

# 1 Individual differences link sensory processing 2 and motor control

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## 9 **Abstract**

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

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## 28 Introduction

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

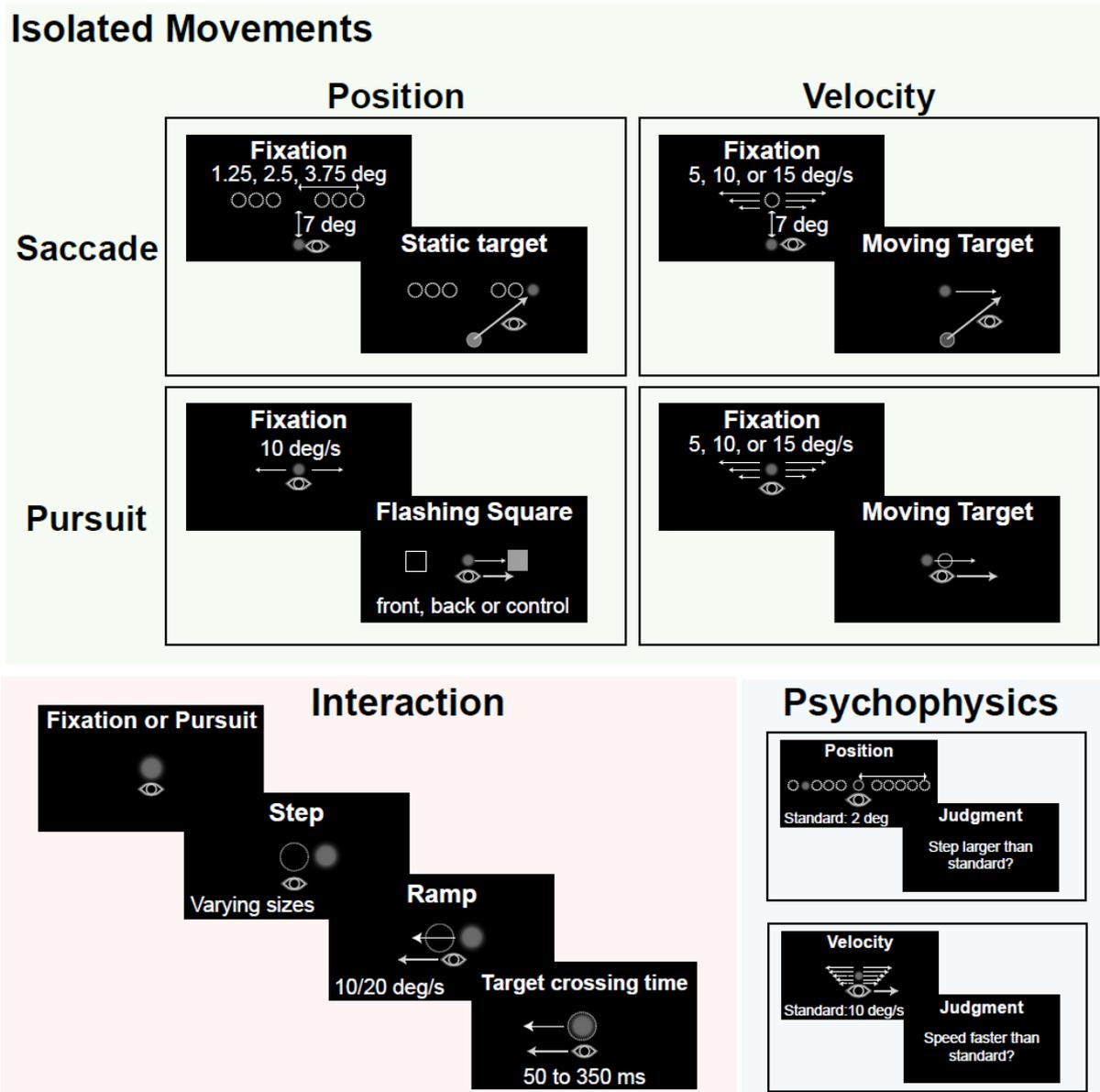
48 First, during natural behavior saccadic and pursuit always occur together to allow for optimal  
49 tracking. Interactions and shared information between saccade and pursuit have been shown  
50 for complex natural movements in highly dynamic situations <sup>16-18</sup>, but also with simpler  
51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

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

64 massive Individual differences have been shown for the control of both saccadic <sup>35-39</sup> and  
65 pursuit eye movements <sup>40-42</sup>, and in how saccadic and pursuit eye movements are combined  
66 to track a moving target. The same stimulus that is tracked with smooth pursuit by one  
67 observer, is tracked by a combination of saccadic and pursuit eye movements by another  
68 observer <sup>43,44</sup>. These interindividual differences in oculomotor behavior are strong and stable,  
69 so that even ideas of an 'oculomotor signature' or 'oculomotor fingerprint' have been proposed  
70 <sup>36,45-47</sup>. The focus on average behavior might miss out on a substantial amount of interesting  
71 information.

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

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



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.

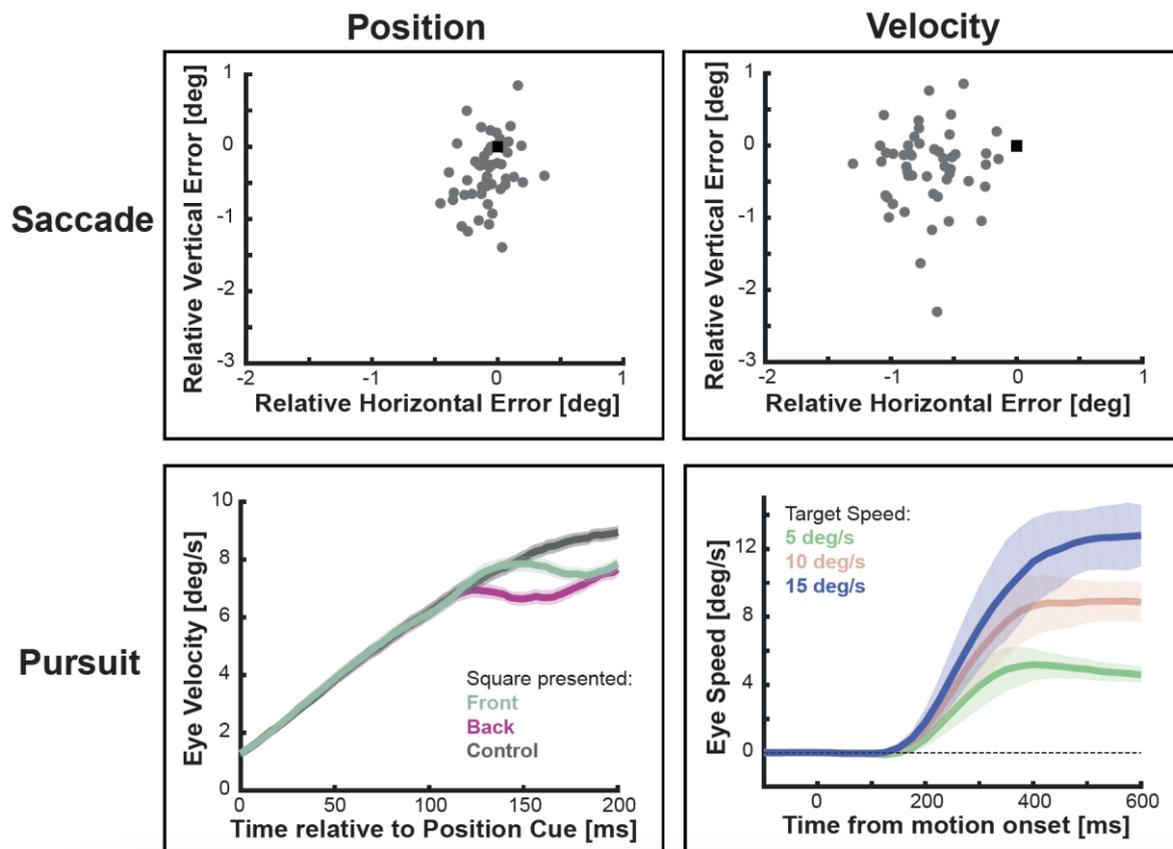
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## 116 **Results**

### 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<sup>28</sup>. 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).



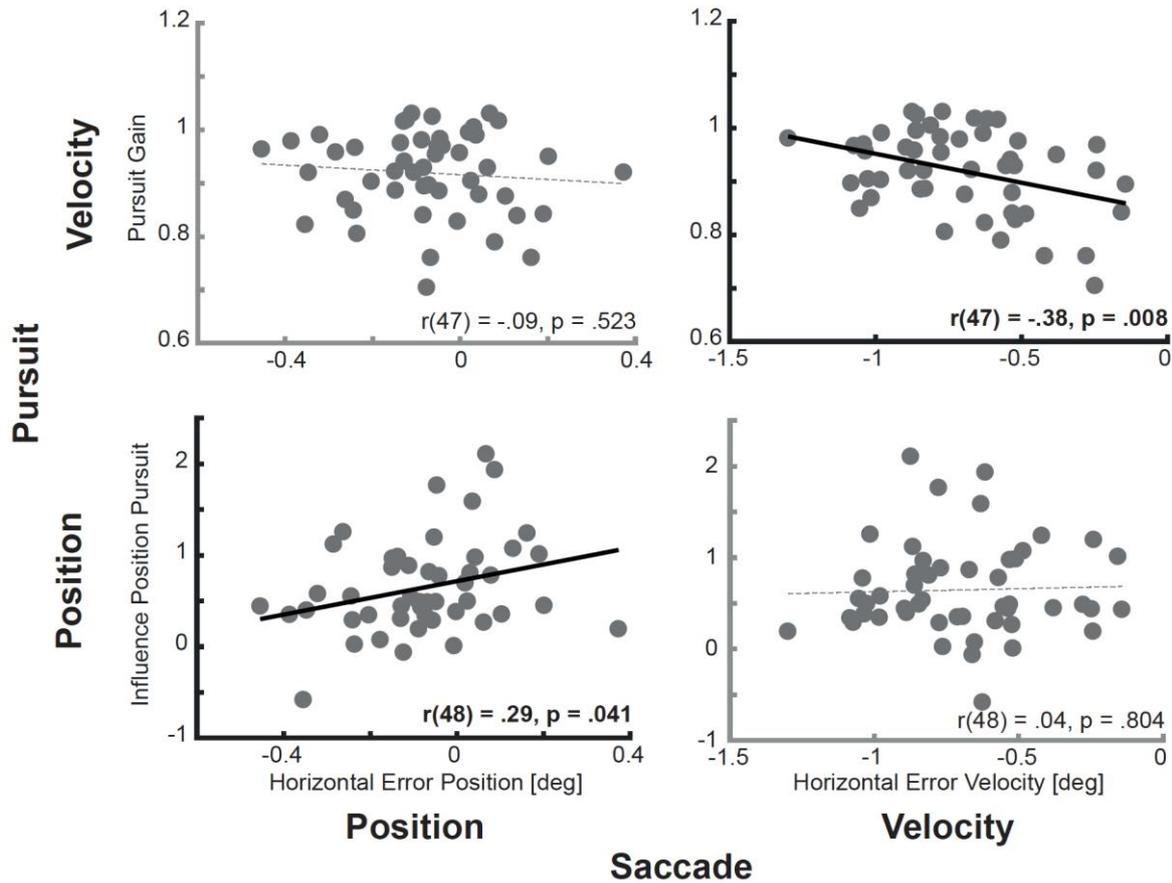
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151 **Figure 2. Overview over data from other experiments. Top row.** Average relative saccade endpoint  
 152 for each observer for stationary (left) and moving (right) targets. All endpoints are aligned, such that the  
 153 target is at 0,0 (black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

160

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

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



177

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

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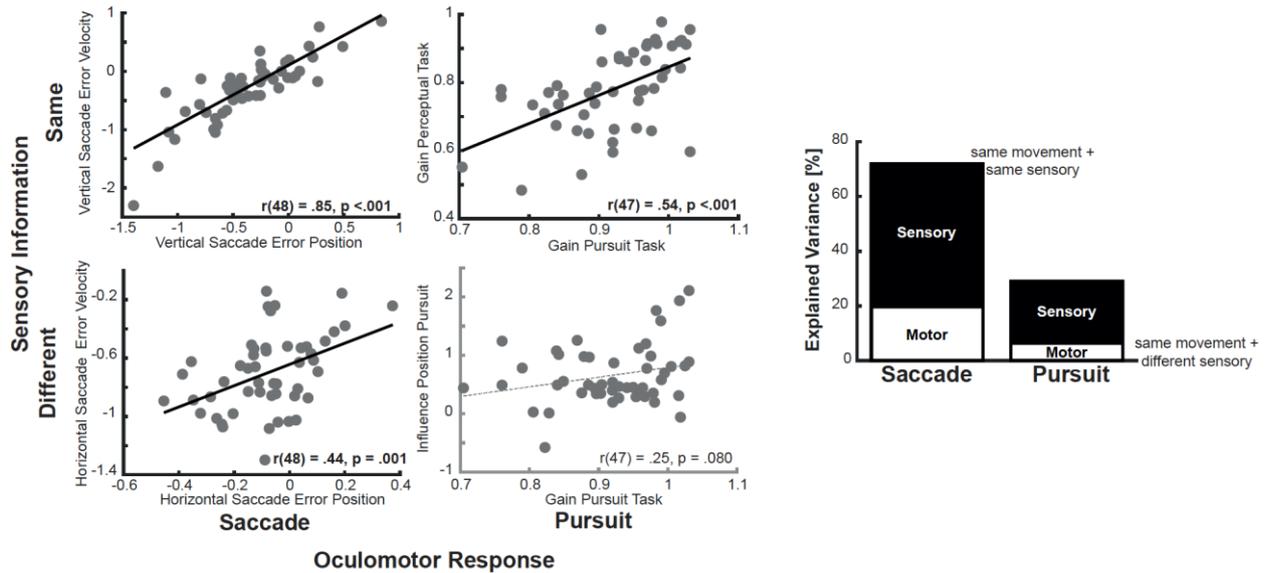
185 Together, these results show that assuming independent and separate systems while only  
 186 comparing saccades to static targets with pursuit to moving targets is missing critical links in  
 187 the control of saccadic and pursuit eye movements<sup>24,25</sup>. For position information, a larger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

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

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

### 199 **Contributions of sensory information and motor behavior across different tasks**

200 To estimate the contributions of sensory information for variations in oculomotor behavior  
201 across tasks, we compared the correlations for the same motor responses (either saccade or  
202 pursuit) when related to the same sensory information and once across metrics when related  
203 to different sensory information (see Figure 4 and Methods for more details). If the executed  
204 oculomotor response is the relevant factor (e.g., someone is generally good at making  
205 saccades), we would not expect a large difference between the correlations. As a baseline, we  
206 observed highly significant correlations between the same oculomotor responses (see Figure  
207 4 left) when the metric was related to the same sensory response (saccade:  $r(48) = .85$ ,  $p <$   
208  $.001$ ; pursuit:  $r(47) = .54$ ,  $p < .001$ ). This shows that individual differences in oculomotor  
209 behavior across tasks are highly reliable. For comparison, we correlated performance for the  
210 same oculomotor behavior, but with different relevant sensory information. In this case, the  
211 correlations were reduced by about half (saccade:  $r(48) = .44$ ,  $p = .001$ ; pursuit:  $r(47) = .25$ ,  $p$   
212  $= .080$ ). To estimate the contribution of the relevant sensory information for saccadic and  
213 pursuit eye movements across tasks, we computed the proportion of the explained variance  
214 when different sensory-information was used in comparison to the explained variance in the  
215 baseline with the same sensory information (see Figure 4 right). Sensory information explained  
216 roughly three quarters of the total explainable variance (Saccade: 73%, Pursuit: 78%), leaving  
217 one quarter of explainable variance for the oculomotor response.



218

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

229

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

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

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

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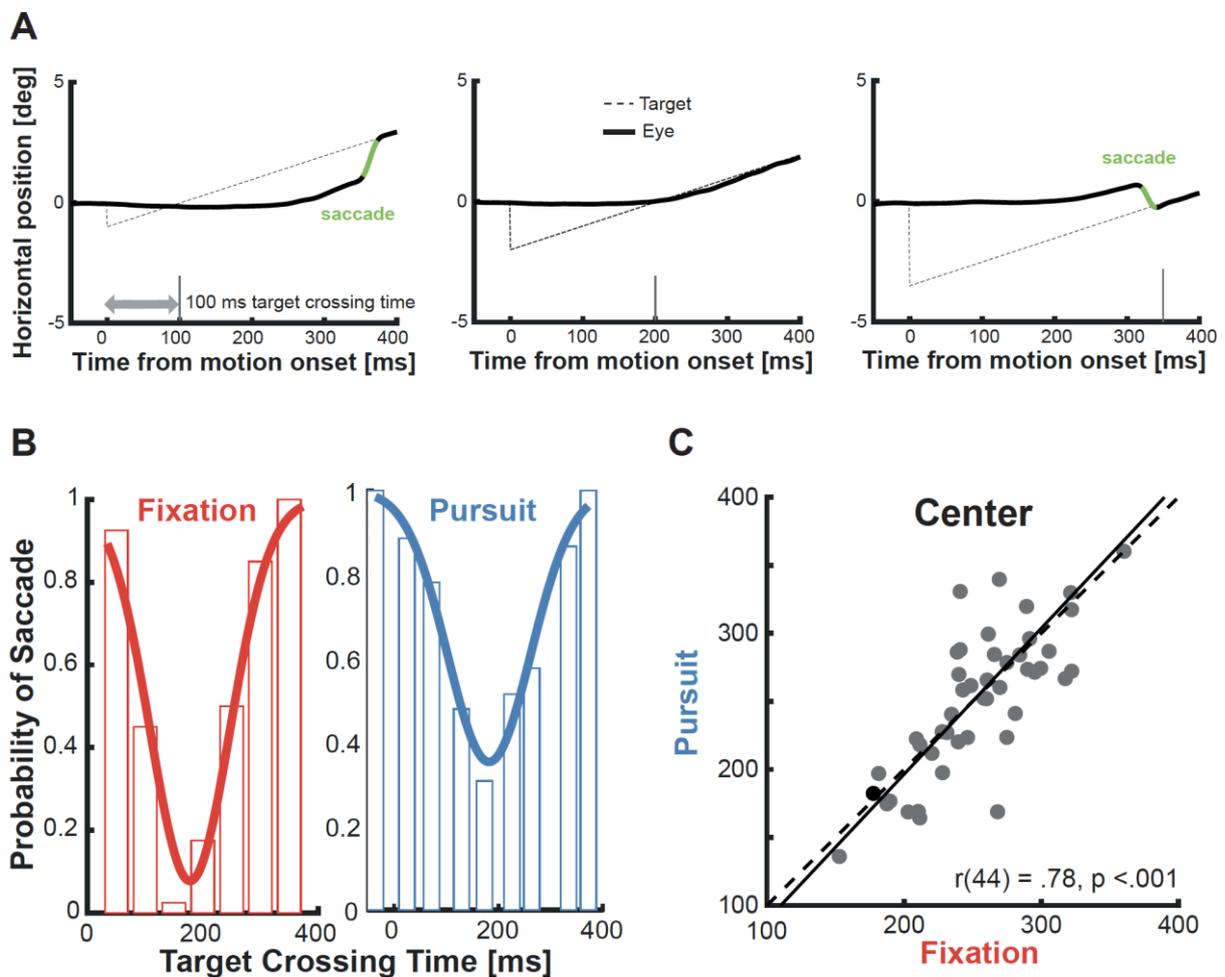
248 Together, these results converge on the fact that variations in oculomotor behavior across  
249 different tasks are mainly driven by the relevant sensory information. We did not observe  
250 evidence for the often-present assumption of separate systems for the control of saccadic and  
251 pursuit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

## 258 **Variability in the coordination of saccadic and pursuit eye movements**

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

265 We operationalized saccade-pursuit interactions as the combination of position and velocity  
266 errors that are related to triggering a corrective saccade during pursuit (see Figure 5A; <sup>22,51</sup>).  
267 The combination of both error signals can be summarized as the target crossing time (the time  
268 the target needs given its current position and velocity to cross the current eye position). Across  
269 different target crossing times, it is possible to fit a “smooth zone” for each observer (see Figure  
270 5B; four observers were excluded from the analysis due to unreliable fits - see Methods for

271 details), which contains trials with a lower probability of corrective saccades <sup>43</sup>. At the center  
 272 of the smooth zone is the combination of position- and velocity-error that led to the minimum  
 273 number of corrective saccades. The smooth zone was measured during fixation or out of  
 274 steady-state pursuit, due to potentially faster pursuit dynamics and different relevant  
 275 information while already pursuing a target <sup>48,52</sup>. Similar to the investigation of isolated eye  
 276 movements, we found substantial variability in the center of the smooth zone across observers  
 277 (see Figure 5C). It ranged between target crossing times of 150 to 400 ms across observers.  
 278 This means that the same combination of errors could be tracked exclusively with pursuit by  
 279 some observers, while other observers would mainly exhibit corrective saccades.



280

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

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

295 We observed that the center of the smooth zone was comparable when measured for fixation  
296 or during steady-state ( $t(45) = 0.92$ ,  $p = .362$ ) and the similarity was accompanied by a high  
297 correlation between the two estimates (with  $r(44) = .78$ ,  $p = <.001$ ). This suggests similar  
298 mechanisms for triggering corrective saccades during fixation and pursuit (see Badler et al.,  
299 2019), which combine position- and velocity-related signals independent of potential  
300 differences in dynamics<sup>48,52</sup>. There were also some significant differences. The probability of  
301 saccades at the center of the smooth zone was higher during steady-state pursuit ( $M = 0.21$   
302 for fixation vs  $M = 0.29$  for steady state,  $t(45) = 3.49$ ,  $p = .001$ ), and the smooth zone got wider  
303 during steady-state ( $M = 88.65$  ms for fixation vs  $M = 102.98$  ms for steady state,  $t(45) = 2.66$ ,  
304  $p = .011$ ). Together, these results can be explained in the context of a recent model<sup>54</sup>: A noisier  
305 sensory signal during pursuit<sup>55</sup> in combination with a fixed threshold for triggering saccades  
306 leads to a larger variability in target crossing times that elicit a corrective saccade<sup>56</sup>, which  
307 matches the observed increase of the minimum and width of the smooth zone during steady-  
308 state pursuit.

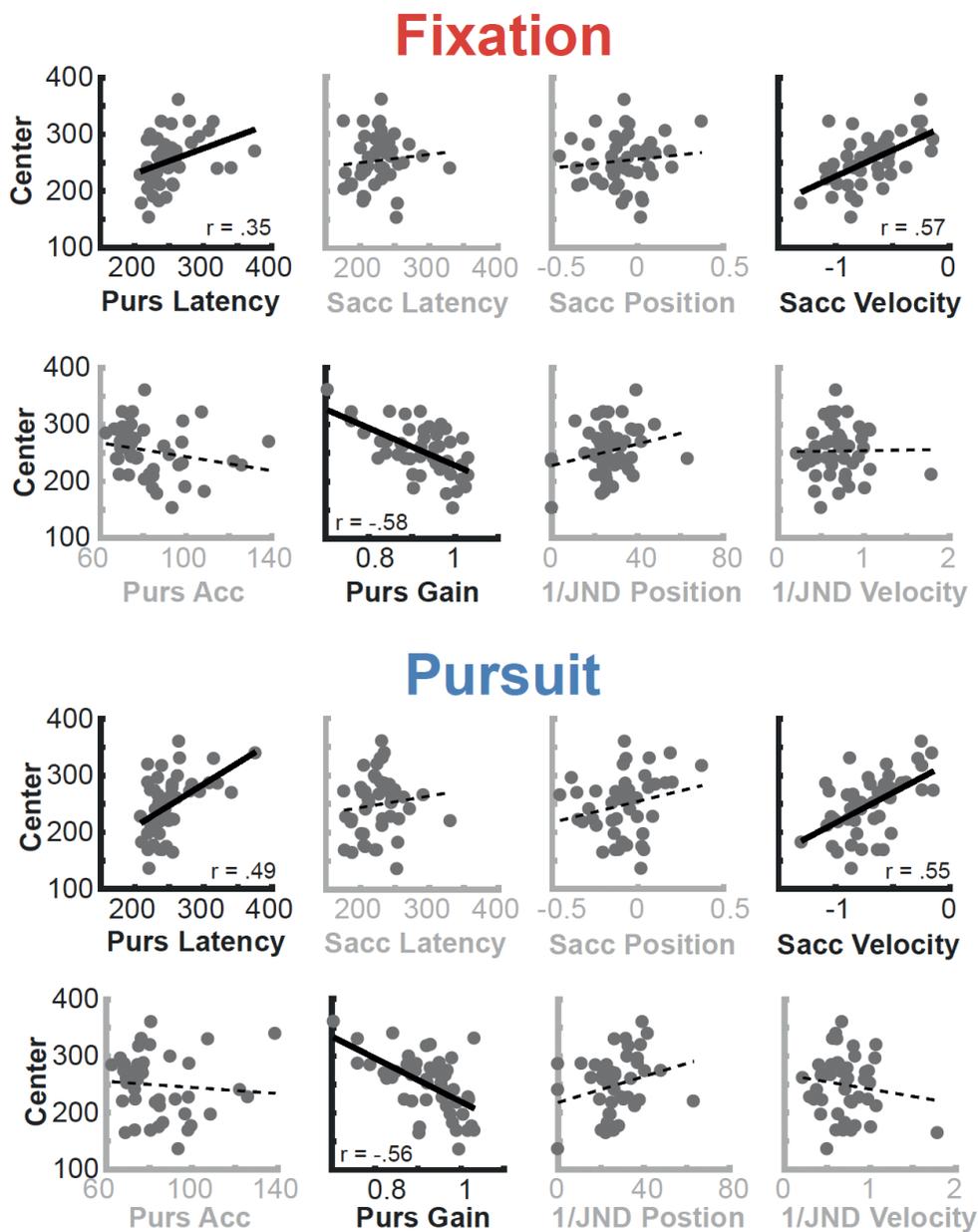
### 309 **Tracking behavior is tailored to the respective strengths of the observer**

310 To link the results of the oculomotor tasks with the parameters of the smooth zone, we  
311 computed correlations between the performance in the other oculomotor and two additional  
312 psychophysics tasks (see Method for more details) and the center of the smooth zone,  
313 separately for the fixation, as well as the steady-state pursuit condition (see Figure 6 for a  
314 selection of correlations). For the fixation condition, we observed significant correlations  
315 between the center of the smooth zone and pursuit latency ( $r(44) = .35$ ,  $p = .02$ ), the horizontal  
316 saccade error for the velocity task ( $r(44) = .57$ ,  $p <.001$ ) and pursuit gain ( $r(44) = -.58$ ,  $p <.001$ ).  
317 For the links to the smooth zone in the steady-state pursuit condition, we observed the same  
318 pattern of results: The center of the zone correlated significantly with pursuit latency ( $r(44) =$   
319  $.49$ ,  $p <.001$ ), the horizontal saccade error ( $r(44) = .55$ ,  $p <.001$ ), and pursuit gain ( $r(44) = -$   
320  $.56$ ,  $p <.001$ ). The other metrics did not show a significant correlation.

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

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

339



340

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

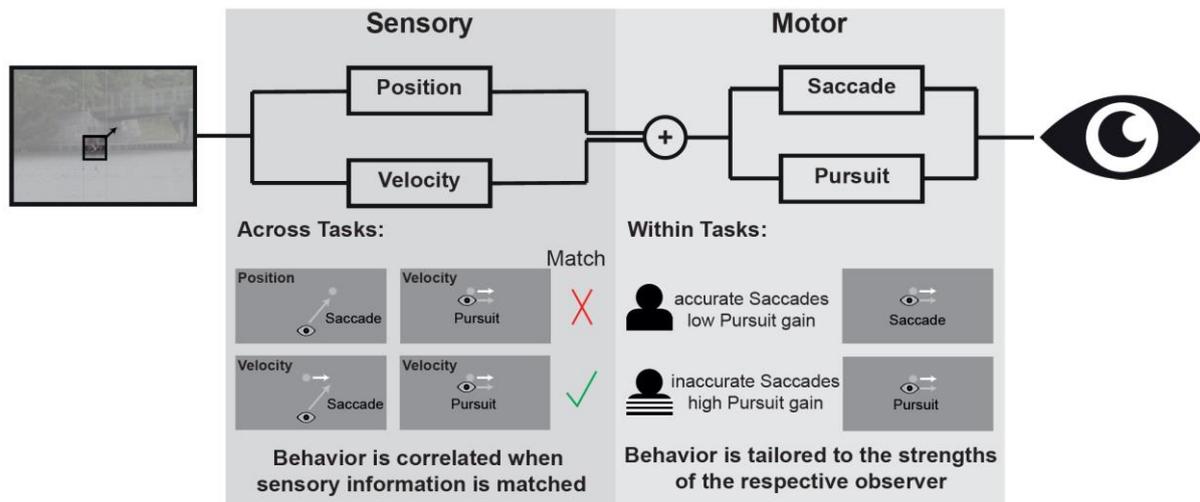
343 different metrics extracted from the other experiments. Each data point reflects the data from one  
344 observer. Lines reflect a linear regression fitted to the data; the line is solid if the correlation reached  
345 significance. **Bottom.** Same as on the top, but this time with the center of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

## 347 **Discussion**

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

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

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



379

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

389

390 Our findings have far reaching consequences. In most previous studies, the paradigms used  
 391 for saccadic or pursuit eye movements differ fundamentally with respect to the relevant sensory  
 392 information (position-related information for saccades and velocity-related information for  
 393 pursuit). Neuroimaging studies often have used these comparisons to dissociate areas in the  
 394 brain responsive to saccadic or pursuit eye movements<sup>32–34,67,68</sup>. Our results suggest that this  
 395 confound could lead to unintentionally specious interpretations, since these studies cannot  
 396 distinguish between a motor-related response (saccade vs pursuit) and a sensory-related  
 397 response (position vs velocity). In neurophysiology, some studies already tried to tackle this  
 398 problem. For example, the superior colliculus, which is mainly thought to be related to saccade  
 399 control<sup>69,70</sup>, seems to provide a more general position error signal, which is also relevant for  
 400 pursuit eye movements<sup>71,72</sup>. Moreover, the middle temporal area, mainly thought to be involved  
 401 for pursuit control<sup>73,74</sup>, seems to provide a more general velocity-related signal, since lesioning  
 402 it affects the control of pursuit and saccadic eye movements to moving, but not to stationary  
 403 targets<sup>75,76</sup>. Even the well-known omnipause neurons in the brain stem<sup>77</sup>, which are thought  
 404 to be a gating mechanism for saccadic eye movements, are involved in the control of pursuit  
 405 eye movements<sup>78</sup>. Therefore, there seems to be converging evidence on the  
 406 neurophysiological level, that responses in single brain regions are not always related to the  
 407 control of a specific type of eye movement<sup>79,80</sup>. We emphasize that the assumption that there  
 408 are still some areas selectively related to the control of saccadic and pursuit eye movements

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

416 When focusing on the coordination of saccadic and pursuit eye movements within the same  
417 task for the same type of sensory information, we noticed that observers tailored their behavior  
418 to their respective strengths (Figure 6). Importantly, there was a negative correlation between  
419 the performance of saccades to moving targets and pursuit. This rules out that these  
420 relationships can be explained by an overall better oculomotor performance (saccade and  
421 pursuit eye movements were not both more accurate across observers), or a general improved  
422 accuracy for one of the eye movements (e.g., accuracy of saccades to stationary targets was  
423 not related to the interaction). It rather shows a specific optimization of behavior within a certain  
424 task, that is based on the performance of the individual eye movements under these  
425 circumstances. With the previously established importance of shared sensory information that  
426 links saccade and pursuit control across tasks, this leaves the puzzling question of why  
427 saccadic and pursuit eye movements do not show comparable performance when tracking a  
428 moving target. We believe that this reflects a hierarchical organization in the control of  
429 oculomotor behavior. There is an underlying distinction in the processing of position- and  
430 velocity-related information<sup>23</sup>, which can explain the links in performance across tasks, but for  
431 a specific task with the same sensory information, there is a further specialization in the control  
432 of individual eye movements.

433 So how could the performance of saccadic and performance differ despite shared sensory  
434 information? The origin of variability in eye movement responses has been debated  
435 extensively for eye movements<sup>81</sup>. While some reports concluded that variability was to a large  
436 extent based on sensory information alone<sup>82,83</sup>, other studies reported an important role of  
437 motor and decision noise<sup>84-86</sup>. Either way, any form of additional motor noise, central decision  
438 noise, or differences in how the sensory signals are transformed into the respective eye  
439 movement could explain a negative correlation between saccadic and pursuit eye movement  
440 performance within the same task, despite shared sensory information. The reasons behind  
441 such a specialization could be manifold and, unfortunately, cannot be addressed with our  
442 correlational data alone. On the one hand, observers could have learned that one type of their  
443 eye movements is more accurate when tracking moving targets, so they rely on that one more  
444 frequently. On the other hand, if observers for example initially relied more on corrective

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

447 It is discussed elsewhere how position- and velocity-related sensory errors are integrated into  
448 decisions whether to perform corrective saccades <sup>22,25,51,54,56</sup>. Our results show that the  
449 decision criteria differ widely across observers. They are probably based on a life-long learning  
450 process and optimized for each individuals tracking performance. The fact that variability in  
451 behavior is more than just noise in measurements, but can be related to the strengths of the  
452 particular observer has already been suggested for the relation between eye movements and  
453 face perception. Although there is a theoretical optimum for where to look at a face, each  
454 observer has their own preferred location for where to fixate, and this correlates with their face  
455 identification performance <sup>87</sup>. In addition, people who spend more time looking at faces are  
456 also better at recognizing faces <sup>36</sup>. Related to that, a recent study showed that Super-  
457 Recognizers <sup>88</sup>, people with exceptional abilities to recognize faces, spend significantly more  
458 time looking at faces than controls and also look closer at a theoretical optimal location for face  
459 identification <sup>89</sup>. Thus, individual differences might in general reflect the strengths and  
460 weaknesses of sensory processing and motor behavior for each observer.

461 Our results provide direct empirical evidence that saccade and pursuit performance is  
462 correlated across different tasks, but only when tested with matched sensory information. This  
463 suggests that the high-level dissociation often assumed to occur between the control of  
464 saccadic and pursuit eye movements, is instead related to the difference in the relevant  
465 sensory information. Both types of eye movements are controlled by a combination of  
466 independent position- and velocity-related information <sup>23</sup>. This is quite similar to the control of  
467 other kinds of actions, for example interception <sup>90,91</sup>. When coordinating saccadic and pursuit  
468 eye movements, differences across observers revealed that they adjust their tracking behavior  
469 according to their individual strengths <sup>87</sup>. These new insights make it very clear that future  
470 studies addressing the underlying brain areas and mechanisms for motor control need a  
471 careful control for the relevant sensory stimuli and can provide exciting pathways towards a  
472 deeper understanding of the underlying neurophysiological circuits. Furthermore, the  
473 differentiation of relevant sensory information and executed eye movement might provide new  
474 insights for clinical research, for example by demonstrating that patient groups have no deficits  
475 related to a certain type of movement, but to the sensory processing relevant for the  
476 characteristics of the task <sup>92</sup>.

## 477 **Methods**

### 478 **Observer**

479 50 observers (mean age: 24.42, std = 3.86, range: 19:35) took part in the study, 37 identified  
480 as female, 13 as male. The number of participants, study design, and parts of the analysis

481 were preregistered<sup>93</sup>. All observers were naïve with respect to the purpose of the study and had  
482 normal or corrected-to-normal vision. Before the start of the experiment, they gave informed  
483 consent, and all tasks were approved by the local ethics committee (Giessen University LEK  
484 2017-0029) and were conducted in accordance with those guidelines at the ZPID in Trier.  
485 Observers were compensated with money for their effort during the experiment.

## 486 **Setup & Experimental Conditions**

487 Observers were seated at a table in a dimly illuminated room with their head positioned on a  
488 chin rest. In this position, their eyes were roughly aligned with the height of the center of a  
489 monitor (53 cm x 30 cm, 1920 x 1080 pixel, 144 Hz, BenQ, Taipeh, Taiwan) with a viewing  
490 distance of 90 cm. Under these circumstances the monitor spanned approximately 34 x 19  
491 degrees of visual angle. The tasks were programmed and controlled with Matlab 2020a  
492 (MathWorks, Natick MA) using Psychtoolbox<sup>94</sup>. Gaze was recorded from one eye with a desk-  
493 mounted eye tracker (EyeLink 1000 Plus, SR Research, Kanata, ON, Canada) at a sampling  
494 frequency of 1000 Hz. To ensure accurate recordings before each block a nine-point calibration  
495 was performed, and additional drift checks were used at the start of each trial. The drift checks  
496 allowed the observers to perform each task in a self-paced manner. To start a trial, they needed  
497 to press the space bar when looking at the central fixation.

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

## 507 **Individual Tasks**

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

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

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

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

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

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

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

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

575 **Task 7: Psychophysical judgment of position steps.** The goal of this task was to measure  
576 the perceptual ability to discriminate different target steps. In this task observers had to judge  
577 the size of a target step. Each trial again started with the target in the center of the screen for  
578 a random time between 1 and 1.5s. Afterwards the target could again step either to the left or  
579 to the right by 1.2, 1.6, 2, 2.4 or 2.8 deg. After the step the target stayed stationary and visible  
580 for a random time between 500 and 700 ms. Then observers had to judge whether the just  
581 observed target step was larger than the size of a standard target step. The standard step was  
582 2 deg. To reduce the number of trials, we didn't use a 2 AFC task, but a memorized standard,  
583 where we presented the labelled standard target 5 times in a row randomly stepping to the left  
584 or the right. The standard was shown at the beginning of the task and again before trial 10, 30,  
585 60 and 100. The standard was the average of all visible target speeds. The judgements of the  
586 different target steps allowed to compute a psychometric curve. Overall, observers completed  
587 150 trials (2 directions x 5 step sizes x 15 repetitions).

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

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

## 597 **Data Analysis & Pre-Processing**

598 Eye movement data were analyzed offline using our custom software programmed in  
599 MATLAB. Saccades were detected by using the Eyelink criteria of a speed and acceleration  
600 threshold of 30 deg/s and 4,000 deg/s<sup>2</sup>, respectively. Blinks in the data were linearly  
601 interpolated. Eye positions were filtered using a second-order Butterworth filter with a cutoff  
602 frequency of 30 Hz and afterwards we calculated the horizontal and vertical eye velocity by  
603 taking the difference between consecutive samples of the filtered position traces and  
604 multiplying it by the sampling frequency to represent it in degrees per second. Eye velocity  
605 was then again filtered by a second-order Butterworth filter with a cutoff frequency of 20 Hz.  
606 To analyze the data for leftward and right movements or leftward and rightwards steps  
607 together, we flipped the horizontal positions of the eye movement for targets that moved or  
608 stepped to the left. Pursuit onset was detected by a custom algorithm. To calculate pursuit  
609 onset, we used a velocity trace where detected saccades were linearly interpolated in the  
610 velocity trace (saccade +/- 30 ms). Then, as a baseline, the velocity and standard deviation of  
611 the eye velocity was computed from 25 ms before to 25 ms after target movement onset.  
612 Pursuit onset was the point where the eye velocity was above three times the standard  
613 deviation of the baseline and stayed from there for more than 50 ms above 30% of the target  
614 speed.

## 615 **Metrics**

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

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

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

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

662 **Statistical Analysis.** To assess the structure of the data we had two approaches: The first  
663 was looking at specific combination of correlations to test and visualize along which dimension  
664 (motor behavior or sensory signals) observers varied. We computed correlations between  
665 metrics reflecting saccadic and pursuit behavior in response to position- and velocity-related  
666 sensory information. To estimate the relative contributions of sensory signals and motor  
667 behavior, we computed the correlations for pursuit eye movements based on the same sensory  
668 input (pursuit gain in task 3 & 8) and with different sensory input (pursuit gain in task 3 & and  
669 position influence measured in task 4). We then computed the difference between the  
670 explained variance of the correlation based the same sensory input and the explained variance  
671 based on the correlation with different sensory input. This allowed us to express the relative  
672 contribution of sensory information. We took the same approach for saccadic eye movements  
673 (same sensory input: vertical error in task 1 & 2; different sensory input: horizontal error in task  
674 1 & 2). Our second approach was purely data driven, where we used a principal component  
675 analysis based on all metrics extracted for the tasks that investigated isolated eye movements.  
676 The PCA was conducted in JASP, with the settings of relevant factors with an eigenvalue  
677 above 1. Factors needed to be orthogonal and we tried to increase the interpretability of the  
678 individual factors by using the varimax setting.

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

## 682 **Exclusion Criteria**

683 Single trials were excluded from the analysis if during a single trial there were more than 500  
684 ms of missing data due to blinks or other reasons. For saccade measurements (Task 1 & 2),  
685 trials were excluded if no valid saccade was detected that had a latency between 50 and 700  
686 ms and a position error above 5 deg. For pursuit measurements (Tasks 3, 4 & 8), trials were  
687 excluded if no valid pursuit onset with a latency between 50 and 700 ms was found or the  
688 computed gain following pursuit onset was below 0.3 or above 2. Please note that for  
689 experiment 8, trials not reaching the pursuit criteria were only excluded from the oculomotor  
690 analysis, but not from the perceptual analysis. Based on these criteria across all tasks we used  
691 70.873 out of 73000 trials (97%). The proportion of valid trials across experiments was: Task  
692 1 = 92%, Task 2 = 90%, Task 3 = 95%, Task 4 = 95%, Task 5 = 99%, Task 6 = 99% Task 7 =  
693 99%, Task 8 = 98 % for psychometric data, 93 % for oculomotor behavior.

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

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

## 700 **Deviations from Preregistration**

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

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

## 719 **Author contributions**

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

## 723 **Acknowledgements**

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

## 728 **Data Availability**

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

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