32–34,67,68}. Our results suggest that this confound could lead to unintentionally specious interpretations, since these studies cannot distinguish between a motor-related response (saccade vs pursuit) and a sensory-related response (position vs velocity). In neurophysiology, some studies already tried to tackle this problem. For example, the superior colliculus, which is mainly thought to be related to saccade control^{69,70}, seems to provide a more general position error signal, which is also relevant for pursuit eye movements^{71,72}. Moreover, the middle temporal area, mainly thought to be involved for pursuit control^{73,74}, seems to provide a more general velocity-related signal, since lesioning it affects the control of pursuit and saccadic eye movements to moving, but not to stationary targets^{75,76}. Even the well-known omnipause neurons in the brain stem⁷⁷, which are thought to be a gating mechanism for saccadic eye movements, are involved in the control of pursuit eye movements⁷⁸. Therefore, there seems to be converging evidence on the neurophysiological level, that responses in single brain regions are not always related to the control of a specific type of eye movement^{79,80}. We emphasize that the assumption that there are still some areas selectively related to the control of saccadic and pursuit eye movements

is valid. Not every region initially identified by comparing eye movements across different tasks has to be related to sensory information. However, due to the potential confound in the relevant sensory information, the interpretability of such comparisons is often limited. Future studies should make use of additional control conditions, for example by measuring saccades to moving targets or by comparing variations in the combination of saccadic and pursuit eye movements due to trial-by-trial variability^{43,44} to be able to directly dissociate eye movement-related from sensory-related areas.

When focusing on the coordination of saccadic and pursuit eye movements within the same task for the same type of sensory information, we noticed that observers tailored their behavior to their respective strengths (Figure 6). Importantly, there was a negative correlation between the performance of saccades to moving targets and pursuit. This rules out that these relationships can be explained by an overall better oculomotor performance (saccade and pursuit eye movements were not both more accurate across observers), or a general improved accuracy for one of the eye movements (e.g., accuracy of saccades to stationary targets was not related to the interaction). It rather shows a specific optimization of behavior within a certain task, that is based on the performance of the individual eye movements under these circumstances. With the previously established importance of shared sensory information that links saccade and pursuit control across tasks, this leaves the puzzling question of why saccadic and pursuit eye movements do not show comparable performance when tracking a moving target. We believe that this reflects a hierarchical organization in the control of oculomotor behavior. There is an underlying distinction in the processing of position- and velocity-related information²³, which can explain the links in performance across tasks, but for a specific task with the same sensory information, there is a further specialization in the control of individual eye movements.

So how could the performance of saccadic and performance differ despite shared sensory information? The origin of variability in eye movement responses has been debated extensively for eye movements⁸¹. While some reports concluded that variability was to a large extent based on sensory information alone^{82,83}, other studies reported an important role of motor and decision noise^{84–86}. Either way, any form of additional motor noise, central decision noise, or differences in how the sensory signals are transformed into the respective eye movement could explain a negative correlation between saccadic and pursuit eye movement performance within the same task, despite shared sensory information. The reasons behind such a specialization could be manifold and, unfortunately, cannot be addressed with our correlational data alone. On the one hand, observers could have learned that one type of their eye movements is more accurate when tracking moving targets, so they rely on that one more frequently. On the other hand, if observers for example initially relied more on corrective

saccade when tracking moving targets, accuracy of these movements could just have improved with practice.

It is discussed elsewhere how position- and velocity-related sensory errors are integrated into decisions whether to perform corrective saccades^{22,25,51,54,56}. Our results show that the decision criteria differ widely across observers. They are probably based on a life-long learning process and optimized for each individuals tracking performance. The fact that variability in behavior is more than just noise in measurements, but can be related to the strengths of the particular observer has already been suggested for the relation between eye movements and face perception. Although there is a theoretical optimum for where to look at a face, each observer has their own preferred location for where to fixate, and this correlates with their face identification performance⁸⁷. In addition, people who spend more time looking at faces are also better at recognizing faces³⁶. Related to that, a recent study showed that Super-Recognizers⁸⁸, people with exceptional abilities to recognize faces, spend significantly more time looking at faces than controls and also look closer at a theoretical optimal location for face identification⁸⁹. Thus, individual differences might in general reflect the strengths and weaknesses of sensory processing and motor behavior for each observer.

Our results provide direct empirical evidence that saccade and pursuit performance is correlated across different tasks, but only when tested with matched sensory information. This suggests that the high-level dissociation often assumed to occur between the control of saccadic and pursuit eye movements, is instead related to the difference in the relevant sensory information. Both types of eye movements are controlled by a combination of independent position- and velocity-related information²³. This is quite similar to the control of other kinds of actions, for example interception^{90,91}. When coordinating saccadic and pursuit eye movements, differences across observers revealed that they adjust their tracking behavior according to their individual strengths⁸⁷. These new insights make it very clear that future studies addressing the underlying brain areas and mechanisms for motor control need a careful control for the relevant sensory stimuli and can provide exciting pathways towards a deeper understanding of the underlying neurophysiological circuits. Furthermore, the differentiation of relevant sensory information and executed eye movement might provide new insights for clinical research, for example by demonstrating that patient groups have no deficits related to a certain type of movement, but to the sensory processing relevant for the characteristics of the task⁹².

Methods

Observer

50 observers (mean age: 24.42, std = 3.86, range: 19:35) took part in the study, 37 identified as female, 13 as male. The number of participants, study design, and parts of the analysis

were preregistered⁹³. All observers were naïve with respect to the purpose of the study and had normal or corrected-to-normal vision. Before the start of the experiment, they gave informed consent, and all tasks were approved by the local ethics committee (Giessen University LEK 2017-0029) and were conducted in accordance with those guidelines at the ZPID in Trier. Observers were compensated with money for their effort during the experiment.

Setup & Experimental Conditions

Observers were seated at a table in a dimly illuminated room with their head positioned on a chin rest. In this position, their eyes were roughly aligned with the height of the center of a monitor (53 cm x 30 cm, 1920 x 1080 pixel, 144 Hz, BenQ, Taipeh, Taiwan) with a viewing distance of 90 cm. Under these circumstances the monitor spanned approximately 34 x 19 degrees of visual angle. The tasks were programmed and controlled with Matlab 2020a (MathWorks, Natick MA) using Psychtoolbox⁹⁴. Gaze was recorded from one eye with a desk-mounted eye tracker (EyeLink 1000 Plus, SR Research, Kanata, ON, Canada) at a sampling frequency of 1000 Hz. To ensure accurate recordings before each block a nine-point calibration was performed, and additional drift checks were used at the start of each trial. The drift checks allowed the observers to perform each task in a self-paced manner. To start a trial, they needed to press the space bar when looking at the central fixation.

All observers completed a total of eight different tasks (see Figure 1): (1) saccades to stationary targets, (2) saccades to moving targets, (3) pursuit of moving targets, (4) pursuit with flashed stationary target, (5) smooth-zone measurement out of fixation, (6) smooth-zone measurement out of steady-state pursuit, (7) psychophysical judgment of position steps, (8) psychophysical judgements of target speed. Tasks 1, 2, 3, 7 and 8 consisted of one block and took about 15 minutes; tasks 5,6, and 7 consisted of two blocks and took approximately 30 minutes. All tasks were completed across three one-hour sessions on separate days. The order of tasks was randomized for each observer. At the beginning of the first session additional demographic information was collected. Across all tasks, each observer completed a total of 1460 trials.

Individual Tasks

Task 1 Saccades to stationary targets. The goal of this task was to measure saccade accuracy to static targets. After the drift check, observers were asked to always look at and then fixate a Gaussian blob target (SD = 0.3 deg, maximum contrast = 0.2) presented in front of a gray background. The target initially appeared at the horizontal meridian, but shifted downwards by 7 deg. After a random time between 1 and 1.5 seconds the target then disappeared and directly reappeared at one of six different positions. It always appeared at the vertical meridian, but shifted by either 1.25, 2.5 or 3.75 deg to the left or to the right. These positions were chosen to match the position of the moving target in task 2 after 250 ms of movement with the different target speeds. Gaze was monitored online to ensure that

observers only moved their eyes to the new target after it actually appeared. If observers moved their eyes too early, an error message appeared and the task continued with the next trial. The horizontally shifted target then stayed on the screen for 1s, the trial ended and the drift check for the next trial followed. Overall, each observer completed 120 trials (3 horizontal positions x 2 directions x 20 repetitions).

Task 2: Saccades to moving targets. The goal of this task was to measure saccade accuracy to moving targets. The trial structure of task 2 was identical to task 1. After an initial fixation on the target on the bottom half of the screen, after a random time between 1 and 1.5s the target again jumped to the center. However, here instead of being horizontally shifted, the target appeared in the center of the screen and immediately moved either to the left or the right. The target could move with 5, 10, or 15 deg/s and disappeared after 1s. Overall, each observer completed 120 trials (3 speeds x 2 directions x 20 repetitions).

Task 3: Pursuit of moving targets. The goal of this task was to measure pursuit accuracy to moving targets. Each trial started with Gaussian blob target in the center of the screen for a random time between 1 and 1.5s. After this time the target stepped either to the left or the right and immediately started to back to the center of the screen. The target could move again with either 5, 10, or 15 deg/s and the size of the step was adjusted so that the target reached the center of the screen after 200 ms with the respective velocity. After crossing the center, the movement continued for 1s and the target disappeared. Overall, each observer completed 120 trials (3 speeds x 2 directions x 20 repetitions).

Task 4: Pursuit with flashed stationary target. The goal of this task was to measure the influence of positional information on the pursuit system. The design of this paradigm was inspired by a recent paper of Buonocore and colleagues ²⁸. Each trial again started with the Gaussian blob target in the center of the screen for a random time between 1 and 1.5s. Then the target stepped either 2 deg to the left or 2 deg the right and moved with 10 deg/s towards the center. Just when the target crossed the center of the screen additional squares could be flashed on the screen for one frame (around 7ms). The squares were grayish (Contrast: 0.1) and 2 by 2 deg large, and could either appear at 4 deg left of the center or 4 deg right of the center. Across trials the squares were therefore either presented in front of the pursuit, behind of the pursuit or as a control was not shown. Observers were told to ignore the squares and just continue tracking the moving target, which appeared after 1 second of movement. Observers completed two blocks of 120 trials each (2 directions x 3 squares x 20 repetitions) leading to a total of 240 trials.

Task 5: Smooth-zone measurement out of fixation. The goal of this task was to asses saccade-pursuit interactions via the smooth zone out of fixation. To assess the smooth zone, we systematically varied the target crossing time. Again, the target stayed in the center of the

screen for a random time between 1 and 1.5s. Then the target stepped to the left or the right and immediately moved with 10 deg/s towards the center. The time the target took to reach the center was varied between 50, 100, 150, 200, 250, 300 or 350 ms by adjusting the size of the initial step accordingly. The target kept moving for 700 ms after it crossed the center of the screen and then disappeared. Each block consisted of 140 trials (2 directions x 7 target crossing times x 10 repetitions) and observers completed 2 blocks for a total of 280 trials.

Task 6: Smooth-zone measurement out of steady-state pursuit. The goal of this task was to assess saccade-pursuit interactions via the smooth zone out of steady-state pursuit. For this we aimed at creating the same eye crossing times with comparable position and velocity errors during steady state pursuit. Trials could move either to the left or right and this time depending on the direction of the movement, the target started at 15 deg to the left or right in the opposite direction of the target movement. After a random time between 0.75 and 1.25s the target started to move with 10 deg/s and an eye crossing time of 200 ms. The target kept moving towards the center for a random duration between 0.75 and 1.25s. During this time the eyes were in steady-state pursuit following the target. After the random time a second step occurred, where the target stepped backwards and afterwards started moving with 20 deg/s. The size of the step was chosen to match the eye crossing times of 50, 100, 150, 200, 250, 300 or 350 ms (by not using the 20 deg/s of the velocity, but 10 deg/s velocity since the eyes were supposed to be already moving at 10 deg/s). In this way the smooth zone could be compared with comparable target movements during fixation or steady-state pursuit. After the second step, the target again kept moving for 700 ms and then disappeared. Overall, observers completed a total of 280 trials (2 blocks x 2 directions x 7 target crossing times x 10 repetitions).

Task 7: Psychophysical judgment of position steps. The goal of this task was to measure the perceptual ability to discriminate different target steps. In this task observers had to judge the size of a target step. Each trial again started with the target in the center of the screen for a random time between 1 and 1.5s. Afterwards the target could again step either to the left or to the right by 1.2, 1.6, 2, 2.4 or 2.8 deg. After the step the target stayed stationary and visible for a random time between 500 and 700 ms. Then observers had to judge whether the just observed target step was larger than the size of a standard target step. The standard step was 2 deg. To reduce the number of trials, we didn't use a 2 AFC task, but a memorized standard, where we presented the labelled standard target 5 times in a row randomly stepping to the left or the right. The standard was shown at the beginning of the task and again before trial 10, 30, 60 and 100. The standard was the average of all visible target speeds. The judgements of the different target steps allowed to compute a psychometric curve. Overall, observers completed 150 trials (2 directions x 5 step sizes x 15 repetitions).

Task 8: Psychophysical judgment of target speed. The goal of this task was to measure the perceptual ability to discriminate different target speeds. The design of the task was

identical to task 7. However, instead of size of the target step, we varied the velocity of the moving target. The target stayed in the center for a random time between 1 & 1.5 s and then stepped to the left or right and immediately started moving towards the center of the screen. The velocity varied between 8, 9, 10, 11 or 12 deg/s and the size of step was again chosen so that the target crossed the center of the screen in 200 ms. These velocities had then to be compared with the standard velocity of 10 deg/s, which again was introduced as a memorized standard. Overall, observers completed 150 trials (2 directions x 5 speeds x 15 repetitions).

Data Analysis & Pre-Processing

Eye movement data were analyzed offline using our custom software programmed in MATLAB. Saccades were detected by using the Eyelink criteria of a speed and acceleration threshold of 30 deg/s and 4,000 deg/s², respectively. Blinks in the data were linearly interpolated. Eye positions were filtered using a second-order Butterworth filter with a cutoff frequency of 30 Hz and afterwards we calculated the horizontal and vertical eye velocity by taking the difference between consecutive samples of the filtered position traces and multiplying it by the sampling frequency to represent it in degrees per second. Eye velocity was then again filtered by a second-order Butterworth filter with a cutoff frequency of 20 Hz. To analyze the data for leftward and right movements or leftward and rightwards steps together, we flipped the horizontal positions of the eye movement for targets that moved or stepped to the left. Pursuit onset was detected by a custom algorithm. To calculate pursuit onset, we used a velocity trace where detected saccades were linearly interpolated in the velocity trace (saccade +/- 30 ms). Then, as a baseline, the velocity and standard deviation of the eye velocity was computed from 25 ms before to 25 ms after target movement onset. Pursuit onset was the point where the eye velocity was above three times the standard deviation of the baseline and stayed from there for more than 50 ms above 30% of the target speed.

Metrics

For tasks measuring performance of isolated eye movements (Task 1-4) we computed individual metrics. If not noted differently, we computed each of the following metric for each trial and then averaged them across both directions for each of the factor steps (e.g., target step or target velocity). To compare the results across tasks we then averaged across the factor steps to have one value per subject per task. In the saccade tasks (Task 1 & 2) we computed the *horizontal and vertical saccade error* (respective difference between eye position and target position at saccade offset) as well as *saccade latency*. The target positions in these tasks were designed in a way that saccades landed at comparable positions, which allowed for a direct comparison. For the pursuit-velocity task (Task 3) we computed *pursuit latency* based on pursuit onset detection as well as *pursuit acceleration* (defined as the slope of a

linear regression fitted to the velocity in a temporal window of 50 around the pursuit onset) and *pursuit gain* (defined as the average velocity from 200 to 300 ms after pursuit onset divided by target speed). Note that for the computation of pursuit gain, saccadic velocity epochs ± 30 ms were eliminated from the analysis. For pursuit-position task (Task 4) we computed the mean difference between the average eye velocity between 100 and 180 ms after the presentation of the square in front or behind the pursuit eye movement to quantify the influence of positional information on pursuit. We obtained this time window, by looking at the difference in the average eye velocity across subjects for the different conditions (see Figure 2).

For the tasks measuring the coordination of saccadic and pursuit eye movements by establishing a “smooth zone” (see Figure 5), we labelled each trial as a saccade trial if a saccade occurred within the first 400 ms after target motion onset. If no saccade happened during that interval, the trial was labelled a pursuit trial. We then wanted to compute the average probability of a saccade trials across the different presented target crossing times. However, we noticed that especially in estimating the smooth zone during steady-state, the eyes were not always perfectly on the target and the position (Average = 1.98 deg for fixation vs 1.86 deg for steady-state) and velocity errors (Average = -9.82 deg/s for fixation vs -10.63 deg/s for steady-state) were therefore not directly comparable. To account for that we performed the analysis with a corrected target crossing time. For that, we computed the horizontal position error between eye and target position after the relevant target step as well as the velocity error (for the eye we took the average horizontal eye velocity between 75 ms before to 25 ms after the target step) and calculated the corrected target crossing time based on the negative position error divided by the velocity error. We grouped the computed target crossing times in bins between 0 and 400 ms in 50 ms steps. One additional bin was capturing negative target crossing times between -100 and 0 ms. For bins that had more than 3 trials, we computed the average probability of a saccade, as well as the median of the computed target crossing time. Based on these values, we then estimated the smooth zone by fitting an inverse Gauss function, which allowed us to extract three relevant parameters. The mean of the function indicated the *center of the smooth zone* (e.g. minimum number of saccades at 250 ms target crossing time), the standard deviation of the function reflected the *width of the smooth zone* (e.g. low number of saccade across a width of 80 ms, and the amplitude of function gave us the *minimum of the smooth zone* (e.g. at the center of the smooth zone the probability of a saccade is 0.1).

For task psychometric tasks (Task 7 & 8), we fitted a cumulative Gaussian as psychometric functions to the average ratings across factor steps. We used the inverse of the JND's as indicator of the *discrimination performance*. For the motion judgement task, we used the same computation as for Task 3, to estimate the pursuit gain per observer in this task.

Statistical Analysis. To assess the structure of the data we had two approaches: The first was looking at specific combination of correlations to test and visualize along which dimension (motor behavior or sensory signals) observers varied. We computed correlations between metrics reflecting saccadic and pursuit behavior in response to position- and velocity-related sensory information. To estimate the relative contributions of sensory signals and motor behavior, we computed the correlations for pursuit eye movements based on the same sensory input (pursuit gain in task 3 & 8) and with different sensory input (pursuit gain in task 3 & position influence measured in task 4). We then computed the difference between the explained variance of the correlation based the same sensory input and the explained variance based on the correlation with different sensory input. This allowed us to express the relative contribution of sensory information. We took the same approach for saccadic eye movements (same sensory input: vertical error in task 1 & 2; different sensory input: horizontal error in task 1 & 2). Our second approach was purely data driven, where we used a principal component analysis based on all metrics extracted for the tasks that investigated isolated eye movements. The PCA was conducted in JASP, with the settings of relevant factors with an eigenvalue above 1. Factors needed to be orthogonal and we tried to increase the interpretability of the individual factors by using the varimax setting.

For the investigation of coordination of saccadic and pursuit eye movements, we computed correlations between the center of the smooth zone and the metrics extracted in the tasks focusing on isolated eye movements.

Exclusion Criteria

Single trials were excluded from the analysis if during a single trial there were more than 500 ms of missing data due to blinks or other reasons. For saccade measurements (Task 1 & 2), trials were excluded if no valid saccade was detected that had a latency between 50 and 700 ms and a position error above 5 deg. For pursuit measurements (Tasks 3, 4 & 8), trials were excluded if no valid pursuit onset with a latency between 50 and 700 ms was found or the computed gain following pursuit onset was below 0.3 or above 2. Please note that for experiment 8, trials not reaching the pursuit criteria were only excluded from the oculomotor analysis, but not from the perceptual analysis. Based on these criteria across all tasks we used 70.873 out of 73000 trials (97%). The proportion of valid trials across experiments was: Task 1 = 92%, Task 2 = 90%, Task 3 = 95%, Task 4 = 95%, Task 5 = 99%, Task 6 = 99% Task 7 = 99%, Task 8 = 98 % for psychometric data, 93 % for oculomotor behavior.

In addition to the exclusion of single trials, we excluded the results from one observer when analyzing Task 5, due to a really high trial exclusion rate (> 70%) and an average pursuit gain below 0.5. In addition, we excluded the data from 4 observers from the analysis of the smooth zone experiments, since here the estimated center of the smooth zone was at least 50 ms

outside the range of our tested target crossing times (> 400 ms) and therefore no reliable estimate was possible.

Deviations from Preregistration

In comparison to the preregistration, we focused the story and analysis presented in the manuscript on two of the three initial hypotheses: the structure of the tasks and the relation of different metrics to the center of the smooth zone. The third hypothesis regarding the comparison of the smooth zone between fixation and steady-state pursuit is still included and discussed. With respect to the analysis, we needed to exclude a few participants from parts of the analysis (see exclusion criteria). With respect to the analysis, we slightly adjusted our initial plan. With such a large data set, there are a lot of potentially interesting results and possible comparisons and in the preregistration, we mentioned a lot of different metrics to compute. To keep the analysis more focused, we only selected a subset of the proposed metrics (e.g., we didn't analyze saccade precision or the psychometric PSEs).

To search for structure in the data, we performed the PCA on the isolated metrics alone, since the interaction measurements were already directly related to multiple different saccadic and pursuit measurements. Instead of an additional multidimensional scaling approach, we explored the data with selected correlations to directly test the interaction of different sensory information and different oculomotor behavior and to estimate the relative contributions of sensory and motor information. For studying saccade-pursuit interactions, we decided against the use of additional t-tests to compare good and bad performers for each eye movements, but stucked with the proposed correlational approach.

Author contributions

Conceptualization, A.G.; Methodology, A.G. and K.G.; Formal Analysis, A.G.; Writing – Original Draft, A.G.; Writing – Review & Editing, A.G. and K.G.; Visualization, A.G.; Funding Acquisition, A.G. and K.G.

Acknowledgements

The authors thank Bianca Baltaretu and Jolande Fooker for helpful comments on the initial draft of the manuscript. AG & KG were supported by the Deutsche Forschungsgemeinschaft (DFG; project number 222641018–SFB/TRR 135 Project A1). Data collection of the present study was funded by PsychLab, a service of the Leibniz Institute for Psychology (ZPID)

Data Availability

All Data, the experimental and analysis code will be made available on psycharchive.

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