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Running head: MOTION EXPECTATION IN PERCEPTION AND ANTICIPATORY PURSUIT

**Expectations about motion direction affect
perception and anticipatory smooth pursuit differently**

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Abstract

1
2 Smooth pursuit eye movements and visual motion perception rely on the integration of current
3 sensory signals with past experience. Experience shapes our expectation of current visual events
4 and can drive eye movement responses made in anticipation of a target, such as anticipatory
5 pursuit. Previous research revealed consistent effects of expectation on anticipatory pursuit—eye
6 movements follow the expected target direction or speed—and contrasting effects on motion
7 perception, but most studies considered either eye movement or perceptual responses. The
8 current study directly compared effects of direction expectation on perception and anticipatory
9 pursuit within the same direction discrimination task to investigate whether both types of
10 responses are affected similarly or differently. Observers ($n = 10$) viewed high-coherence
11 random-dot kinematograms (RDKs) moving rightward and leftward with a probability of 50, 70,
12 or 90% in a given block of trials to build up an expectation of motion direction. They were asked
13 to judge motion direction of interleaved low-coherence RDKs (0-15%). Perceptual judgements
14 were compared to changes in anticipatory pursuit eye movements as a function of probability.
15 Results show that anticipatory pursuit velocity scaled with probability and followed direction
16 expectation (attraction bias), whereas perceptual judgments were biased opposite to direction
17 expectation (repulsion bias). Control experiments suggest that the repulsion bias in perception
18 was not caused by retinal slip induced by anticipatory pursuit, or by motion adaptation. We
19 conclude that direction expectation can be processed differently for perception and anticipatory
20 pursuit.

21 **Introduction**

22 How we perceive and interact with the visual world depends not only on current visual
23 input but also on our experience with past sensory events. In Bayesian inference, this experience
24 informs a prior—one’s expectation of the probability of an event before any sensory evidence is
25 present (de Lange et al. 2018; Seriès and Seitz 2013). This study investigates how visual motion
26 priors, based on long-term experience, affect visual perception and movement, and whether these
27 two outcomes are controlled in the same way or differently by expectation. We use smooth
28 pursuit eye movements—the eyes’ continuous response to moving objects—as a model system
29 for visually-guided movement to investigate this question. Smooth pursuit eye movements are
30 closely related to the perception of visual motion (Gegenfurtner 2016; Schütz et al. 2011;
31 Spering and Montagnini 2011). They rely on the integration of current motion information with
32 priors based on experience across just a few trials or across a longer-term context (Darlington et
33 al. 2017; Deravet et al. 2018; Yang et al. 2012). Moreover, smooth pursuit can be triggered by the
34 expectation of a certain motion direction even before the object’s motion onset, a phenomenon
35 known as anticipatory smooth pursuit (Kowler et al. 1984, 2019).

36 Previous research has revealed highly consistent effects of expectation on pursuit but
37 contrasting effects on motion perception. For example, anticipatory pursuit can be triggered
38 when observers repeatedly view stimuli moving into the same direction (Kowler 1989; Kowler et
39 al. 2019). The eyes are then attracted to the expected motion direction prior to the onset of the
40 stimulus (attraction bias in direction). These responses are not purely habitual but finely tuned to
41 the strength of expectation (Damasse et al. 2018; Jarrett and Barnes 2002; Santos and Kowler
42 2017). Congruently, anticipatory pursuit velocity is proportional to the average velocity of the
43 target across previous trials (attraction bias in speed), and strongly affected by events in the

44 previous two trials (Maus et al. 2015). Furthermore, Bayesian integration models have been used
45 to describe how priors would lead to attraction effects in visually-guided pursuit when combined
46 with noisy visual motion signals (Behling and Lisberger 2020; Darlington et al. 2017; Deravet et
47 al. 2018).

48 By contrast, perceptual studies have found evidence for both an attraction bias as well as
49 for responses to be repelled away from the expected direction (repulsion bias; Jazayeri and
50 Movshon 2007). In studies reporting attraction biases, estimates of direction, velocity, or
51 orientation in a current trial are affected by events in previous trials such that an observer's
52 perception would be biased in line with the motion information observed in previous trials. Such
53 biases can build up quickly, within a few trials (Alais et al. 2017; Cicchini et al. 2018) or can be
54 based on implicitly learning the statistical properties of a stimulus environment over many trials
55 (Chalk et al. 2010; Kok et al. 2013; Seriès and Seitz 2013), as described by Bayesian integration
56 models. Perceptual repulsion biases have been observed across different visual tasks and
57 features. In a speed estimation task in which observers had to judge whether the speed in the
58 current trial was faster or slower than the average speed across all previous trials, observers
59 tended to overestimate a current target's velocity when the average velocity across previous trials
60 was slow and vice versa for fast velocity (Maus et al. 2015). Similar repulsion biases have been
61 found in studies in which observers had to adjust the orientation of a test stimulus relative to an
62 inducer stimulus, when both stimulus orientations differed by more than 60° between the
63 previous and current trial (Fritsche et al. 2020). In this scenario, observers' adjustment responses
64 were sometimes repelled away from the previous trial's stimulus orientation. In sum, expectation
65 built across different timescales can result in a perceptual bias either in the same direction as the
66 cue, prompt, or adaptor (attraction bias), or in the opposite direction (repulsion bias).

67 The current study directly compared effects of direction expectation on perception and
68 anticipatory pursuit within the same trials to investigate whether both types of responses are
69 affected similarly or differently, and how they interact. On one hand, attraction biases are
70 commonly found in pursuit, and in most perceptual studies that did not use adjustment tasks or
71 reference comparisons. On the other hand, one study that directly compared velocity expectation
72 effects reported opposite biases in speed discrimination and anticipatory pursuit (Maus et al.
73 2015). Overall, it remains unclear whether motion priors affect perception and pursuit similarly
74 or differently. We introduced different probabilities of motion direction in the current study,
75 leading to an implicit expectation bias for future motion direction based on previous trial history.
76 This manipulation allows us to investigate the effect of a general motion prior on perception and
77 pursuit. In the following, we refer to effects of expectation as the behavior triggered by
78 manipulations of this statistical bias.

79

80

Methods

81 All three experiments were similar in terms of procedure and analyses. Experiment 1 was
82 the main experiment, and the purpose was to compare the effect of expectation on motion
83 direction discrimination and anticipatory pursuit. Control experiments 2 and 3 investigated
84 alternative explanations for findings obtained in Experiment 1, testing interactions between
85 anticipatory pursuit and perception, and effects of stimulus features, respectively. General
86 methods are described for experiment 1. Deviations in stimuli and procedures for control
87 experiments are briefly described in Results.

88

89 *Observers*

90 We recruited 10 observers (age $M = 26.20$, $std = 5.41$ years; six females) with normal or
91 corrected-to-normal visual acuity (at least 20/20 as assessed using an Early Treatment Diabetic
92 Retinopathy Study chart) and no history of ophthalmologic, neurologic, or psychiatric disease.
93 All observers participated in experiment 1, eight of these observers (age $M = 27.38$, $std = 5.40$
94 years; four females) also participated in experiment 2, and nine (age $M = 26.56$, $std = 5.61$ years;
95 six females) also participated in experiment 3. The sample size is comparable to previous studies
96 ($n = 9$ in Maus et al. 2015; $n = 8$ in Santos et al. 2012; $n = 6$ in Santos and Kowler 2017). The
97 University of British Columbia Behavioral Research Ethics Board approved all experimental
98 procedures, and all observers participated after giving written informed consent. Observers
99 received \$35 Canadian Dollars remuneration for participation per experiment.

100

101 *Visual stimuli and setup*

102 Stimuli were random dot kinematograms (RDKs) presented in a static aperture of 20°
103 diameter centered in the middle of the screen. Each RDK consisted of about 470 (density 1.5
104 dot/deg²) uniformly distributed white dots (98 cd/m²) on a grey background (22 cd/m²). Each dot
105 (diameter 0.14°) moved at a constant speed of $10^\circ/s$. The dots were labeled as signal or noise
106 dots. Labels were updated and randomly reassigned every four frames (about 47 milliseconds,
107 ms). Signal dots always moved in the global motion direction of the RDK (left or right), while
108 each noise dot moved in a random direction other than the signal direction with unlimited
109 lifetime. When a dot moved out of the aperture, it reentered from the opposite side of the
110 aperture. The coherence of the RDK was defined as the proportion of signal dots (0-100%).

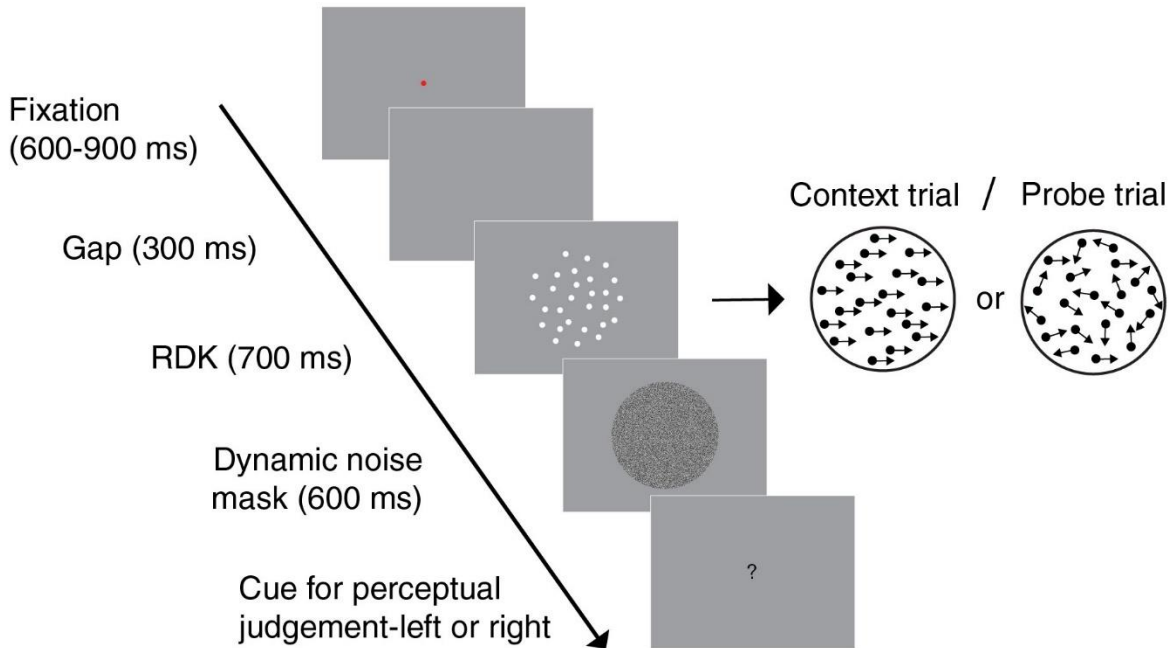
111 Observers were seated in a dimly-lit room and viewed all stimuli on a gamma-corrected
112 39 cm \times 29 cm CRT monitor (ViewSonic G255f; resolution 1280 \times 1024 pixel; refresh rate 85

113 Hz). The viewing distance was 55 cm. Each observer's head was stabilized using a chin-and-
114 forehead-rest. Stimuli and procedure were programmed in MATLAB R2018b (The MathWorks
115 Inc., Natick, MA) and Psychtoolbox Version 3.0.12 (Brainard 1997; Kleiner et al. 2007; Pelli
116 1997).

117

118 *Procedure and design*

119 **Figure 1** shows the trial timeline in experiment 1. Observers were asked to fixate the
120 center of the screen when the red fixation point was on for 600-900 ms. Fixation was monitored
121 online: if eye position was further than 2° from the center of the fixation point, the fixation point
122 turned white and the countdown of fixation duration was paused until the observer regained
123 accurate fixation. A blank screen (gap; 300 ms) was shown to help induce anticipatory pursuit
124 (Krauzlis and Miles 1996). Observers were then asked to smoothly follow the global motion of
125 the RDK (700 ms) with their eyes. A dynamic white-noise mask with luminance noise randomly
126 assigned pixel by pixel (luminance range within 7 cd/m^2 to 46 cd/m^2) was shown after RDK
127 offset for 600 ms to reduce potential motion aftereffects. At the end of each trial, they were asked
128 to report whether it moved left or right using the “left” or “right” arrow keys on the computer
129 keyboard.



131 **Figure 1.** Trial timeline in experiment 1. A fixation point was shown for 600-900 ms, followed
132 by a blank screen for 300 ms, and the RDK for 700 ms. A dynamic white-noise mask was
133 presented after the RDK for 600 ms. Two types of trials were presented: context trials with
134 highest-coherence RDKs, and probe trials with low-coherence RDKs. The stimuli's relative size
135 and contrast are increased for presentation purposes.

136
137 In each block, two types of trials were shown: 500 context trials containing non-
138 ambiguous motion direction (100% coherence) were randomly interleaved with 182 probe trials
139 containing ambiguous motion (0, 5, 10 or 15% coherence). The purpose of the context trials was
140 to build up an expectation of motion direction in a given block. In each of three blocks of trials,
141 presented in random order, we introduced different probabilities of motion direction in context
142 trials, either 50%, 70%, and 90% probability of rightward or leftward motion. Blocks with higher
143 probability of rightward and leftward motion were presented in different sessions; half of our
144 sample of observers ($n = 5$) saw only higher probabilities of rightward motion, the other half saw
145 only higher probabilities of leftward motion. The experiment was split up that way to reduce
146 workload for each observer, because each block of trials took 60 minutes to complete for a total
147 of 3 hours per observer. The first 50 trials in each block were always context trials. The purpose

148 of the probe trials was to measure the effect of expectation on perception of motion direction,
149 which would be prominent when visual input provided little evidence. In order to fairly compare
150 perception and oculomotor anticipation we also analyzed anticipatory pursuit in probe trials only.
151 For all observers, probe trials consisted of equal numbers of leftward/rightward trials.

152

153 *Eye movement recording and analysis*

154 In all three experiments, the position of the right eye was recorded using a video-based
155 eye tracker at a sampling rate of 1000 Hz (EyeLink 1000 desk-mounted, SR Research Ltd.,
156 Kanata, ON, Canada). Eye movements were then analyzed offline using custom-made MATLAB
157 functions. Eye position, velocity, and acceleration data were filtered with a second-order
158 Butterworth filter (cutoff frequencies of 15 Hz for position and 30 Hz for velocity and
159 acceleration). Saccades were detected based on an acceleration criterion: the acceleration trace
160 was segmented by zero-crossing points, and peak acceleration within each segment was
161 calculated. If at least two consecutive segments had absolute peak acceleration larger than
162 $400^\circ/\text{s}^2$, these segments were defined as saccades. An acceleration threshold was used to
163 accurately detect saccades of small amplitude and velocity during the anticipatory pursuit phase.
164 Saccade detection was confirmed by visual inspection of the velocity traces in each trial.
165 Saccades were then excluded from the analysis of smooth pursuit. Following previous studies
166 (Maus et al. 2015; Santos and Kowler 2017; Watamaniuk et al. 2017), anticipatory pursuit
167 velocity was defined as the average horizontal eye velocity during the time window from 50 ms
168 before to 50 ms after RDK onset. We also analyzed eye velocity gain (eye velocity relative to
169 target velocity) during visually-guided pursuit, calculated during the time window from 300 to
170 600 ms after target onset. Trials with blinks during RDK presentation were manually labeled as

171 invalid and excluded (1% across observers in experiment 1, 0.5% in experiment 2, and 0.7% in
172 experiment 3). Leftward direction is negative by convention.

173

174 *Perceptual response analysis*

175 We did not observe systematic differences between the effects of rightward and leftward
176 motion probability on the magnitude of anticipatory pursuit (experiment 1: $t(4) = 0.76$, $p = .49$,
177 Cohen's $d = 0.94$) or perceptual bias (experiment 1: $t(4) = 1.07$, $p = .34$, Cohen's $d = 0.83$) and
178 therefore merged data for different motion directions, presenting data as if higher probabilities of
179 rightward motion were presented. Under each probability condition for each observer, we fitted a
180 psychometric curve using the logistic function as shown below:

181

$$P(\text{perceiving right}) = (1 - \lambda) \frac{1}{1 + e^{-\beta(x-\alpha)}}$$

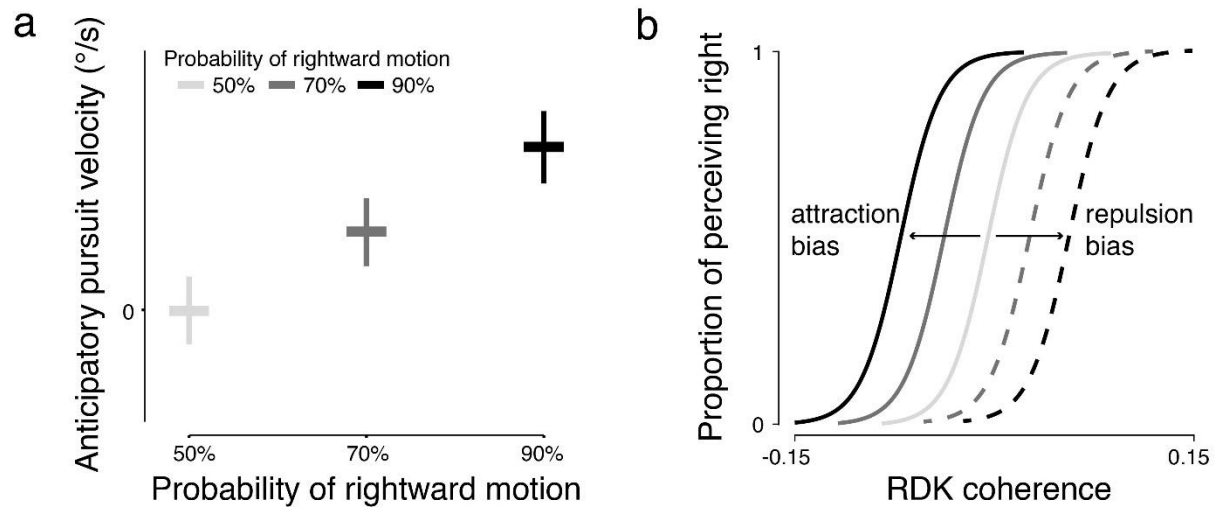
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183 Specifically, x is the signed motion coherence of RDK (negative for leftward motion), α
184 is the point of subjective equality (PSE) where observers reported both motion directions equally
185 often (50% of the time), β is the slope representing the sensitivity of perception, and λ is the
186 lapse rate (restricted to below 0.1 when fitting). In this study, a shift of the PSE across
187 probability conditions would indicate a perceptual bias. A shift to the left indicates a perceptual
188 attraction bias (i.e. with direction judgments being attracted toward the direction expectation of
189 rightwards), and a shift to the right indicates a repulsion bias. A change in slope across
190 probability conditions would indicate a change in sensitivity of perceptual judgments, where a
191 steeper slope corresponds to higher sensitivity. Curve fitting was performed using the Palamedes
192 toolbox version 1.9.0 in MATLAB (Prins and Kingdom 2018).

193

194 *Hypotheses and statistical analysis*

195 In experiment 1, we aimed to test the following hypotheses. First, anticipatory pursuit is
196 affected by direction expectation: the velocity of anticipatory pursuit scales positively with the
197 target's direction probability (attraction bias); a higher probability of rightward motion will lead
198 to a higher velocity in anticipatory pursuit (**Fig. 2a**). Second, direction perception is affected by
199 direction expectation: observers preferentially perceive the expected motion direction (attraction
200 bias; **Fig. 2b**). Alternatively, perception could be biased away from the expected direction
201 (repulsion bias; **Fig. 2b**), as has sometimes been reported in the literature. We further examined
202 if expectation affected slope to investigate whether different prior probabilities might result in
203 differences in sensitivity. To examine the expected effects of probability on anticipatory pursuit
204 velocity, the magnitude of perceptual bias (shift of the PSE), and the sensitivity of perception
205 (slope), we used one-way repeated-measures analyses of variance (ANOVA) with *probability* as
206 factor. In addition, to examine whether anticipatory pursuit velocity and the strength of any
207 potential perceptual bias were correlated across conditions and observers, we fitted a linear
208 mixed-effects model of PSE with *probability* and *anticipatory pursuit velocity* as fixed effects,
209 and individual intercept as the random effect (formula: $\text{PSE} \sim \text{anticipatory pursuit velocity} +$
210 $\text{probability} + (1 \mid \text{observer})$). Finally, we also examined the potential link between visually-
211 guided pursuit and perception, and effects of probability on the velocity gain of visually-guided
212 pursuit. Experiments 2 and 3 investigated alternative explanations of findings obtained in
213 experiment 1. Their logic and underlying hypotheses are described in Results.



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Figure 2. Hypotheses for (a) attraction bias in anticipatory pursuit velocity and (b) attraction or repulsion bias in perception. (a) Anticipatory pursuit velocity increases with increasing probability of rightward motion in each block, reflecting an attraction bias. (b) The perceptual bias is reflected by a shift of the PSE at higher probabilities (70% and 90%) when compared to the 50% probability condition; a leftward shift (solid lines) indicates an attraction bias, a rightward shift (dashed lines) indicates repulsion bias. Negative value of RDK coherence indicates that the global motion direction is left.

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Across experiments, we report generalized eta-squared (η_g^2) as the effect size in one-way ANOVAs, and partial eta-squared (η_p^2) in two-way ANOVAs. For all experiments, we also report mean and 95% confidence interval (CI) of anticipatory pursuit velocity, and PSE from 1000 bootstrap simulations to supplement statistical hypothesis testing and provide quantitative estimates of the variability of sample estimates. The statistical tests were conducted in R Version 3.6.0 (package "lme4", Bates et al. 2015; package "ez", Lawrence 2016; R Core Team 2019) and MATLAB R2020a.

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Results

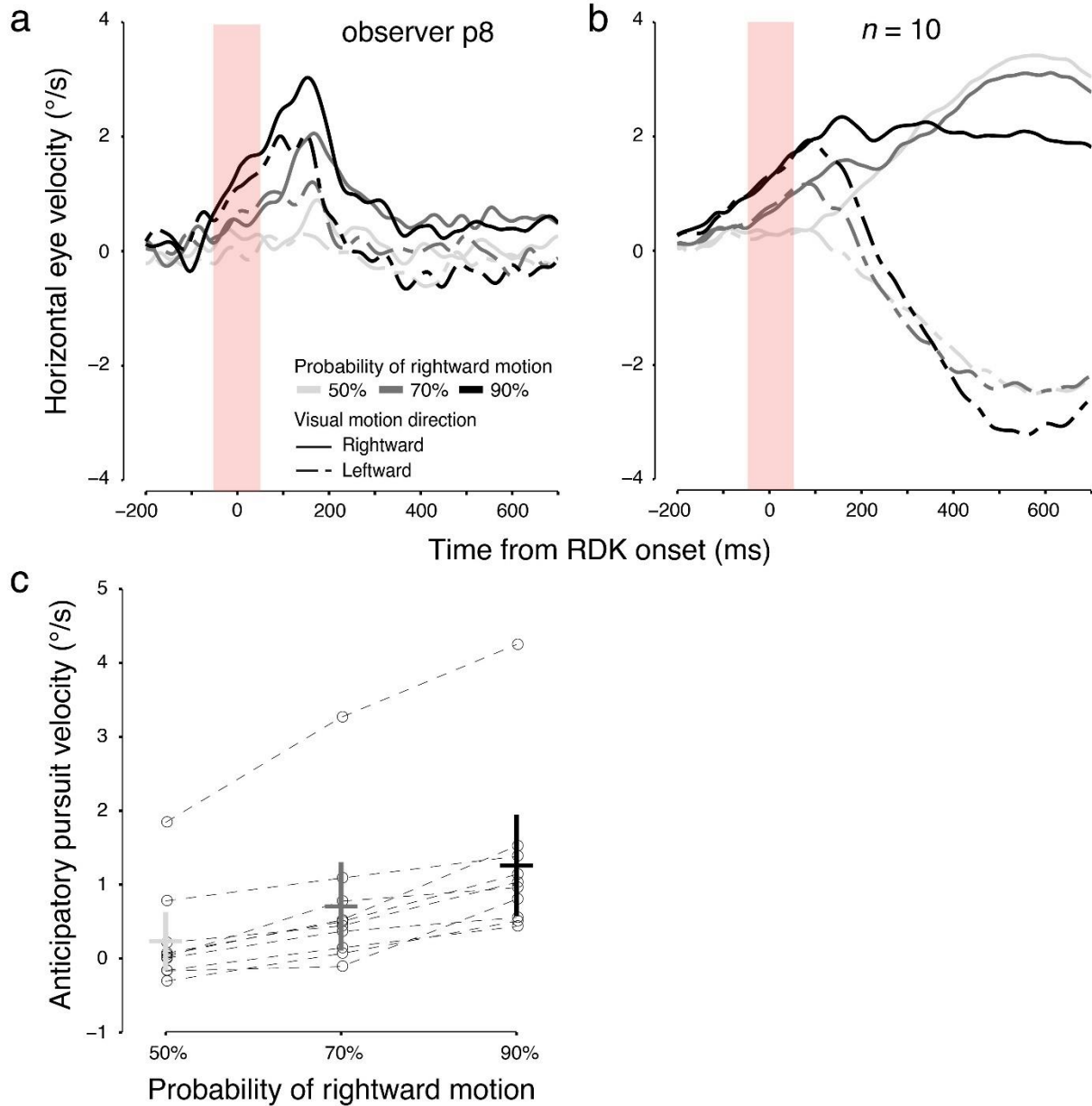
Experiment 1

Evidence for attraction bias in anticipatory pursuit

235

Across observers and trials, we found that the velocity of the anticipatory pursuit

236 response scaled positively with the probability of a given motion direction. **Figure 3a** shows an
237 example of individual eye velocity traces and **Figure 3b** shows group-averaged eye velocity
238 traces in probe trials, indicating that anticipatory pursuit velocity increases with increasing
239 probability of rightward motion. These observations were confirmed by a significant main effect
240 of *probability* on anticipatory pursuit velocity (**Fig. 3c**), $F(2,18) = 28.19, p = 2.84 \times 10^{-6}, \eta_g^2 = .19$.
241 As a complementary method to these statistics, the bootstrapped mean and 95% CI of
242 anticipatory pursuit velocity confirmed our findings (50%: $0.24 \pm 0.01^\circ/\text{s}$; 70%: $0.70 \pm 0.01^\circ/\text{s}$;
243 90%: $1.26 \pm 0.01^\circ/\text{s}$).



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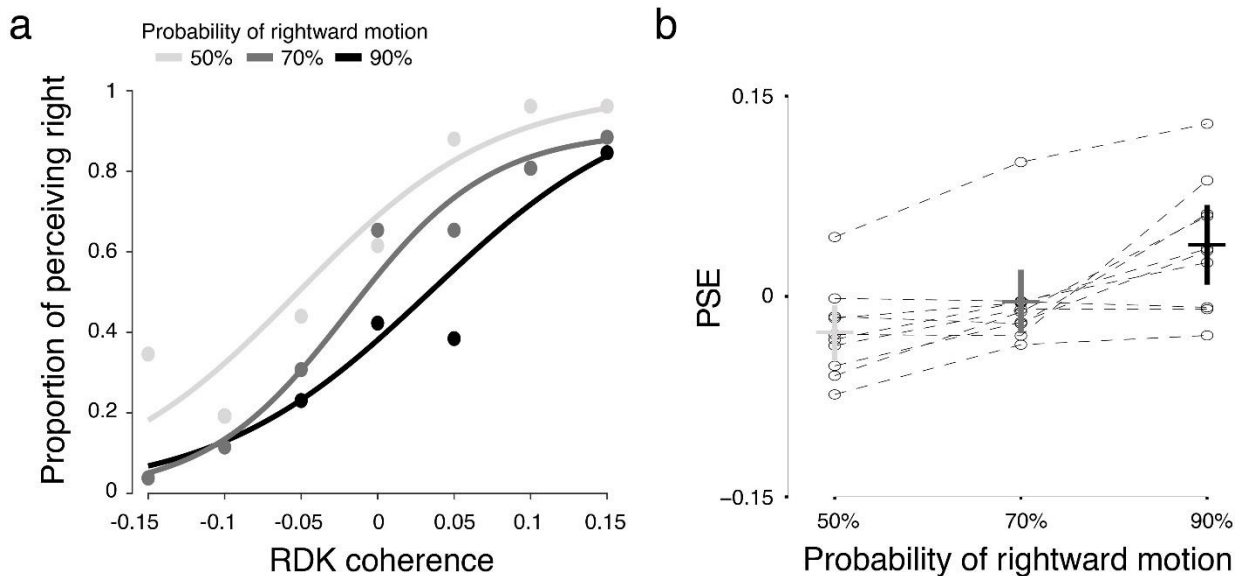
246 **Figure 3.** (a) Example trial-average horizontal eye velocity traces in probe trials (leftward or
247 rightward motion direction as indicated by line type) for different probability conditions
248 (indicated by line color) for one representative observer in experiment 1. The red shaded area
249 indicates the analysis window for anticipatory pursuit. This particular observer had little visually-
250 guided pursuit in probe trials. (b) Group-average horizontal eye velocity traces in probe trials for
251 different probability conditions in experiment 1 for $n = 10$. Line types in panels a and b denote
252 motion direction and probability of rightward motion. (c) Horizontal anticipatory pursuit velocity
253 in experiment 1 averaged across the time interval indicated as shaded area in panel a. Horizontal
254 bars indicate the mean anticipatory pursuit velocity across observers, and vertical bars indicate
255 the 95% CI. The circles indicate the mean anticipatory pursuit velocity of individual observers,
256 connected by dashed lines across probability conditions. Results were the same even if excluding
257 the one outlier who had relatively high anticipatory pursuit velocity.

258

259 *Evidence for repulsion bias in direction perception*

260 Perceptual results are incongruent with what we observed for anticipatory pursuit. We
261 found a systematic rightward shift in the PSE at the individual observer level (**Fig. 4a**) as well as
262 across observers (**Fig. 4b**), indicating a perceptual bias away from the high-probability motion
263 direction. When rightward trials had a higher probability in context trials, observers tended to
264 perceive leftward direction more often in probe trials. These observations were confirmed by a
265 significant main effect of *probability* on the PSE (**Fig. 4b**), $F(2,18) = 20.36, p = 2.39 \times 10^{-5}, \eta_g^2$
266 $= .34$. The bootstrapped mean and 95% CI of the PSE confirmed these statistical results (50%: -
267 $0.02 \pm .002$; 70%: 0.0003 ± 0.002 ; 90%: 0.04 ± 0.0002). We did not observe any significant
268 effects of *probability* on slope ($F(2,18) = 0.78, p = .48, \eta_g^2 = .02$), indicating that sensitivity did
269 not change across probability conditions. The bootstrapped mean and 95% CI of slope were
270 31.31 ± 5.26 for 50%, 31.72 ± 2.14 for 70%, and 29.87 ± 3.93 for 90%.

271



272

273 **Figure 4.** (a) Example psychometric curves from the same individual observer shown in Fig. 3a.
274 Negative coherence represents leftward direction. (b) PSE in experiment 1 ($n = 10$).

275
276 We did not find any dependencies between PSE and anticipatory pursuit velocity in
277 addition to the fact that they both changed with probability. The fixed effect of anticipatory
278 pursuit velocity in the linear mixed-effects model of PSE (PSE \sim anticipatory pursuit velocity +
279 probability + (1 | observer)) was not significant (estimate \pm std = -0.002 ± 0.01 , $t(20.31) = -0.16$,
280 $p = .87$), and only the fixed effect of probability was significant (estimate \pm std = 0.002 ± 0.0004 ,
281 $t(30.00) = 4.60$, $p = 7.12 \times 10^{-5}$).

282 Taken together, our results point at a differential effect of motion direction probability on
283 anticipatory pursuit, reflecting an attraction bias, and direction perception, reflecting a repulsion
284 bias. To explore this further, we next examined the potential link between visually-guided pursuit
285 and perception, and analyzed the effect of probability on visually-guided pursuit velocity gain.

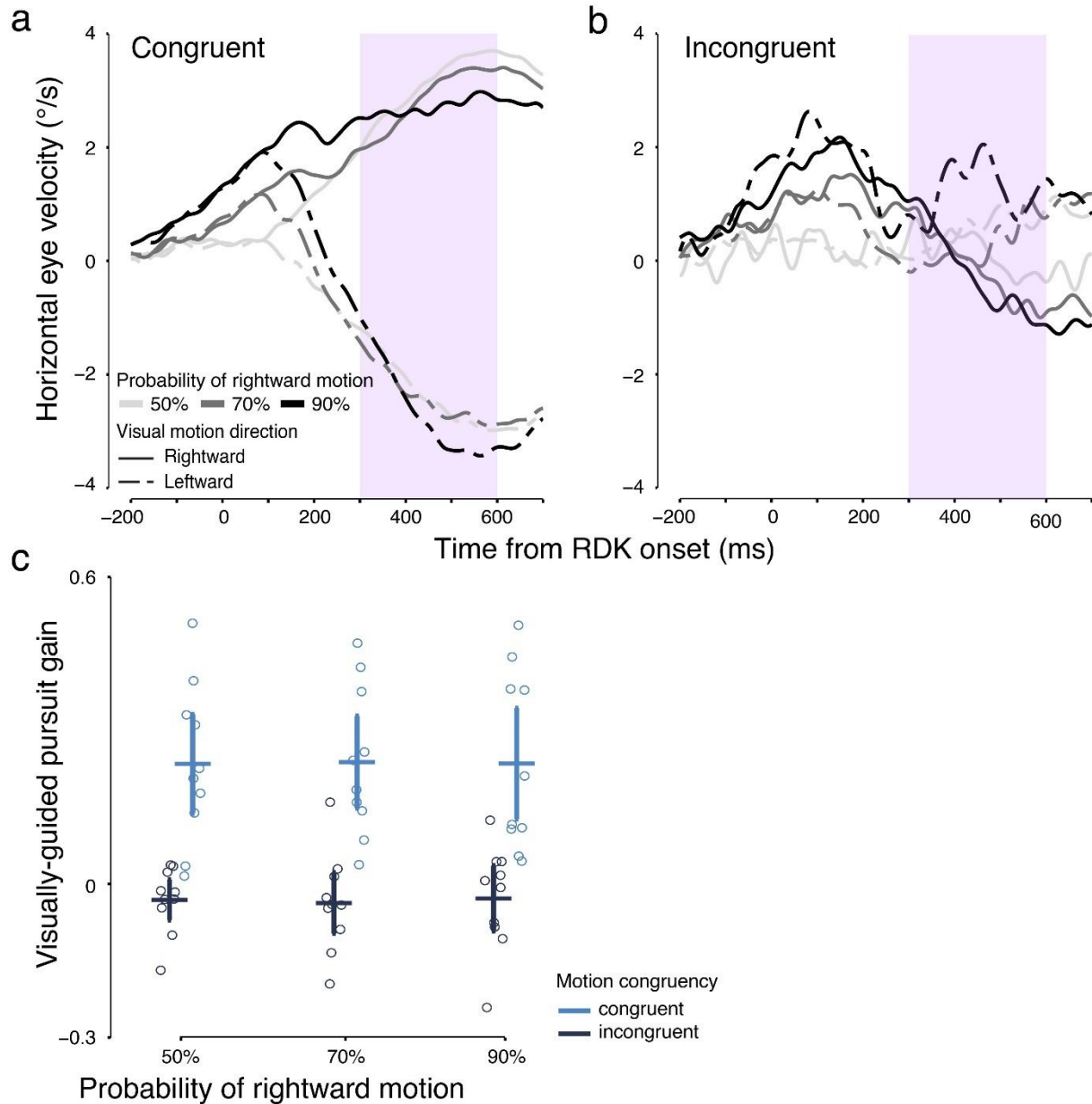
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287 *Visually-guided pursuit is aligned with direction perception*

288 Whereas anticipatory pursuit is mostly driven by expectation, visually-guided pursuit is
289 tuned to the visual properties of the target and is known to strongly covary with motion
290 perception (Spering and Montagnini 2011). Previous research has demonstrated that smooth
291 pursuit can be elicited by perceived illusory motion rather than by physical motion (Madelain
292 and Krauzlis 2003; Montagnini et al. 2006). Therefore, visually-guided pursuit could follow
293 different result patterns from anticipatory pursuit and be more aligned with perception.

294 Here we investigated whether visually-guided pursuit was more in line with an attraction
295 bias (as in anticipatory pursuit) or followed a repulsion bias (as in perception). We compared eye
296 velocity gain in conditions in which the perceptual judgment corresponded to the physical
297 motion direction (congruent) with conditions where perceptual judgments went in the opposite
298 direction to the physical motion (incongruent). **Figure 5** shows average velocity traces in probe

299 trials across all observers for congruent (**Fig. 5a**) versus incongruent trials (**Fig. 5b**). Note that
300 this categorization of congruency is agnostic on whether perception followed the expected
301 motion direction or the opposite one and merely reflects how closely perception matched
302 physical target motion. Whereas late visually-guided pursuit followed the visual motion direction
303 in congruent trials (shaded areas in **Fig. 5a**), pursuit followed visual motion direction less in
304 incongruent trials (**Fig. 5b**) with a tendency to be directed into the opposite (perceived) direction,
305 resulting in smaller or negative gains. This is confirmed by a significant main effect of
306 *congruency* on velocity gain (**Fig. 5c**; $F(1,9) = 20.65, p = .001, \eta_p^2 = 0.70$). The main effect of
307 *probability* ($F(2,18) = 0.049, p = .953, \eta_p^2 = .005$) or the *congruency* \times *probability* interaction
308 ($F(2,18) = 0.051, p = .950, \eta_p^2 = .006$) were not significant. This difference in visually-guided
309 pursuit between congruent and incongruent conditions persisted across different levels of motion
310 coherence (not shown).

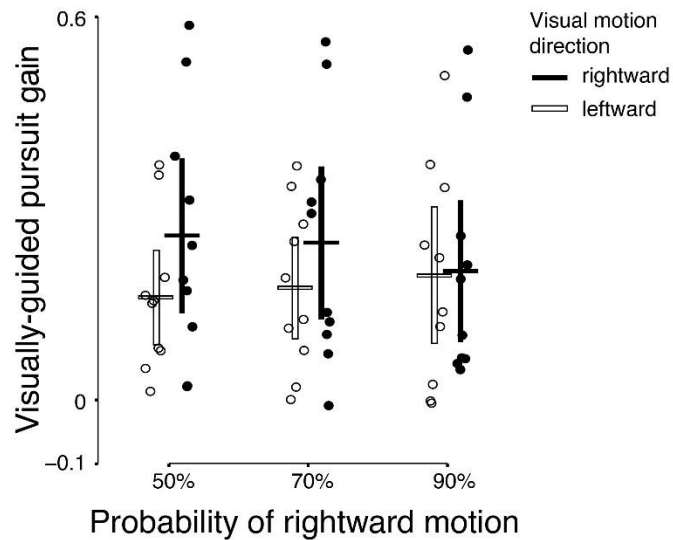


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312 **Figure 5.** (a) Group-averaged ($n = 10$) horizontal eye velocity traces in probe trials in which
313 visual motion directions were congruent (3967 trials total) with perceived directions across
314 different probability conditions in experiment 1. The purple shaded area indicates the analysis
315 window for late-phase pursuit; an early cutoff was applied to reduce the effect of anticipatory
316 deceleration before the end of each trial (at 700 ms). (b) Group-averaged ($n = 10$) horizontal eye
317 velocity traces in probe trials in which visual motion directions were incongruent (649 trials
318 total) with perceived directions across different probability conditions in experiment 1. (c) Late-
319 phase visually-guided pursuit gain in probe trials grouped by motion congruency across different
320 probability conditions in experiment 1 ($n = 10$). Higher gain indicates that the eyes follow the
321 visual motion better, and negative gain indicates that the eyes are moving in the opposite
322 direction to the visual motion direction. Horizontal bars indicate the mean visually-guided
323 pursuit gain across observers, and vertical bars indicate the 95% CI. The circles indicate the

324 mean visually-guided pursuit gain of individual observers.
325

326 Further, we examined if expectation had an effect on visually-guided pursuit, by
327 analyzing the effect of *probability* on visually-guided pursuit gain. Late-phase visually-guided
328 pursuit in rightward probe trials seemed to have lower velocity in blocks with higher probability
329 of rightward motion (see **Fig. 3b**, can also be seen in **Fig. 5a** with majority of probe trials). Since
330 direction expectation might affect visually-guided smooth pursuit differently for rightward and
331 leftward motion trials, we included *visual motion direction* as a second factor in the two-way
332 ANOVA on visually-guided pursuit gain. If the observed decrease in eye velocity with increased
333 probability across blocks was true, a significant main effect of *probability* and possibly a
334 significant interaction effect of *probability* \times *visual motion direction* could be observed.
335 However, the interaction effect ($F(2,18) = 1.54, p = .24, \eta_p^2 = .15$; **Fig. 6**), the main effect of
336 *probability* ($F(2,18) = 0.58, p = .57, \eta_p^2 = .06$), or the main effect of *visual motion direction*
337 ($F(1,9) = 1.87, p = .20, \eta_p^2 = .17$) were non-significant. This could be due to the large individual
338 variability—some observers had little visually-guided pursuit in probe trials across probability
339 conditions (gain close to zero), likely due to the low RDK coherence.



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Figure 6. Late-phase visually-guided pursuit gain in probe trials grouped by visual motion direction across different probability conditions in experiment 1 ($n = 10$).

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Notwithstanding a lack of evidence for expectation effects on visually-guided pursuit, this part of the pursuit response was more aligned with perception than anticipatory pursuit. This finding indicates that late-phase pursuit is driven by signals that are more coherent with those signals driving perceptual judgments than those driving anticipatory pursuit.

350 Experiment 2

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To further explore the mechanisms underlying the dissociation between expectation effects on anticipatory pursuit and perception, we conducted two control experiments. One potential problem with our paradigm might be that anticipatory pursuit during the earliest phase of the presentation of the low-coherence RDK elicits retinal image motion in the opposite direction than the expected one. This motion signal could have informed the perceptual choice, explaining the repulsion bias. In experiment 2, we therefore tested whether the observed perceptual bias was affected by this negative retinal motion signal by manipulating anticipatory pursuit magnitude. To reduce anticipatory pursuit, we showed the fixation point until RDK onset,

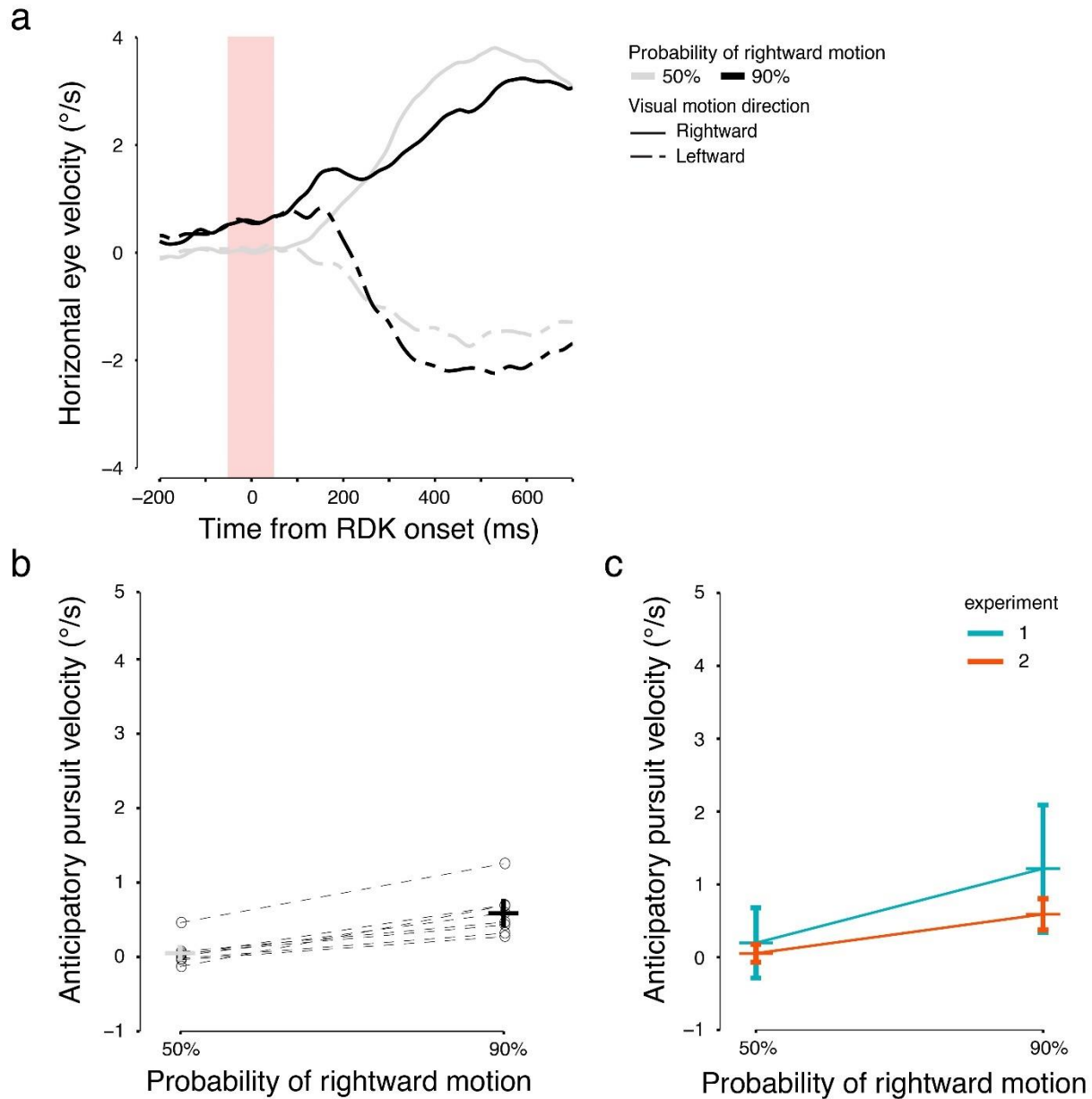
359 omitting the 300-ms gap introduced in Experiment 1, and instructed observers to maintain
360 fixation until the stimulus started moving. Each observer completed two blocks (50% and 90%
361 probability of rightward motion). All other procedures were the same as in experiment 1.

362 To confirm that anticipatory pursuit was reduced in Experiment 2 as compared to
363 Experiment 1, we performed a two-way repeated measures ANOVA with *experiment* and
364 *probability* as factors. An *experiment* × *probability* interaction effect on anticipatory pursuit
365 velocity would indicate a change in anticipatory pursuit magnitude from one experiment to the
366 other. If anticipatory pursuit induced the perceptual bias, reduced anticipatory pursuit magnitude
367 in Experiment 2 should result in a smaller perceptual bias. This interpretation would be
368 supported by a significant *experiment* × *probability* interaction effect on PSE.

369

370 *Anticipatory pursuit was significantly reduced with prolonged fixation*

371 The experimental manipulation of prolonging fixation in Experiment 2 yielded the
372 expected reduction in anticipatory pursuit velocity from $1.26 \pm 1.11^\circ/\text{s}$ ($M \pm \text{std}$) in Experiment 1
373 to $0.57 \pm 0.30^\circ/\text{s}$ in Experiment 2 at the highest probability of rightward motion (**Fig. 7a, b**).
374 This observation was confirmed by a significant *experiment* × *probability* interaction (**Fig. 7c**;
375 $F(1,7) = 7.20, p = .03, \eta_p^2 = .51$). Despite lower overall velocity, higher probability of rightward
376 motion continued to induce higher anticipatory pursuit velocity, reflected in a main effect of
377 *probability* ($F(1,7) = 37.81, p = .0005, \eta_p^2 = .84$). Congruently, the bootstrapped mean and 95%
378 CI of anticipatory pursuit velocity in experiment 2 were $.05 \pm .01^\circ/\text{s}$ for 50% and $.59 \pm .01^\circ/\text{s}$ for
379 90%. The main effect of *experiment* was not significant ($F(1,7) = 2.06, p = .19, \eta_p^2 = .23$).



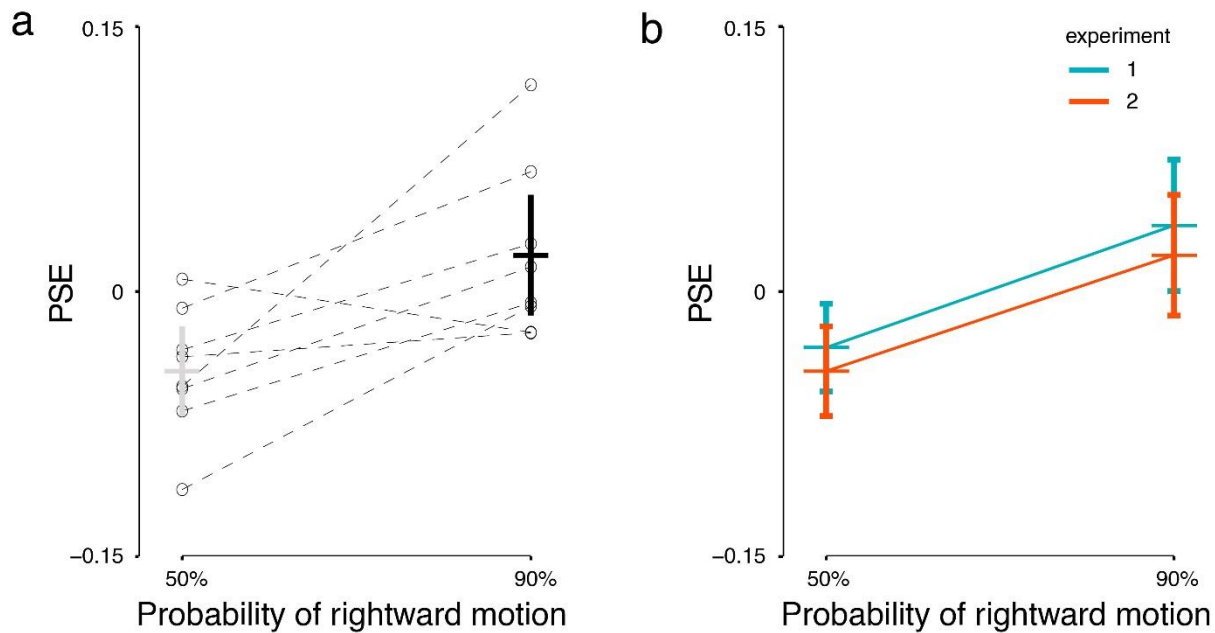
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Figure 7. (a) The group-averaged ($n = 8$) horizontal eye velocity traces in probe trials across different probability conditions in experiment 2. (b) Horizontal anticipatory pursuit velocity in experiment 2 ($n = 8$). (c) The comparison of anticipatory pursuit velocity between experiment 1 and 2. The horizontal bars show the mean across observers ($n = 8$ for both experiments), and the error bars show the 95% CI.

388 *Persistent perceptual bias despite reduced anticipatory pursuit velocity*

389 Despite the successful reduction in anticipatory pursuit velocity, we observed the same
390 repulsion bias (rightward shift of the PSE; **Fig. 8a**) in perceptual judgments in Experiment 2.

391 This observation was confirmed by a significant main effect of *probability*, $F(1,7) = 22.91$, p
392 $= .002$, $\eta_p^2 = .77$, and a lack of *experiment* \times *probability* interaction (**Fig. 8b**; $F(1,7) = 0.001$, p
393 $= .97$, $\eta_p^2 = .0002$). The bootstrapped mean and 95% CI of the PSE were $-.04 \pm .003$ for 50%
394 and $.02 \pm .002$ for 90%. The main effect of *experiment* was not significant ($F(1,7) = 4.54$, p
395 $= .07$, $\eta_p^2 = .39$). These results indicate that the perceptual bias remained stable across
396 experiments, and that negative retinal image motion induced by anticipatory pursuit is unlikely to
397 cause the repulsion bias.
398



399
400 **Figure 8.** (a) PSE in probe trials across different probability conditions in experiment 2 ($n = 8$).
401 (b) The comparison of PSE between experiment 1 and 2 ($n = 8$ in each experiment).
402
403

404 Experiment 3

405 In all experiments presented so far, we used a noise mask following RDK presentation
406 (**Fig. 1**) to reduce potential motion aftereffects. Such aftereffects have been observed in
407 perception (Mather et al. 2008) and pursuit (Braun et al. 2006). An alternative explanation for the

408 perceptual repulsion effect observed in experiments 1 and 2 could be that prolonged exposure to
409 a high-coherence moving stimulus in context trials produces a perceptual aftereffect (a form of
410 low-level sensory adaptation) despite the mask. One way to reduce potential effects of motion
411 aftereffects or other similar forms of sensory adaption is to lower the motion signal strength of
412 the adaptor, for example, by reducing its luminance contrast (Keck et al. 1976). It is well known
413 that the response of neurons in motion-sensitive middle temporal cortex (area MT) is modulated
414 by motion coherence (Händel et al. 2007). In Experiment 3, we therefore reduced the coherence
415 of the RDK in context trials to investigate whether such a manipulation would weaken the
416 perceptual repulsion bias. We reduced motion coherence of RDKs in context trials to 25% on
417 average (coherence levels of 20% and 30% randomly assigned to half of the context trials in each
418 block). This coherence level is considered to be above perceptual thresholds for direction
419 discrimination in adults (Meier and Giaschi 2014) and yielded judgements of >99% correct
420 accuracy in context trials in our experiment. We therefore expected that the perceived probability
421 of context trials (50% and 90%) remained the same as in previous experiments. All other
422 procedures were the same as in experiment 1.

423 First, we assessed whether coherence impacted visually-guided pursuit in context trials to
424 confirm that the coherence manipulation successfully reduced the motion signal. We conducted a
425 two-way repeated-measures ANOVA on pursuit gain with *experiment* and *probability* as factors.
426 A significant main effect of *experiment* would imply a reduction in motion signal due to the
427 reduced coherence. To examine if motion coherence has an effect on anticipatory pursuit, we
428 conducted a two-way repeated-measures ANOVA on anticipatory pursuit velocity with
429 *experiment* and *probability* as factors. A significant interaction would indicate that anticipatory
430 pursuit was modulated by motion signal strength in context trials. Second, to examine whether

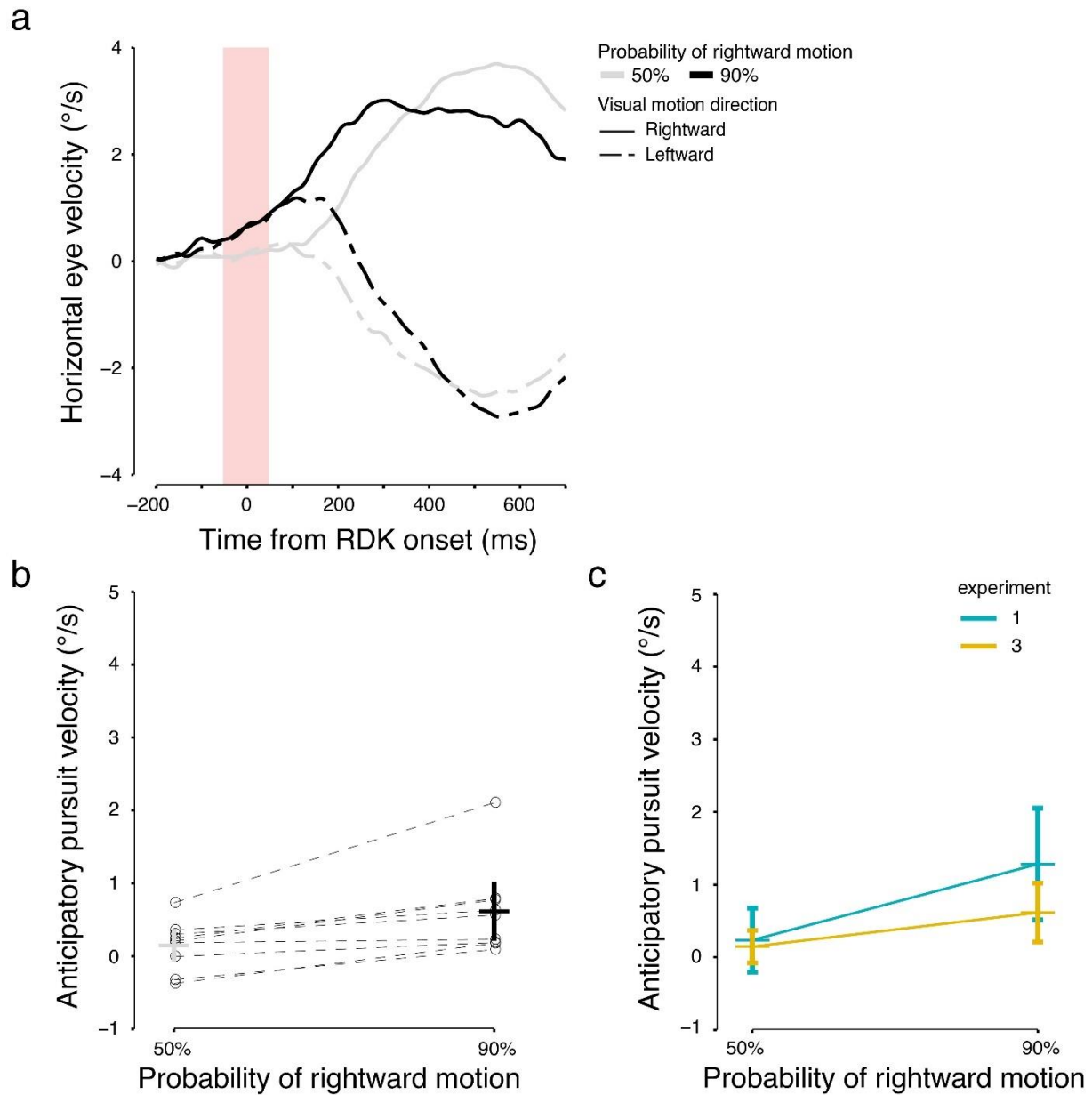
431 RDK coherence in context trials affects perception, we conducted a two-way repeated-measures
432 ANOVA on PSE with *experiment* and *probability* as factors. If RDK coherence in context trials
433 affected the repulsion bias, we should find a significant interaction.

434

435 *Low-coherence context trials elicit weaker visually-guided and anticipatory smooth pursuit*

436 The experimental manipulation of motion coherence yielded the expected reduction in
437 visually-guided pursuit gain in context trials (exp. 1: $M = 0.89 \pm 0.11$ across observers and
438 probability conditions, exp. 3: $M = 0.49 \pm 0.16$). This observation was confirmed by a significant
439 main effect of *experiment* on pursuit gain ($F(1,8) = 192.62, p = 7.03 \times 10^{-7}, \eta_p^2 = .96$). No
440 significant main effect of *probability* ($F(1,8) = 1.66, p = .23, \eta_p^2 = .17$) or interaction ($F(1,8) =$
441 $1.68, p = .23, \eta_p^2 = .17$) were found. This confirmed that a reduction in motion coherence elicited
442 a weaker motion signal and therefore lower pursuit gain in context trials.

443 Similarly, the experimental manipulation of motion coherence in context trials reduced
444 anticipatory pursuit velocity at the highest probability of rightward motion in probe trials (exp. 1:
445 $M = 1.26 \pm 1.11^\circ/\text{s}$; exp. 3: $M = 0.62 \pm 0.62^\circ/\text{s}$, **Fig. 9a, b**). This observation was confirmed by a
446 significant *experiment* \times *probability* interaction effect ($F(1,8)=32.39, p=.0005, \eta_p^2=0.80$),
447 indicating that the effect of *probability* was smaller in experiment 3 than in experiment 1 (**Fig. 3c**).
448 The main effect of *probability* was also significant ($F(1,8) = 23.29, p = .001, \eta_p^2 = .74$), and the
449 main effect of *experiment* was not significant ($F(1,8) = 5.10, p = .05, \eta_p^2 = .39$). The bootstrapped
450 mean and 95% CI of anticipatory pursuit velocity in experiment 3 were $0.17 \pm 0.01^\circ/\text{s}$ for 50% and
451 $0.61 \pm 0.01^\circ/\text{s}$ for 90%.



452

453 **Figure 9.** (a) The averaged ($n = 9$) horizontal eye velocity traces in probe trials across different
454 probability conditions in experiment 3. (b) Horizontal anticipatory pursuit velocity in
455 experiment 3 ($n = 9$). (c) The comparison of anticipatory pursuit velocity between experiment 1
456 and 3 ($n = 9$ in each experiment).

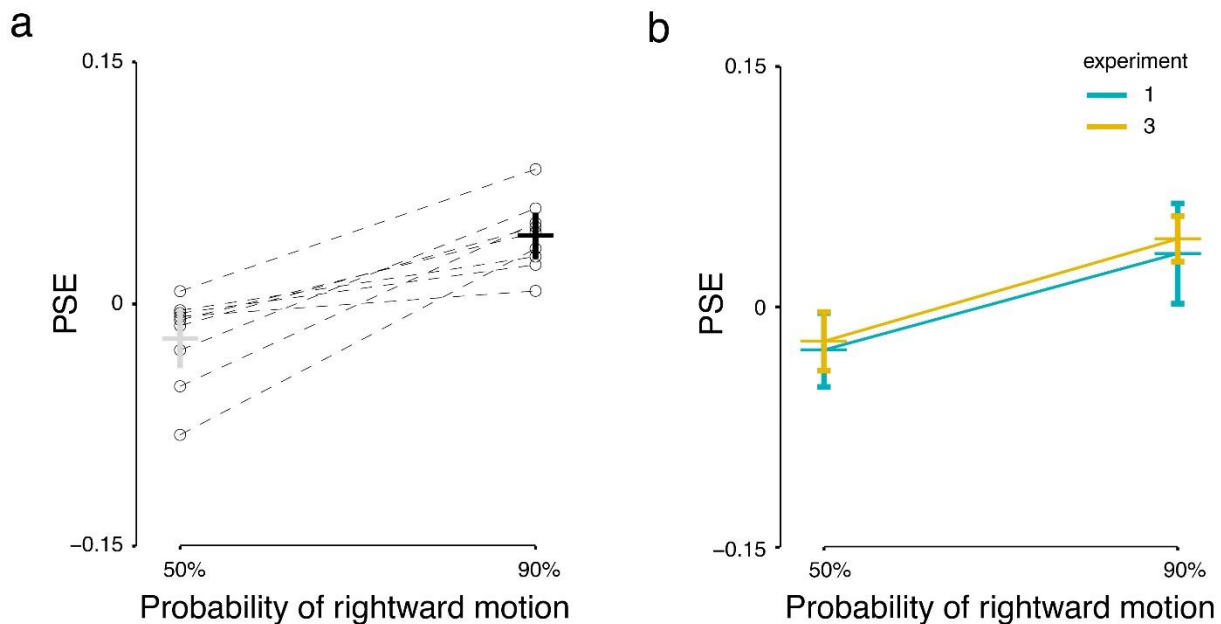
457

458 *Persistent perceptual bias despite reduced motion coherence*

459 Even though we found a reduction in visually-guided pursuit velocity, confirming that a

460 lower-coherence stimulus shown in context trials elicited weaker pursuit, and thus was less likely

461 to cause sensory adaptation, the perceptual bias remained stable (**Fig. 10**). This observation was
462 confirmed by a lack of *experiment* \times *probability* interaction on the PSE ($F(1,8) = 0.53, p = .49,$
463 $\eta_p^2 = .06$), indicating a similar magnitude of perceptual bias in both experiments (**Fig. 10**). The
464 main effect of *probability* was significant ($F(1,8) = 44.97, p = .0002, \eta_p^2 = .85$), and the main
465 effect of *experiment* was not significant ($F(1,8) = 0.13, p = .73, \eta_p^2 = .02$). Congruently, the
466 bootstrapped mean and 95% CI of the PSE were $-.02 \pm .002$ for 50% and $.05 \pm .002$ for 90%.



467
468 **Figure 10.** (a) PSE in probe trials across different probability conditions in experiment 3 ($n = 9$).
469 (b) Comparison of PSE between experiment 1 and 3 ($n = 9$ in each experiment).
470

471 In summary, results from experiment 3 suggest that the perceptual bias was not purely an
472 aftereffect induced by repeated exposure to strong motion signals, because reduced motion
473 coherence in the context trial history did not modulate the perceptual repulsion bias.

474

475

Discussion

476 By introducing a prior based on different probabilities of rightward motion, we tested how

477 expectation affected anticipatory pursuit and direction perception. Anticipatory pursuit was
478 directed toward the highest probability direction in a given block of trials. By contrast, the direction
479 of perceptual judgments was repelled away from the most probable direction. This repulsion bias
480 was not caused by anticipatory pursuit (experiment 2) and unlikely to be caused by sensory
481 adaptation (experiment 3).

482 These results make a novel contribution to the literature on the comparison between
483 perception and pursuit and highlight that motion perception does not necessarily rely on
484 expectation in the same way as early, anticipatory pursuit responses do. These findings are
485 generally congruent with a previous study investigating trial history effects in the velocity
486 domain (Maus et al. 2015). In that study, the authors presented random sequences of brief, dot-
487 motion stimuli with different speeds. Observers were asked to track the motion with their eyes
488 and judge whether the current trial's speed was faster or slower than the speed averaged across
489 previous trials. Whereas anticipatory pursuit scaled with previous target speed, perceptual
490 judgments were faster after slow stimuli and vice versa for fast stimuli, indicating a similar
491 repulsion effect as observed for motion direction in the current study. Taken together, our study
492 and the previous study show that opposite effects on perception and anticipatory pursuit exist
493 regardless of which feature of the stimulus is manipulated (speed vs. direction) and over which
494 time course both responses are compared (long-term prior vs. shorter-term trial history).

495 Such opposite biases and different sensitivities to manipulations of motion signal strength
496 in perception and pursuit are generally compatible with the idea of different information
497 processing for both responses. Perception and visually-guided pursuit eye movements might rely
498 on different information accumulation and integration over time, due to different needs of the
499 perceptual and the oculomotor systems (Spering and Montagnini 2011). The current paper

500 mainly compares perceptual responses to another aspect of pursuit, the earliest, anticipatory
501 phase that is driven by cognitive, memory-related signals rather than by visual signals.
502 Interestingly, the present study did not find a significant effect of direction expectation on the
503 later, visually-guided phase of smooth pursuit. However, in trials in which the perceived
504 direction was incongruent with the physical motion direction (i.e., followed a repulsion bias),
505 visually-guided smooth pursuit was aligned with perception. In the following paragraphs, we will
506 discuss the characteristics of the signals driving motion perception and different phases of
507 smooth pursuit with a main focus on anticipatory pursuit.

508

509 *Different biases in motion perception and pursuit might reflect how both responses adapt to task*
510 *requirements*

511 Studies on perceptual responses to manipulations in short-term or long-term probability
512 have mostly revealed an attraction bias (Alais et al. 2017; Chalk et al. 2010; Kok et al. 2013), in
513 which perception follows the recently viewed or most likely stimulus feature (direction,
514 orientation, etc.). Our paradigm utilized short-duration displays and introduced a statistical bias
515 of motion direction (long-term probability), similar to some of these studies (e.g., Chalk et al.
516 2010). However, we observed a repulsion bias. These different types of biases are interesting
517 because they reveal that the perceptual system might respond to different task and stimulus
518 environments in a flexible way, depending on the requirements of the task (e.g., to sensitively
519 respond to a change or categorize information). A repulsion bias might reflect the need of the
520 perceptual system to stay alert and to quickly respond to changes in the environment in an
521 energy-efficient way: there is no need to be highly sensitive to a stimulus that always appears,
522 whereas a novel stimulus would alert the system and may require priority processing. This is

523 similar to the functional role of adaptation, yet results from experiment 3 suggested that the
524 repulsion perceptual bias in our experiment was not caused by low-level sensory adaptation.

525 Similarly, different result patterns in perception and pursuit might reflect different task
526 requirements as well. Our results resemble those obtained in other studies comparing perception
527 and pursuit (Spering and Gegenfurtner 2007), or pursuit and hand movements (Kreyenmeier et
528 al. 2017). These studies found that pursuit generally followed the motion average of different
529 target and context speeds, whereas perception and manual interception of a target followed the
530 difference of target and background. Akin to the task requirements in our study, perception and
531 action served different functions in these studies as well. Whereas perception's role appeared to
532 be to segregate a target from the background, pursuit's role was to track in the general target
533 direction in the presence of surrounding motion signals, resulting in motion vector averaging. In
534 the present work the tendency for pursuit to rely on integration rather than segmentation of
535 different signals seems to be extended to the trial-history domain, and to the anticipatory phase:
536 integration of visual signals across many trials would drive anticipatory pursuit, whereas
537 perception could be based on the contrast between the current visual input and long-term
538 memory of visual motion.

539

540 *Expectation effects on anticipatory vs. visually-guided pursuit*

541 Anticipatory pursuit has been shown to be not purely habitual (Jarrett and Barnes 2001,
542 2002; Kowler 1989), but also sensitive to different types of cognitive cues and probabilistic
543 context (Pasturel et al. 2020; Santos and Kowler 2017) as well as to reward (Damasse et al.
544 2018). In addition, we show that anticipatory pursuit velocity is modulated by motion coherence
545 in context trials, i.e. motion signal strength in the prior history. Our results together with previous

546 findings suggest that anticipatory pursuit is based on the integration of multiple signals, from
547 low-level visual motion signals (weighted by the sensory strength, or saliency, e.g. RDK
548 coherence), to higher-level cognitive cues such as expectation and reward. This holds across the
549 short time-scale of a single trial for visually-guided early smooth pursuit (e.g., Ferrera and
550 Lisberger 1997) and a much longer time-scale lasting several minutes for anticipatory pursuit, as
551 in our experimental blocks. The assumption that anticipatory pursuit is based on such an
552 integration of multiple signals is reasonable considering that the goal of anticipatory pursuit is to
553 reach accurate tracking as soon as possible, in order to reduce the temporal delay in tracking the
554 visual target.

555 Interestingly, whereas anticipatory pursuit showed an attraction bias scaling with
556 probability, late-phase visually-guided pursuit did not follow the same result pattern. This
557 difference might be expected given that visually-guided pursuit and perception similarly rely on
558 current sensory signals, whereas anticipatory pursuit is driven by expectation. Moreover, it is
559 known that visually-guided pursuit and motion perception interact, and that motion perception
560 can modulate pursuit (Madelain and Krauzlis 2003; Montagnini et al. 2006). It is thus possible
561 that the late-phase visually-guided pursuit observed in our experiment was driven by perception,
562 regardless of the nature of the expectation information.

563

564 *Neural correlates of expectation effects on perceptual bias and anticipatory pursuit*

565 The dissociation between effects of expectation on perception and anticipatory pursuit
566 might be due to perception and pursuit depending on different cortical areas during different
567 processing stages. For perception, modulation by expectation might have affected sensory
568 processing of current stimuli, based on activity in early visual cortical areas. By contrast,

569 anticipatory pursuit is not triggered by current stimuli but instead based on expectation or
570 history, related to activity in frontal cortical areas. In the following paragraphs we will discuss
571 the neural correlates for perception and anticipatory pursuit accordingly.

572 Cortical area MT and the medial superior temporal area (MST) are the major sensory
573 areas for motion processing for both perception and visually-guided smooth pursuit (Born and
574 Bradley 2005; Thier and Ilg 2005). It is unclear which specific cortical areas are responsible for
575 expectation effects on perception. However, there is evidence that modulation in early sensory
576 cortices, from primary visual cortex (V1) to MT and MST, might underlie repulsion and
577 attraction biases in perception. For example, the repulsion bias in perceived orientation was
578 found to be stronger when the current and previous stimuli in a given trial were presented at the
579 same location (Fritsche et al. 2020). These findings indicate that this orientation bias was driven
580 by effects that are spatially specific (and retinotopically congruent), which likely implies
581 modulation of neurons in early sensory cortex, such as V1, responsive to stimuli within small
582 receptive fields. Similarly, spatial specificity has been found in visual motion adaptation in
583 relation to neuronal activity in area MT (Kohn and Movshon 2003). Area MT is known for its
584 large receptive fields and might inherit spatial specificity from V1, but also shows distinct
585 adaptation responses (Kohn and Movshon 2004) that could underlie a repulsion bias. Although
586 our results indicate that such low-level sensory adaptation was unlikely the cause of the repulsion
587 bias in our study, other mechanisms could have resulted in a similar modulation of MT neuronal
588 activity, leading to a repulsion bias in perception. Congruently, for attraction biases induced by
589 expectation, functional magnetic resonance imaging studies (e.g., Kok et al. 2013) showed that
590 representation of visual motion direction in early sensory cortices from V1 to MT was biased
591 toward the expected stimulus. Taken together, these studies indicate that sensory areas as early as

592 V1, and potentially up to MT and MST, play an important role in the effect of expectation on
593 motion perception. Whether the modulation on early sensory cortex comes from higher-level
594 areas remains unclear.

595 The supplementary eye field (SEF) plays a critical role for anticipatory pursuit, as shown
596 in studies using electrical microstimulation in SEF to elicit anticipatory pursuit (Missal and
597 Heinen 2004). Moreover, direction-selective neurons in area SEF showed stronger activity before
598 anticipatory pursuit in their preferred direction, indicating that SEF plays a role in the
599 preparation of anticipatory pursuit (de Hemptinne et al. 2008). The pursuit area of the frontal eye
600 field (FEF_{sem}) could also contribute to anticipatory pursuit, because lesions in FEF could abolish
601 the ipsilateral anticipatory initiation of pursuit (Macavoy et al. 1991). We hypothesize that
602 expectation based on visual and/or motor history might be encoded in SEF and then combined
603 with current sensory evidence in FEF (Darlington et al. 2018; Fukushima et al. 2013; Schall
604 2015). The source of visual motion history might come from MT and MST, but the roles of these
605 areas in anticipatory pursuit remain to be tested (Kowler et al. 2019).

606

607 *Limitations and future directions*

608 One limitation of the current study is that we were not able to analyze the temporal
609 development of the expectation effect in perception in detail due to limited number of probe
610 trials. Anticipatory pursuit and perception rely on history on different temporal scales (Maus et
611 al. 2015). Attraction and repulsion perceptual bias seem to also operate on different time scales
612 (Chopin and Mamassian 2012; Fritsche et al. 2020), and could occur with slight changes of
613 parameters in the same paradigm (Kanai and Verstraten 2005). Therefore, understanding the
614 temporal dependency and development of the effects of expectation would be crucial to

615 understand the complicated interaction between attraction and repulsion biases.

616 We do not know how robust our results are with regard to parametric variations of the
617 visual stimuli. For example, an attraction bias is mostly observed in studies using moving stimuli
618 whose directions differed by about 60° or less (Fritsche et al. 2020) rather than 180° (as in our
619 study). In addition, effects of expectation are often examined with weak motion stimuli, i.e., low
620 contrast (Chalk et al. 2010) or low coherence (probe trials in our study), because the Bayesian
621 integration hypothesis postulates that the effect of expectation would be larger on a stimulus with
622 less reliable sensory signals. However, reducing coherence might introduce changes other than
623 reducing contrast for RDK stimuli, such as inducing the perceptual phenomenon of motion
624 transparency, in which two or more distinct surfaces are perceived as moving in different
625 direction (Qian et al. 1994). Motion characteristics of noise dots in an RDK, together with their
626 lifetime, affect the perception of global motion as well as pursuit quality (Pilly and Seitz 2009;
627 Schütz et al. 2010). Future work is needed to elucidate the potential influence of the
628 characteristics of sensory stimuli—ranging from simplified dots, blobs and RDKs to more
629 complex naturalistic stimuli (Goettker et al. 2020)—on behavioral biases in perception and eye
630 movements.

631 Finally, the perceptual repulsion bias observed in our and other studies does not match
632 predictions of optimal Bayesian integration. Standard Bayesian inference would predict an
633 attraction bias to the prior. Combining this prediction with the efficient coding hypothesis,
634 whereby expectation modulates sensory likelihood, could account for the repulsion biases
635 (“Anti-Bayesian” effects; Wei and Stocker 2015). In the future, this kind of modeling approach
636 might help understand the complicated interaction between attraction and repulsion biases
637 induced by experience-based expectation across different behavioral tasks.

638

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647

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