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Oculomotor freezing indicates conscious detection free of decision bias
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11   *Running head: Oculomotor freezing is independent of decision bias*
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Abstract

The appearance of a salient stimulus rapidly inhibits saccadic eye movements. Curiously, this "oculomotor freezing" reflex is triggered only by stimuli that the observer reports seeing. It remains unknown, however, if oculomotor freezing is linked to the observer's *sensory experience*, or their *decision* that a stimulus was present. To dissociate between these possibilities, we manipulated decision criterion via monetary payoffs and stimulus probability in a detection task. These manipulations greatly shifted observers' decision criteria but did not affect the degree to which microsaccades were inhibited by stimulus presence. Moreover, the link between oculomotor freezing and explicit reports of stimulus presence was stronger when the criterion was conservative rather than liberal. We conclude that the sensory threshold for oculomotor freezing is independent of decision bias. Provided that conscious experience is also unaffected by such bias, oculomotor freezing is an implicit indicator of sensory awareness.

Key words: perceptual awareness; oculomotor freezing; microsaccades; perceptual decision-making

New & Noteworthy

Sometimes a visual stimulus reaches awareness, and sometimes it does not. To understand why, we need objective, bias-free measures of awareness. We discovered that a reflexive freezing of small eye movements indicates when an observer detects a stimulus. Furthermore, when we biased observers' decisions to report seeing the stimulus, the oculomotor reflex was unaltered. This suggests that the threshold for conscious perception is independent of the decision criterion and is revealed by oculomotor freezing.

1

70   **Introduction**

71   You can often gain insight into another person's mind by observing how they move their eyes

72   and what they choose to look at. But even when they attempt to keep their gaze still, tiny

73   involuntary eye movements reveal aspects of their mental state. Interspersed among slower

74   types of fixational eye movements, involuntary *microsaccades* rapidly shift the gaze direction

75   by small amounts (Rolfs 2009; Rucci and Poletti 2015). Microsaccades are in many ways

76   similar to large saccadic eye movements (Hafed 2011; Otero-Millan et al. 2013; Rolfs et al.

77   2008), and their frequency and timing are affected by other cognitive and motor processes.

78   For instance, microsaccade rates decrease in anticipation of sensory events(Abeles et al.

79   2020; Amit et al. 2019; Badde et al. 2020; Denison et al. 2019) and prior to voluntary eye and

80   hand movements (Betta and Turatto 2006; Rolfs et al. 2006).

81   A particularly striking oculomotor phenomenon is oculomotor freezing (White and Rolfs

82   2016): saccadic eye movements are momentarily and automatically inhibited by the

83   appearance of new stimuli(Engbert and Kliegl 2003; Hafed and Ignashchenkova 2013;

84   Reingold and Stampe 2002; Rolfs et al. 2008). Specifically, the onset of a stimulus — be it

85   auditory, tactile, or visual — causes a transient decrease in the spontaneous microsaccade

86   rate that lasts from roughly 100 to 400 ms, which is followed by a brief rebound above

87   baseline (Badde et al. 2020; Bonneh et al. 2015; Engbert and Kliegl 2003; Hafed and

88   Ignashchenkova 2013; Rolfs et al. 2008; Scholes et al. 2015).

89   We recently found that oculomotor freezing is triggered only by stimuli that the observer

90   detects (as measured by explicit report), revealing a possible link to visual awareness (White

91   and Rolfs 2016). In those experiments, we presented brief grating stimuli (Gabor patches) on

92   half the trials and asked the observers to report stimulus presence or absence. We

93   developed an algorithm to convert microsaccade rates into a measure of oculomotor

94   sensitivity (o') that can be compared to perceptual sensitivity (d'). Contrast thresholds for the

95   two sensitivity measures were indistinguishable (consistent with contemporaneous work by

96   others (Bonneh et al. 2015; Scholes et al. 2015)). Crucially, the same physical stimulus gave

97   rise to full-fledged oculomotor freezing when it was detected but caused no change in

98   microsaccade rates when it was missed. Moreover, microsaccades were inhibited if

99   observers reported having seen a stimulus even if none had appeared. Because of this

100   correlation, a Bayesian algorithm could decode from observers' eye movement patterns

101   whether they had detected a stimulus or not. This oculomotor link to perception may provide

102   a new tool for studies of perception in incommunicative patients, children, or non-human

103   animals, and for "no-report" studies of consciousness (Tsuchiya et al. 2015).

104   The present study answers an important question left open by all previous studies: is

105   oculomotor freezing triggered by observers' *sensory experience*, or by their *decision* that a

106   stimulus was present? Those two phenomena can be dissociated, and understanding which

107   one lies at the origin of oculomotor freezing is vital to its interpretation and application. We

108   consider two hypotheses to explain the established covariation between oculomotor

109   responses and explicit perceptual detection (Bonneh et al. 2015; Denniss et al. 2018;

110   Scholes et al. 2015; White and Rolfs 2016). Both assume a classical signal detection model:

111   on each trial, the stimulus evokes an internal response that is compared against a criterion to

112   decide whether to produce a response or not. Even when the physical stimulus and task

113   demands are constant, the sensory response varies across trials, but the criterion is

114   relatively stable. The two hypotheses concern whether the criterion for oculomotor freezing is

115   the same as the criterion for explicit perceptual decisions.

116   (1) *Shared criterion*: There is a single decision criterion that determines both explicit

117   perceptual reports and oculomotor freezing. When the sensory response exceeds the

118   criterion, it triggers both a "yes" decision and oculomotor freezing. The shared criterion

119   can be strategically modified, to maximize expected rewards. In support of this possibility,

120   manipulations of stimulus probability that affect decision bias affect activity in the superior

121   colliculus (Crapse et al. 2018), which is also causally involved in controlling

122   microsaccades (Hafed et al. 2009).

123   (2) *Distinct criteria:* There are distinct criteria for triggering oculomotor freezing and for

124   deciding that a stimulus was present. However, while the oculomotor criterion is

125   inflexible, the observer can strategically change their perceptual decision criterion to

126   maximize expected rewards as conditions change. Thus, the two criteria can diverge,

127   breaking the link between explicit reports and oculomotor freezing. To explain our prior

128   results(White and Rolfs 2016), this hypothesis assumes that the participants reported

129   exactly what they perceived and set their decision criterion very near the criterion for

130   oculomotor freezing.

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131   We designed two experiments to discriminate between these hypotheses by manipulating
132   observers' decision criterion in a detection task. The first experiment used weighted payoffs
133   (real money won or lost on each trial), and the second varied the expected probability that a
134   stimulus would appear on each trial. Such manipulations shift the theoretically optimal
135   criterion to a point that corresponds to a particular likelihood ratio β_{opt} of target presence to
136   absence, and have been shown to work empiricalally (Macmillan and Creelman 2005; Mulder
137   et al. 2012; Swets et al. 1961). Our question here is whether and how these bias
138   manipulations affect the prevalence of oculomotor freezing. To answer it, we conduct two
139   main analyses of microsaccade rates: the first separates trials according to the physical
140   stimulus presence, and the second additionally separates trials according to the participants'
141   reports of stimulus presence or absence. The shared-criteria hypotheses predict an effect of
142   bias condition in the first analysis but not the second, the distinct-criteria hypothesis predicts
143   the opposite.

144   **METHODS**

145   Both experiments were pre-registered (https://osf.io/ycjgr; https://osf.io/s9myc/). The Ethics
146   Committee of the German Society for Psychology (DGPs) approved the study.

147   **Experiment 1**

148   *Participants:* We recruited a total of 16 observers from the Humboldt-Universität zu Berlin
149   community, with normal or corrected-to-normal vision. They participated in exchange for a
150   payment that depended on performance (details below). Of the 14 observers who completed
151   the study (see below), 6 were male, 8 were female, and their ages ranged from 19 to 34
152   years (mean 26.3). All were naive as to the research aims, and gave informed consent.

153   The sample size was chosen on the basis of a power analysis based on the data from White
154   & Rolfs (2016). In Experiment 3 of that study, we found an effect of orientation adaptation on
155   microsaccade rates. That effect size was modest: the maximal difference at 350 ms post-
156   stimulus was 0.2 Hz. Averaging over the time window when the overall inhibitory effect of
157   stimulus presence was significant, the mean effect was 0.13 Hz.

158   We made the conservative assumption that if there is an effect of payoff condition, it is 75%
159   as large as the effect of orientation adaptation, at each individual timepoint. We conducted a

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power analysis to determine how many participants would be necessary to find such an effect with a power of 0.8. For each possible sample size (N) between 10 and 20, we simulated 100 experiments. For each experiment, we conducted a bootstrapping analysis: in each of 1000 repetition, we drew N observers with replacement from the original data set in White & Rolfs (2016). For each observer, we computed the difference in microsaccade rate between the unadapted and adapted condition, at each time point post-stimulus, multiplied by 0.75. We then averaged those differences across the resampled participants. Over 1000 repetitions we built up a distribution of differences at each time-point, from which we could extract a p-value. We applied the false discovery rate correction to determine at which time-points the difference was significant by applying. For each simulated experiment, we considered the overall effect to be significant if the difference was significant in at least 10 individual time-points. For each N, we defined power as the proportion of experiments with a significant effect. The minimal N to have a power over 0.8 was 14 (estimated power = 0.87).

Two participants began the study but did not finish it and were not included in the analyses. One was unable to finish all the sessions, and another discontinued after three sessions with d' far above the acceptable range, due to threshold estimation failure. Thus, the final sample included 14 participants.

Apparatus and Stimuli

Observers sat in a darkened room with their head on a chin rest, 270 cm from a projection screen that displayed stimuli with a gamma-linearized ProPixx projector (VPixx Technologies; 120 Hz, 1920 x 1080 pixel resolution). We recorded the gaze position of both eyes at 500 Hz with a head-mounted Eyelink 2 system (SR Research, Ontario, Canada). Stimuli were controlled and data collected with the Psychophysics and Eyelink toolboxes (Brainard 1997; Cornelissen et al. 2002; Pelli 1997). The grayscale display (1920 x 1080 pixels, 120 Hz refresh rate) had 8 bits of resolution in luminance. The background luminance was set to 35% of its maximum (18.15 cd/m^2).

The fixation mark was a 4 by 4-pixel black-and-white checkerboard pattern of width 0.09 degrees of visual angle (dva). In between trials, this mark was replaced by a circle (0.27 dva radius) of alternating black and white pixels. The target stimulus was a Gabor pattern: a 0.75 cycles/dva, vertically oriented sinusoidal grating windowed by a two-dimensional Gaussian (σ = 0.67 dva).

191   *Procedure*

192   Observers began each trial by fixating on the central mark. After 0.5–2.5 s, the target Gabor

193   stimulus flashed for 8.3 ms. The target's onset time had a roughly flat hazard rate: on each

194   trial, the onset time was set to 0.5 s plus a value drawn from an exponential distribution

195   (Mean = 0.65 s) clipped at 2 s. The target's phase on each trial was randomly set to either 0º

196   or 180º. On 50% of the trials, the target had non-zero contrast (target-present trials). On the

197   remaining trials, its contrast was set to 0, causing no change on the screen (target-absent

198   trials). The fixation mark remained visible at the center of the Gabor. 492 ms after target

199   onset, a beep (400 Hz, 50 ms, delivered through headphones) indicated that the trial was

200   over.

201   The observer's task was to indicate whether the target was present or absent by pressing the

202   up or down arrow, respectively, with the right hand. Response time was unlimited, but

203   responses were not allowed before the beep. Tones delivered immediately after the

204   response indicated whether the response was correct or incorrect, and how many points

205   were won or lost (details in the next section). After an inter-trial interval (700 ms) containing

206   only the circular fixation mark, the next trial began.

207   The first session began with practice and then two blocks of staircase trials to estimate the

208   observer's contrast threshold. During the staircase blocks, the contrast was adjusted after

209   each trial according to the single-interval adjustment matrix (SIAM) staircase procedure

210   (Kaernbach 1990). The contrast adjustment depended on the stimulus and response: after a

211   hit, -0.3 $\log_{10}$ units; miss, $+0.3$ $\log_{10}$ units; false alarm, $+0.6$ $\log_{10}$ units; correct rejection, no

212   adjustment. The magnitudes of these steps were halved after the 1st and 2nd staircase

213   reversals. In each block, we interleaved two staircases, one starting at a relatively high and

214   the other at a low level of contrast. The block ended when both staircases underwent 10

215   additional reversals. The mean contrast of all but the first 2 reversal points provided the

216   threshold estimate. We defined the observer's contrast threshold as the mean of 4 threshold

217   estimates (2 from each of 2 blocks).

218   In the main experimental blocks (80 trials each), the target's contrast was set to the

219   observer's estimated threshold. The mean stimulus contrast in included trials was 9%

220   (ranging across individuals from 7% to 12%).

221   *Payoff conditions*

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222   Our main manipulation is to the reward structure for correct and incorrect responses on

223   target-present and target-absent trials. On each trial the observer won or "points", which at

224   the end of the experiment were converted to a monetary payment (1600 points = €1). By

225   varying payoffs, we aimed to manipulate the observer's *detection criterion:* that is, how much

226   internal sensory evidence is required for the participant to report "target present" (Macmillan

227   and Creelman 2005; Swets et al. 1961). In the main experimental blocks, there were two

228   payoff conditions: conservative and liberal. Additionally, a neutral condition was used in the

229   initial staircase blocks to estimate contrast threshold. Following classic signal detection

230   theory, we assumed that on each trial the observer bases their decision on a single value r,

231   which is the amount of sensory evidence in favor of target presence. The probability

232   distribution of r on target-absent trials is $f_a(r)$, a Gaussian with $\mu=0$ and $\sigma=1$. The probability

233   distribution of r on target-present trials is $f_p(r)$, a Gaussian with $\mu=d'$ and $\sigma=1$. d' is the

234   observer's sensitivity to the target. The observer's criterion can be expressed as c, the cutoff

235   value of r needed to report presence. A related measure is the observer's bias, the likelihood

236   ratio β:

$$\beta = \frac{f_p(c)}{f_a(c)} \qquad \text{(Eq. 1)}$$

238   After substituting the full Gaussian formulas for f_p and f_a, we can reduce the equation to:

$$\beta = e^{cd' - \frac{d'^2}{2}} \qquad \text{(Eq. 2)}$$

240   The payoffs in each condition were set to achieve a desired optimal criterion β_{opt}: the value of

241   β that maximizes the expected reward. The values of β_{opt} were 3 for the conservative

242   condition, 1 for the neutral condition, and 1/3 for the liberal condition. We set the payoffs

243   such that the optimal observer, with a d' of 1.5, would earn an average of 6.4 points per trial.

244   Over 1280 trials, that would yield a payment of €5.12 at our exchange rate of 1600 points/€.

245   By setting the target luminance contrast to detection threshold, we aimed to keep each

246   observer's d' near 1.5. Given the average expected reward/trial (6.4 points) and the expected

247   d', we computed the payoff matrix that would lead an ideal observer to set their criterion to

248   the desired β_{opt}. Specifically, we computed the payoffs for target-present trials, R_p, and for

249   target-absent trials, R_a. For each trial type j ($j=p$ for target-present; $j=a$ for target-absent), the

250   reward for correct responses is R_j points and the reward for errors is $-R_j$ points.

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251   On any given trial, there were four possible outcomes: hits or misses if a target was present,

252   or correct rejections or false alarms if there was no target. Given d' and β, we can compute

253   the probabilities of each of those outcomes. Given R_p and R_a, we can then compute the

254   expected reward V per trial:

255 $$V = p(hit)R_p - p(miss)R_p + p(correct\ reject)R_a - p(false\ alarm)R_a \qquad \text{(Eq. 3)}$$

256   Given that the prior probabilities of target presence and absence were both equal to 0.5, the

257   optimal likelihood ratio criterion is the ratio of payoffs:

258 $$\beta_{opt} = \frac{R_a}{R_p} \qquad \text{(Eq. 4)}$$

259   Therefore, greater payoffs on target-absent trials should induce a conservative (higher)

260   criterion, whereas greater payoffs on target-present trials should induce a liberal (lower)

261   criterion. In our conservative condition (β_{opt} = 3), payoffs on target-absent trials should be

262   three times payoffs on target-present trials. The inverse is true in the liberal condition.

263   Working backwards from the equations above, and given our desired d' and expected reward

264   per trial (V), we computed the payoff matrix shown in **Table 1**.

265   **Table 1**: Payoff matrix. For each condition, this table lists the number of points that can be
266   won (positive values) or lost (negative values) for each type of response. The neutral
267   condition was only used in the initial staircase blocks.

Condition	Hit (R_p)	Miss ($-R_p$)	Correct reject (R_a)	False alarm ($-R_a$)
Conservative	4.9	-4.9	14.8	-14.8
Liberal	14.8	-14.8	4.9	-4.9
Neutral	11.7	-11.7	11.7	-11.7

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269   The payoff on each trial was indicated by a feedback tone immediately after the response.

270   These tones were composed of one, two, or three beeps, depending on the absolute value of

271   the payoff (as shown in **Table 1**, there were three possible magnitudes). When there were

272   multiple beeps, their pitches ascended in a major scale for correct responses or descended

273   in a minor scale for incorrect responses. Each beep was separated by 20 ms of silence. In

274   the liberal condition, for example, hits won 14.8 points and were followed by three ascending

275   beeps, whereas false alarms cost 4.9 points and were followed by one low-pitched beep. The

276   three beeps used for correct tones were: 75 ms of 440 Hz; 80 ms of 587 Hz; and 85 ms of

277   659 Hz. The three beeps used for incorrect feedback tones were: 75 ms of 196 Hz; 80 ms of

278   155 Hz; and 85 ms of 131 Hz.

279   The total number of points won were displayed at the end of each block. Prior to each block,

280   instructions regarding the payoff structure were displayed on the screen. These instructions

281   consisted of a 2x2 table showing the number of points that could be won or lost for reporting

282   "Yes" or "No" depending on whether a target was present or absent. The values in this table

283   were the same as in the corresponding condition's row in **Table 1**, rounded to the nearest

284   integer. A single sentence was written above the table: in the Conservative condition,

285   "Rewards and penalties are greatest when the target is absent."; in the Liberal condition,

286   "Rewards and penalties are greatest when the target is present."

287   Importantly, the words "liberal" or "conservative" were never said to the participants, nor did

288   experimenters tell them what the optimal strategy was for any given condition. However, in

289   the first training session, the participant read a longer document of instructions that said, "In

290   the main part of the experiment, we will vary the number of points you can win or lose

291   depending on presence of the target and the response you make. There are two types of

292   blocks that differ in the relative rewards and penalties on trials when the target was really

293   present or absent. To win the most money, you should adjust how sure you need to be to say

294   'yes' or 'no', depending on the points available for each type of response in the current

295   block." When introducing the conservative condition, the instructions said: "You will win three

296   times as many points when the target is absent and you say no, than when a target is

297   present and you say yes…and lose three times as many points when the target is absent

298   and you say yes, than when a target is present and you say no." Complementary instructions

299   followed for the liberal condition. Observers were also instructed that they could win points

300   and earn money during the staircase blocks as well as the main blocks.

301   In the first session, we informed observers that they would be paid a base hourly rate of

302   €7/hour, plus a bonus equal to the total number of points they accumulated during the trials,

303   divided by 1600. The maximum bonus they could earn in any given hour-long session was

304   €4. The mean bonus paid for two main experimental sessions was €4.66 (range €4.13 to

305   €5.30).

306   Each participant completed a total of 8 blocks of each condition (for a total of 640

307   trials/condition). The first session began with practice, the staircase to estimate threshold,

308   and if time permitted, some main experimental blocks. In each subsequent session (about

309   one hour each), the typical observer completed 8 blocks: the first four of one payoff

310   condition, and the next four of the other condition. In each session, observers thus did an

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311 equal number of blocks of the two payoff conditions. The order of conditions alternated

312 across sessions, and a random half of the observers started with the liberal condition.

313 Completing all 16 blocks required a total of three sessions for the typical participant

314 (including the first staircase session). At the start of the 2nd and 3rd sessions, a practice block

315 established whether the prior session's contrast threshold was still appropriate; in some

316 cases, it was necessary to re-evaluate the threshold and re-set the contrast level for that

317 session to keep *d'* near 1.5. If the overall *d'* in a full session (~8 blocks) was above 2.0 or

318 below 1.0, we excluded those blocks from analysis and re-ran them in an extra session. This

319 occurred when our threshold estimate was significantly inaccurate. A total of three sessions

320 from three participants were excluded and re-run in that fashion. The reason to exclude them

321 is that our analyses of interest depend on the target stimulus being at threshold visibility.

322 Importantly, we always excluded and re-ran the same number of blocks of each payoff

323 condition.

324 *Eye-tracking*

325 At the start of each block, we performed a 9-point calibration within a central square region,

326 21 dva wide. Every 28 trials, we performed a standard drift correction by having the observer

327 press a key while fixating a dot at the screen's center. If either eye's gaze position deviated

328 more than 2 dva from the fixation mark between the start of a trial start and the beep, that

329 trial was immediately terminated and repeated at the end of the block. We also detected

330 fixation breaks offline by defining, for each trial, the fixation position as the median gaze

331 coordinates during the first 100 ms of the trial, and fixation breaks as deviations >2 dva from

332 that. Trials with offline-detected fixation breaks were excluded from the analysis, but that only

333 excluded an average of 1 trial per participant (maximum 3).

334 **Experiment 2**

335 *Participants:* We recruited a total of 20 observers from the Humboldt-Universität zu Berlin

336 community. All had normal or corrected-to-normal vision, participated in exchange for

337 payment, and gave informed consent. Of the 14 observers who completed the study and

338 were included in the analysis (see below), 4 were male, 10 were female, and their ages

339 ranged from 20 to 37 years (mean 25.4).

340 We used the same number of participants as in Experiment 1, but with twice as many trials

341 per condition. The reason is that this experiment contained a condition in which the target

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342   was half as likely to appear (and we needed to separately analyze trials with and without

343   targets). 6 participants were not included in the analysis because they discontinued

344   participation before completing the study (in two cases because their d' was out of range in

345   one or more completed sessions and they declined to repeat them). Thus, the final sample

346   included 14 observers.

347   *Procedure*

348   All stimuli and methods in Experiment 2 were the same as in Experiment 1, except as noted

349   here. Observers began each trial by fixating on the central mark. Then a *probability cue*

350   appeared for 1 s. The target probability cues were formed of 12 dots (each 0.2 dva in

351   diameter) arranged in a ring around fixation (radius 3 dva). The dots on each trial were all of

352   the same color, either cyan or magenta. For half the observers, a cyan cue indicated low

353   target probability and magenta indicated high target probability. For the other half of

354   observers, the colors were reversed. Then, after a variable delay of 0.5–2.5 s, the target

355   Gabor stimulus flashed for 1 frame (8.3 ms), and the trial proceeded as in Experiment 1. The

356   mean stimulus contrast in included trials was 6% (ranging across individuals from 5% to 9%).

357   *Feedback and rewards*

358   The feedback and reward structures were matched to the "neutral" condition in Experiment 1

359   (used in the staircase blocks). The participants won 11.7 points on correct trials (hits or

360   correct rejections) and lost 11.7 points on incorrect trials (misses or false alarms). The

361   feedback tones were two ascending beeps or two descending beeps.

362   *Probability conditions*

363   Our main manipulation was the probability of a target being present on each trial (p_T). In "low-

364   probability" trials, $p_T = 0.25$, and on "high probability" trials, $p_T = 0.75$. Those trials were

365   randomly intermixed, because if they were in separate blocks, there could be hysteresis

366   effects due to different amounts of stimulation in each block. The cyan or magenta pre-cue

367   indicated the target probability condition at the start of each trial.

368   Given the average expected reward/trial (6.4 points) and the expected d' (1.5), we computed

369   the target probabilities that would lead an ideal observer to set their criterion to the desired

370   β_{opt}. Using the expected reward on each trial (Eq. 3), we can compute β_{opt} from the ratio of

371   payoffs, scaled by the ratio of the probability of no target and the probability of a target:

372
$$\beta_{opt} = \frac{R_a}{R_p} \frac{(1-p_T)}{p_t}$$
(Eq. 5)

373   See Swets et al. (1961) for an equivalent derivation. In Experiment 2, $R_a = R_p = 11.7$ points.

374   Therefore,

375
$$\beta_{opt} = \frac{(1-p_T)}{p_T}$$
(Eq. 6)

376   In the low-probability condition, $p_T = 0.25$ and $\beta_{opt} = 3$, the same as in the conservative payoff

377   condition of Experiment 1. In the high-probability condition, $p_T = 0.75$ and $\beta_{opt} = 1/3$, the same

378   as in the liberal payoff condition of Experiment 1. We therefore label the low-probability

379   condition as the conservative condition, and the high-probability condition as the liberal

380   condition.

381   At the start of the experiment, the observer was instructed to pay attention to the colored

382   probability cues and was told their exact meaning. We did not tell the observers *how* to use

383   the cues, but we did tell them, "If you pay attention to the colored dots and adjust your

384   responses accordingly, you could gain roughly 20% more money than if you ignore them!".

385   Prior to each block, we displayed a reminder about what the probability cues mean.

386   Each participant completed a total of 32 blocks of the experiment (80 blocks per trial, for a

387   total of 2560 trials, 1280 per condition). Completing all 32 blocks required a total of five or 6

388   sessions for the typical participant (including the first staircase session). The mean bonus

389   paid for the main experimental sessions was €10.67 (range €7.61 to €13.64).

390   As in Experiment 1, we excluded and re-ran sessions with d' above 2.0 or below 1.0. That

391   occurred for a total of 5 sessions, one per each of 5 observers. On average, less than 0.1%

392   of trials were excluded for offline fixation breaks (max 0.3%).

393   **Analyses**

394   *Perceptual data analysis*

395   We excluded trials with reaction times >4 SDs above the observer's median. Across

396   participants, this criterion excluded an average of 1% of trials in Experiment 1 (maximum

397   1.6%), and an average of 0.7% in Experiment 2 (maximum 1.4%). We then computed

398   perceptual sensitivity in each condition using the observer's hit rate (HR, the proportion of

399   'yes' responses on target-present trials) and false alarm rate (FR, the proportion of 'yes'

400   responses on target-absent trials):

401 $$d' = z(\text{HR}) - z(\text{FR}) \qquad\qquad (\text{Eq. 7})$$

402 where z is the inverse of the normal cumulative distribution function. To avoid undefined d'

403 values, HR and FR were not allowed to fall below 1/(2N) nor to exceed (1−1/(2N)), where N

404 is the number of target-present or absent trials. For example, if the hit rate was 1, we

405 assumed that, had we run twice as many trials, there would have been 1 miss. We also

406 report the observer's criterion

407 $$c = z(1\text{-FR}) \qquad\qquad (\text{Eq. 8})$$

408 From that, we compute the bias β, the likelihood ratio, using Equation 2 defined above.

409 To evaluate the effect of payoff condition on these perceptual measures (d' and β), we used

410 bootstrapping to estimate 95% confidence intervals between pairs of conditions. A difference

411 is deemed significant if the 95% confidence interval excludes 0 (a two-tailed test).

412 *Microsaccade detection*

413 The trial exclusion criteria applied in the perceptual data analysis (see above) also applied to

414 the eye movement analysis. Our analysis of eye movement traces followed the procedure

415 reported in our previous paper (White and Rolfs 2016). We first transformed the raw gaze

416 positions into velocities (dva/s) and smoothed them by averaging over neighboring pairs of

417 two samples. Then, we identified microsaccadic events as shifts in gaze position with 2D

418 velocities that exceed—for at least 3 samples—an ellipse with horizontal and vertical radii

419 equal to five times the horizontal and vertical median-based standard deviations, respectively

420 (Engbert and Mergenthaler 2006). However, for 6 observers in Experiment 1, and 3 in

421 Experiment 2, the fixed threshold of 5 SDs yields very few microsaccades, so we lowered the

422 threshold to 4.

423 Monocular microsaccadic events less than 10 ms apart were merged. We defined binocular

424 microsaccades as those with at least 1 sample of overlap between the two eyes, and again,

425 merged binocular microsaccades less than 10 ms apart. We defined microsaccade onset as

426 the time the first of the two eye velocities exceeded the threshold, and offset as the timepoint

427 just before the last eye's velocity dropped below threshold. Other parameters (e.g.,

428 amplitude) were averaged over the two eyes. We included in the analysis only binocular

429 microsaccades with durations ≥ 6 ms, amplitudes ≤ 1 dva, and peak velocities ≤ 250 dva/s.

430 *Microsaccade rate analysis*

13

431   We then determined the time-varying microsaccade rate for each experimental condition with

432   a smoothing procedure. First, we counted the number of microsaccades detected at each

433   millisecond t relative to target onset, across all trials in each condition. Then, for each time

434   point t, we computed a weighted sum of microsaccades in the local interval, using a "causal"

435   kernel:

436
$$\omega(\tau) = \alpha^2\, \tau\, e^{-\alpha\tau} \tag{Eq. 9}$$

437   ω describes the weight given to microsaccades τ ms before time point t. We shifted the filter

438   by $1/\alpha$ ms to avoid a temporal bias and give the most weight to microsaccades at point t

439   (Rolfs et al. 2008; Widmann et al. 2014). The parameter α was set to 1/25. The smoothed

440   rate r(t) is the weighted sum of microsaccades divided by the total number of trials in the

441   sample, and converted into Hz by multiplying by 1000. Microsaccade rates were computed

442   from −350 to +500 ms relative to target onset.

443   To estimate the statistical significance of changes in microsaccade rates, we bootstrapped

444   them by simulating 1000 repetitions of the experiment (Efron and Tibshirani 1993). On each

445   repetition, we resampled with replacement from the set of observers then took the mean

446   between conditions. That gave us distributions of differences at each time point. The two-

447   tailed bootstrapped p-value is defined as twice the proportion of differences that fell below 0.

448   When evaluating differences at many time points, we applied the false discovery rate

449   correction (Benjamini and Hochberg 1995). Two conditions are deemed significantly different

450   if the 95% confidence interval of differences does not include zero (corrected p<0.05). (Note:

451   this bootstrapping procedure differs from what we pre-registered, in that it is simpler and

452   focuses on variability across observers rather than variability across trials within each

453   observer, thus being a nonparametric analogue of a t-test).

454   To directly compare changes in microsaccade rate to perceptual sensitivity, we computed an

455   analogous estimate of oculomotor sensitivity (White and Rolfs 2016). At each millisecond,

456   the lack of a microsaccade following a stimulus is a "hit", and the lack of a microsaccade

457   following no stimulus is a "false alarm". From the resulting oculomotor hit rate (HR) and false

458   alarm rates (FAR), we can compute oculomotor d'_o at each time point t relative to stimulus

459   onset (0<=t<=500):

460
$$d'_o(t) = z(HR(t)) - z(FAR(t)) \tag{Eq. 10}$$

461   Like perceptual *d'*, this measure requires correction if HR or FAR reach extreme values. This

462   can happen if no microsaccade were detected during a period around t as wide as the base

463   B of the filter (~200 ms). Therefore, both rates will not be allowed to fall below 1/(2NB) nor to

464   exceed (1–1/(2NB)), where N is the number of target-present or absent trials, respectively.

465   That is, we assume that had we run twice as many trials, we would have found at least 1

466   microsaccade (a 'miss') in the 200 ms time-window surrounding any given time point.

467   Nonetheless, because microsaccades occur only about once or twice every second, both HR

468   and FAR at individual (millisecond) time points will be high (above 0.999). But because HR

469   rose even higher than FAR after stimulus presentation, we found positive values of d'_o.

470   To extract a single oculomotor sensitivity measure from an entire rate time course for a given

471   condition, we defined a value *o'*, the maximum of the cumulative sum of d'_o values across

472   time (within 200 to 550 ms post-stimulus). *o'* is unaffected by rate rebounds following

473   inhibition, which result in negative d'_o. Pairwise differences in *o'* (across payoff conditions)

474   were tested with bootstrapping, similar to perceptual *d'* as described above.

475   In addition to the pre-registered analyses reported thus far, we conducted two exploratory

476   analyses. First, to simplify the comparison of microsaccade rates across conditions (without

477   relying on hundreds of noisy tests at many individual time points), we computed the

478   microsaccade rates integrated across two time windows: for the baseline microsaccade rate

479   on target absent trials, we used the time window 0 to 500 ms. For target present trials, we

480   used the time window within which the microsaccade rate on target present trials was

481   significantly lower than the rate on target absent trials, for both bias conditions (bootstrapped

482   FDR-corrected p<0.05). This is the *time window of significant oculomotor freezing* (see

483   results).

484   Second, compared to our previous studies, we found that baseline microsaccade rates were

485   lower on average and more variable across, which complicates comparing rates by taking

486   simple differences (liberal-conservative) between conditions. We therefore computed

487   *modulation indices* that are more robust to variation across observers in overall

488   microsaccade rates: (A – B) / (A + B), where A and B refer to a measure in specific

489   conditions (e.g., microsaccade rate on conservative vs liberal trials; or report-present vs

490   report-absent trials). This index ranges from -1 to 1, where positive values indicate higher

491   microsaccades rates in A as compared to B, and negative values indicate the opposite.

492   Finally, we supplement our pairwise tests with Bayes Factors (BFs), which quantify strength

493   of evidence. In this context, a BF is the ratio of the probability of the data under the alternate

494   hypothesis (that two conditions differ), relative to the probability of the data under the null

495   hypothesis (that there is no difference) (Rouder et al. 2009, 2012). As an example, a BF of

496   10 indicates that the data are ten times more likely under the alternate hypothesis than the

497   null hypothesis. Typically, BFs between 1 and 3 are regarded as weak evidence for the

498   alternate hypothesis, BFs between 3 and 10 as substantial evidence, and BFs between 10

499   and 100 as strong evidence (Kass and Raftery 1995). Conversely, BFs between than 1/3 and

500   1/10 are considered substantial evidence for the null hypothesis, etc. We computed BFs for

501   pairwise t-tests and two-way repeated measures ANOVAs using the bayesFactor toolbox by

502   Bart Krekelberg (https://github.com/klabhub/bayesFactor: DOI: 10.5281/zenodo.4394422).

503

504   **RESULTS**

505   *Explicit perceptual reports: Bias manipulations affect decision criteria but not sensitivity*

506   On each trial, observers reported the presence or absence of a brief Gabor stimulus with a

507   luminance contrast that had been set to their individual detection threshold. The time of the

508   target's onset was unpredictable, but the end of each trial was indicated by a beep 500 ms

509   after the time of (potential) target appearance. The observers' goal was to win "points" that

510   were converted to bonus monetary payments. Correct responses (hits and correct rejections)

511   gained points and incorrect responses (misses and false alarms) lost points.

512   In Experiment 1, we introduced asymmetric monetary payoffs to manipulate decision bias. In

513   the liberal condition, rewards were three times greater for hits than correct rejections, and

514   penalties were three times greater for misses than false alarms. This reward structure places

515   the optimal criterion at the level of sensory evidence that is three times as likely to be

516   observed when the target is absent than present. Thus, the optimal likelihood ratio β_{opt} = 1/3).

517   In the conservative condition, rewards were three times greater for correct rejections than

518   hits, and penalties were three times greater for false alarms than misses. That makes β_{opt} =

519   3. The reward structure varied across blocks of trials and was known to the participant in

520   advance. Feedback at the end of each trial indicated the reward magnitude.

521   In Experiment 2, we manipulated probability that a target would appear, and informed

522   observers of that probability on each trial. In the liberal condition, there was a 75% chance

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523   that a target would appear (3x likelier to be present than absent), which lowered the optimal

524   criterion such that β_{opt} = 1/3. In the conservative condition, there was a 25% chance that a

525   target would appear, raising the optimal criterion such that β_{opt} = 3 (as in Experiment 1).

526   These trial types were randomly intermingled within blocks, but a cue in the form of colored

527   dots presented at the start of each trial informed the participant of the target probability.

528   Payoffs on target-presence and target-absent trials were of equal magnitude.

529   In both experiments, the bias manipulation strongly affected explicit perceptual reports of

530   target presence. The mean hit and false alarm rates, their mean differences between bias

531   conditions, and the 95% confidence interval (CI) of those differences, are listed in **Table 2**.

532   Hit rates and false alarm rates were much lower in the conservative than liberal condition,

533   indicating that participants were less willing to report seeing a target when the potential

534   payoffs were greater on target absent trials (Experiment 1), and when target presence was

535   unlikely (Experiment 2). Response times are plotted in **Supplementary Figure 1**

536   (https://osf.io/t9by7/).

|		Conservative	Liberal	Diff	Diff 95% CI
Hit rate	*Expt 1*	0.57 (0.02)	0.79 (0.01)	0.22 (0.03)	[0.18 0.27]
	Expt 2	0.41 (0.02)	0.73 (0.04)	0.32 (0.05)	[0.22 0.40]
False alarm rate	*Expt 1*	0.06 (0.01)	0.38 (0.04)	0.31 (0.04)	[0.24 0.40]
	Expt 2	0.07 (0.01)	0.45 (0.07)	0.38 (0.07)	[0.27 0.52]
d'	*Expt 1*	1.95 (0.12)	1.90 (0.10)	-0.05 (0.08)	[-0.22 0.09]
	Expt 2	1.12 (0.09)	1.27 (0.07)	0.15 (0.11)	[-0.02 0.40]
β	*Expt 1*	2.32 (0.38)	0.42 (0.02)	-1.89 (0.39)	[-2.72 -1.29]
	Expt 2	1.80 (0.09)	0.59 (0.06)	-1.21 (0.11)	[-1.39 -0.99]

537   **Table 2: Explicit reports in each condition of each experiment.** The first two columns list the
538   across-subject mean values, with the standard error in parentheses. The column labeled "Diff" is the
539   average (and SEM) difference: liberal – conservative. The final column is the 95% bootstrapped
540   confidence interval (CI) of the difference. When a CI excludes 0, we conclude there is a significant
541   effect of the bias condition. *d' and β* are sensitivity and bias measures assuming unequal variance of
542   sensory evidence on target-present and target-absent trials (see text).

543   To interpret these psychophysical data, we adopt the classic signal detection model: the

544   participant reports target presence if the magnitude of sensory evidence E exceeds a

545   criterion level c. The variances of E on target-absent and target-present trials are often

546   unequal, and can be estimated with a receiver operating characteristic (ROC) graph (Swets

547   et al. 1961). The ROC in **Figure 1a** plots false alarm rates vs hit rates, each z-transformed

548   through the inverse normal cumulative distribution function. For each participant, one line

549   connects their points for the liberal (blue) and conservative (red) conditions. If the

550   distributions of sensory evidence have equal variance, then these lines should have slopes

551   equal to 1 (illustrated with thick diagonal black lines). The empirical slopes are consistently

552   shallower: in Experiment 1, the mean slope was 0.53 (95% CI = [0.46 0.60]), and in

553   Experiment 2 it was 0.60 (95% CI = [0.50 0.69]).   Assuming that the target-absent

554   distributions have standard deviations (SDs) equal to 1, the SD of the target-present

555   distributions are equal to the inverse of the ROC slopes: 1.90 in Experiment 1 and 1.66 in

556   Experiment 2. These best-fitting signal detection models are shown in **Figure 1b**, with the

557   mean criteria (computed directly from false alarm rates) as vertical blue and red lines.

558   Using these estimated variances, we computed d', a measure of sensitivity (**Figure 1c**), and

559   β, a measure of bias (**Figure 1d**). d' is the distance between the mean E (sensory evidence)

560   on target-present trials and the mean E on target-absent trials. β is the likelihood ratio of

561   target presence to target absence when $E = c$. Using the formulas for β and d' (Equations 2

562   and 7) that typically assume equal variance, we substituted the best-fitting SDs into the

563   probability and cumulative density functions. Statistics for both measures are reported in

564   **Table 2.** d' did not significantly differ between the liberal and conservative conditions (CIs

565   include 0), but β was significantly higher in the conservative condition, for all participants.

566   The dashed lines in **Figure 1f** are the optimal β_{opt} in each condition. Most participants did not

567   shift their criteria quite far enough to reach the optimal levels(Kubovy 1977). For the

568   estimates of d' and β that (incorrectly) assume equal variance on present and absent trials,

569   see **Supplementary Figure 2** (https://osf.io/t9by7/).
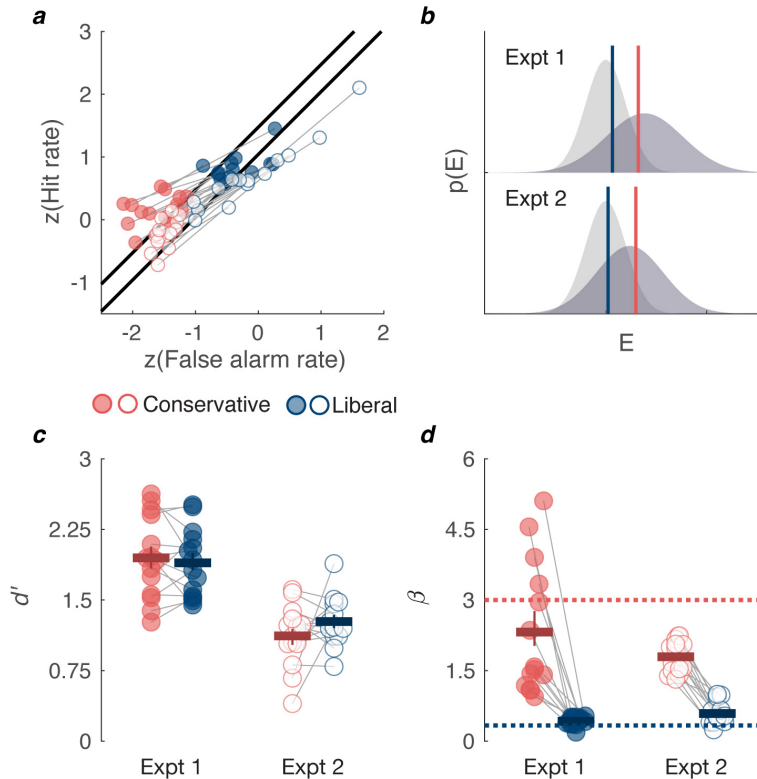
570

Figure 1: Bias manipulations affect explicit perceptual reports. (*a*) The receiver operating characteristic (ROC) showing individual z-transformed hit and false alarm rates. The two black lines with slope 1 are the predictions of an equal-variance model for each experiment (Expt. 1 is the upper black line). The data have slopes consistently less than one, suggesting that the distribution of sensory evidence has higher variance when the target is present rather than absent. (*b*) Signal detection models that account for the empirical hit and false alarm rates. These show probability distributions of sensory evidence E on target-absent trials (light gray distributions) and target-present trials (darker distributions). The standard deviations of the target-present distributions were derived from the average ROC slopes in panel *a*. The blue and red vertical lines are the mean empirical criteria (computed from false alarm rates) in the liberal and conservative conditions, respectively. (*c*) Individual participants' detection sensitivity *d'*, assuming that the sensory evidence distributions have unequal variance as modeled in panel *b*. Experiment 1 is in filled circles, Experiment 2 in open circles. Thin gray lines connect points from the same participant. The horizontal positions of individual data points are jittered to avoid total overlap, but points from the same participant have the same relative jitter. The horizontal lines represent the means, with error bars spanning the 68% bootstrapped confidence interval (approx. ±1SEM). (*d*) Individual participants' decision bias computed as β for each participant, again assuming unequal variance. Format as in panel *c*. Horizontal dotted lines are the optimal β for each condition (dark blue = liberal; light red = conservative).

In sum, both bias manipulations had large effects on decision criteria for explicit judgements, while sensitivity remained unaffected.

19

595 *Microsaccade rates contingent on physical target presence: Bias manipulations do not affect*

596 *oculomotor freezing*

597 **Figures 2a** and **2b** show the mean microsaccade rates plotted as a function of time relative

598 to target onset. The target, when present, was flashed at time point 0. In both experiments

599 we observed oculomotor freezing on target-present trials (solid lines): the microsaccade rate

600 begins to drop roughly 130-150 ms after stimulus onset, and then returns to baseline 300-

601 400 ms later. The key question is whether microsaccade rates differ between the liberal and

602 conservative bias conditions. The *distinct-criteria hypothesis* predicts no difference. The

603 *shared-criterion hypothesis*, which posits that oculomotor freezing is linked to explicit report

604 decisions, predicts a greater drop in microsaccade rates on target-present trials of the liberal

605 condition, in which the participant reports "present" more often. The data do not support the

606 shared-criterion hypothesis. Although the mean rate in the liberal condition (blue line) dips

607 slightly lower than in the conservative condition (red line), that effect is small and not

608 consistent across participants.

609 To simplify this analysis and maximize power, we integrated microsaccades over two key

610 time windows: 0 to 500 ms for target-absent trials and the window of significant oculomotor

611 freezing for target-present trials (shaded windows in **Figures 2a** and **2b;** see **Methods**). In

612 Experiment 1, the window of significant freezing was from 149 ms to 421 ms, and in

613 Experiment 2 it was 145 to 509 ms. As shown in **Figures 2c** and **2d**, there were no reliable

614 effects of bias condition on the mean microsaccade rates in these time windows. We

615 evaluated the effects both as mean differences (L – C, where L is the rate on liberal trials and

616 C on conservative trials) and as modulation indices [(L – C)/(L + C)] that adjust for individual

617 differences in overall microsaccade rate. With one exception, none of those effects were

618 significant: 95% CIs include 0, and Bayes Factors (BFs) support the null hypothesis at least

619 2:1 (BFs<0.5). The one exception is for target-absent trials in Experiment 2: when the effect

620 is expressed as a modulation index, the baseline microsaccade rate was slightly but

621 significantly lower on liberal than conservative trials (mean index = -0.09, 95% CI = [-0.17 -

622 0.02]; BF=1.35. The mean difference was only -0.02 Hz (95% CI = [-0.04 0.03]; BF=0.37).

623
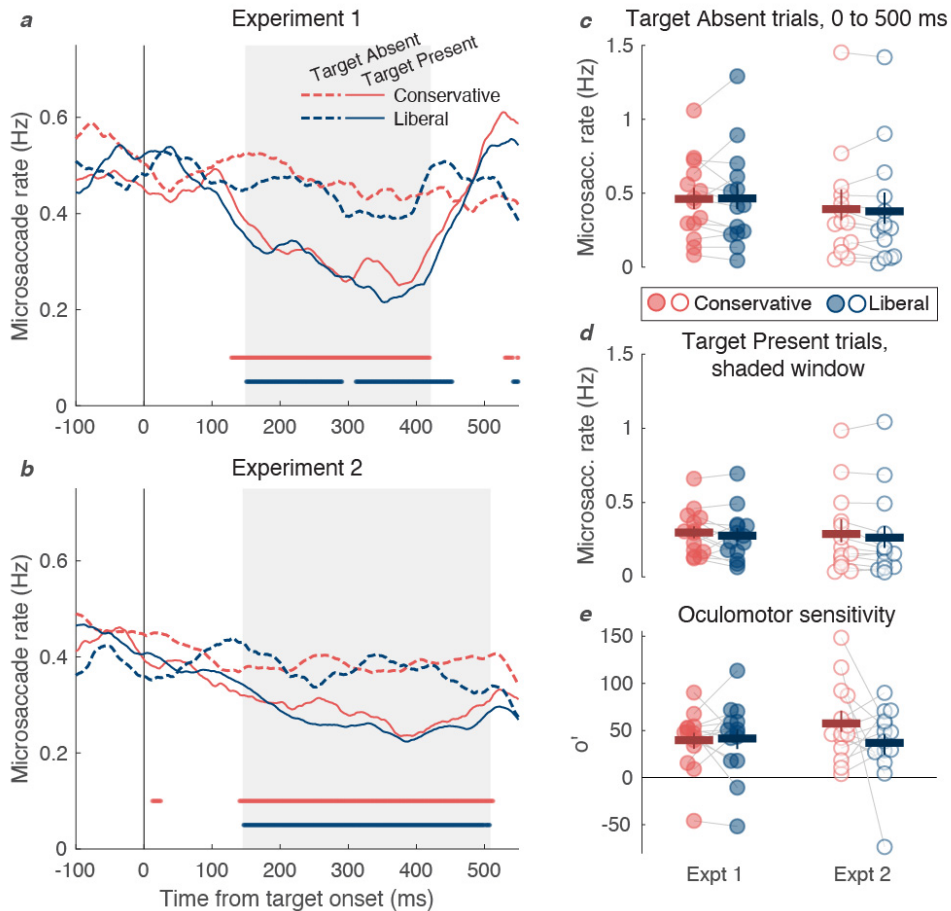
Figure 2: Bias manipulations do not affect overall microsaccade rates on target-present and target-absent trials. (*a,b*) Mean microsaccade rates as a function of time relative to target onset in Experiments 1, for target-absent trials (dotted lines) and target-present trials (solid lines). The horizontal lines at the bottom of each plot indicate time points when the rate on target-present trials is significantly different from the rate on target-absent trials (corrected p<0.05). The gray region of the background indicates the time window when the rate was significantly reduced on target-present trials in both conditions. **(*c*)** Mean microsaccade rates on target-absent trials in the time window between 0 and 500 ms. Format as in Figure 1a. **(*d*)** Mean microsaccade rates on target-present trials in the time windows with significant inhibition in both conditions (shaded portions in panels a and b). There are no significant effects of bias condition. **(*e*)** Oculomotor sensitivity (*o'*), a measure of the difference in microsaccade rates between target-present and target-absent trials over the entire interval 0 to 500 ms. There are no significant effects of bias condition.

To combine across experiments, we entered these data into linear mixed effects models (LMEs), with fixed effects for condition, experiment, and their interaction, as well as random effects for participant. We fit one such model for the target-absent trials and another for the target-present trials. The effect of condition was negligible in both analyses (0.006 and 0.02 Hz, respectively), and not significant (both p>0.10; both BF<0.5). There were no effects of experiment nor interaction between experiment and condition (all p>0.5).

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645 We also computed oculomotor sensitivity (o') as a measure of the strength of oculomotor

646 freezing (White and Rolfs 2016) (**Figure 2e**), comparable to d'. In both experiments, o' did

647 not differ significantly between bias conditions: 95% CIs were far from excluding 0 and Bayes

648 Factors supported the null hypothesis (all BFs<0.5). If anything, the effect in Experiment 2

649 (conservative > liberal) went in the direction opposite predicted by the shared criterion

650 hypothesis, but was not significant (mean modulation index = -0.32, 95% CI = [-1.55 0.11]).

651 An LME combining across experiments found no effect of condition (p=0.32, 95% CI = [-28.4

652 9.5]; BF=0.30) and no main effect of experiment nor interaction (both p>0.2).

653 Altogether, the microsaccade rates in this first analysis are consistent with the distinct-criteria

654 hypothesis: oculomotor freezing is independent of bias manipulations that affect explicit

655 perceptual reports. Next, we sorted the data further by the participant's report on each trial.

656 Based on our prior study (White and Rolfs 2016), we predicted more oculomotor freezing on

657 trials when the participant reports seeing a stimulus than when they don't, but the magnitude

658 of that effect may depend on the bias condition.

659 *Microsaccade rates contingent on explicit perceptual reports: Oculomotor freezing is stronger*

660 *in conservative than liberal bias conditions*

661 When we analyze trials separately according to whether the participant reported target

662 presence or absence, the shared-criterion hypothesis predicts no effect of bias condition.

663 The observer's ultimate decision is the same on liberal hit trials as on conservative hit trials,

664 so the prevalence of oculomotor freezing should be the same. In contrast, the distinct-criteria

665 hypothesis predicts an effect of bias condition: when considering only trials in which the

666 observer reports target presence (hits and false alarms), microsaccade rates should be lower

667 in the conservative condition than liberal condition. This is because in the conservative

668 condition, the sensory evidence must be stronger for the participant to report presence, and

669 therefore it is also likely to trigger oculomotor freezing. In the liberal condition, some explicit

670 reports of target presence are guesses with low sensory evidence, which will not exceed the

671 criterion for oculomotor freezing, so microsaccade rates should be higher.

672 **Figure 3a** plots the mean microsaccade rates on target absent trials, separated by bias

673 condition and the participant's explicit report of whether a target was present or not (correct

674 reject trials in dark lines, false alarm trials in bright lines). In a prior study (White and Rolfs

675 2016), we found that microsaccade rates were lower on false alarm than correct reject trials,

22

676   consistent with the notion that a spurious sensory signal triggered both an explicit false alarm

677   and oculomotor freezing. The distinct-criteria hypothesis predicts that effect (the relative

678   inhibition of microsaccades on false alarm trials) should be weakened in the liberal condition,

679   when many false alarms are guesses without a sensory signal strong enough to inhibit

680   microsaccades.

681   To test these predictions, we integrated microsaccade rates over the 0 to 500 ms time

682   window (shaded region) and then computed the effect of explicit report as a modulation

683   index: (CR – FR) / (CR + FR), where CR is the microsaccade rate on correct reject trials and

684   FR is the microsaccade rate on false alarm trials. The occurrence of oculomotor freezing on

685   false alarm trials predicts a positive index. In addition, the distinct-criteria hypothesis predicts

686   a larger index in the conservative compared to the liberal condition. The mean indices are

687   plotted in **Figure 3b** and listed in Table **2** with 95% CIs and BFs. Only in the conservative

688   condition of Experiment 2 was the effect of report significant. According to a linear mixed

689   effects model that combined experiments, there was a small but significant difference

690   between microsaccade rates on correct reject vs. false alarm trials (mean index = 0.11, CI =

691   [0.004 0.209], p=0.04, BF=1.4), a marginal effect of bias condition (index 0.2 larger in the

692   conservative condition, CI = [0.002 0.41], p=0.053; BF=1.28), and no effect of experiment nor

693   interaction (both p>0.4, BF<0.25). All told, the data in **Figure 3b** support our previous finding

694   that false alarms are associated with inhibition of microsaccades, and are consistent with the

695   distinct-criteria hypothesis. However, this analysis is limited due to the small number of false

696   alarm trials in the conservative condition (on average across participants, only 20 trials in

697   Experiment 1 and 70 in Experiment 2). The target-present trials provide supporting evidence.

698   **Figure 3c** plots microsaccade rates on target-present trials. These traces diverge around

699   stimulus onset (i.e., 0 ms) due to the reductive effect of microsaccades on perceptual

700   sensitivity (Rolfs 2009; Scholes et al. 2018; White and Rolfs 2016; Zuber et al. 1964): a

701   microsaccade that occurs close in time to the stimulus onset can make the participant miss

702   the stimulus, thus miss trials are associated with a peak in the microsaccade rate near time

703   0. That peak is especially large in the liberal condition, when misses are less frequent and

704   require a definite lack of target evidence. Conversely, hits are associated with fewer

705   microsaccades near the time of stimulus onset, and thus there is a dip in microsaccade rate

706   on hit trials. That dip is larger in the conservative condition, when hits require high certainty

707   and would otherwise be turned to misses by microsaccades. We previously confirmed that

708   the drop in microsaccade rates on hit trials ~150-400 ms post-stimulus is not an artifact of the

23

709   divergent dips and peaks observed around 0 ms due to saccadic suppression of perception

710   (White and Rolfs 2016).
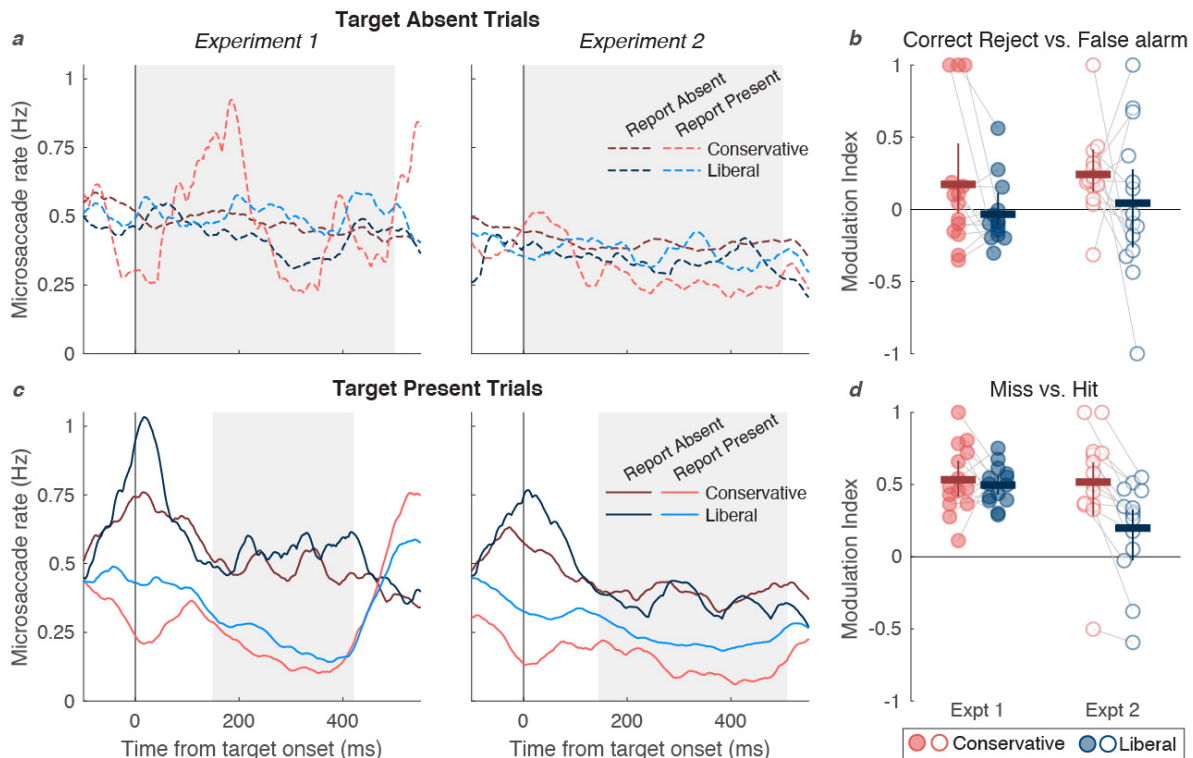
711
Figure 3: Microsaccade rate signatures as a function of bias condition and explicit report outcome. (*a*) Mean rates as a function of time on target absent trials, separated by bias condition and by whether the participant reported target absent (correct reject trials, dark lines) or target present (false alarm trials, bright lines). Note there are very few false alarm trials in the conservative condition (bright red lines) *(b)* The mean modulation indices comparing microsaccade rates on correct reject trials and false alarm trials, integrated over 0 to 500 ms (shaded interval in panel *a*). Format as in Figure 1a, except the error bars are bootstrapped 95% confidence intervals to highlight significant deviations from zero. The overall effect of perceptual report is significant, and marginally higher on conservative than liberal trials. *(c)* Mean microsaccade rates on target present trials, separated by bias condition and by whether the participant reported target absent (miss trials, dark lines) or reported target present (hit trials, bright lines). *(d)* The mean indices comparing microsaccade rates on miss and hit trials, integrated over the intervals with significant stimulus-induced inhibition (shaded in panel c). Microsaccade rates are significantly lower on hit than miss trials, and that effect is significantly larger on conservative than liberal trials.

728   Our current research question focuses on the later time period, starting roughly 150 ms post-

729   stimulus, when stimulus detection is associated with inhibition of microsaccades. We tested

730   whether that effect of perceptual report (misses vs hits) is equal in the two bias conditions.

731   The distinct-criteria hypothesis predicts greater inhibition on hit trials of the conservative

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732   condition, because conservative hits are "purer" (i.e., they contain fewer lucky guesses) and

733   require a strong sensory signal that is also likely to trigger oculomotor freezing.

734   Indeed, the microsaccade rate dips lower on hit trials of the conservative condition (**Figure**

735   **3c**, light red lines) than of the liberal condition (light blue lines). To summarize these effects,

736   we integrated microsaccade rates over the time window with significant inhibition (shaded

737   windows in **Figures 2a**, **2b**, and **3b**). For each bias condition we then computed the effect of

738   explicit detection as a modulation index: (M-H)/(M+H), where M is the microsaccade rate on

739   miss trials and H is the rate on hit trials. The effect of explicit detection was significant (95%

740   CI of the index excludes 0) in all conditions except the liberal condition of Experiment 2 (see

741   **Table 3**). According to a linear mixed effects model, that modulation index was significantly

742   larger in the conservative than liberal condition (by 0.18 on average, CI = [0.08 0.14],

743   p=0.0004; BF=34.0). This is strong evidence that correct reports of target presence in the

744   conservative condition are associated with stronger inhibition of microsaccades than in the

745   liberal condition. The effect of bias condition was also larger in Experiment 2 than

746   Experiment 1 (interaction between condition and experiment, p=0.004; BF=6.32).

		Correct reject - False alarm			Miss - Hit		
	Condition	**Modulation index**	**Index 95% CI**	**BF**	**Modulation index**	**Index 95% CI**	**BF**
Expt. 1	Conservative	0.17 (0.13)	[-0.039 0.437]	0.58	0.53 (0.06)	[0.429 0.657]	1.4×10^4
	Liberal	-0.03 (0.06)	[-0.121 0.116]	0.41	0.50 (0.04)	[0.433 0.566]	2.6×10^6
Expt. 2	Conservative	0.24 (0.08)	[0.128 0.403]	7.47	0.52 (0.10)	[0.248 0.671]	197.6
	Liberal	0.04 (0.14)	[-0.226 0.319]	0.27	0.20 (0.09)	[-0.008 0.333]	1.68

747   **Table 3: Effects of perceptual report on microsaccade rates, expressed as modulation**
748   **indices.** The columns labeled "Modulation index" contain the mean, with standard error
749   across participants in parentheses. The 95% CIs are derived from bootstrapping.

750   These data consistently support the distinct-criteria hypothesis: oculomotor freezing is

751   triggered when a sensory signal crosses a threshold that is independent of the participant's

752   decision bias. The sensory signal is more likely to have crossed that oculomotor threshold on

753   hit trials of the conservative condition, when the criterion for explicit report is higher, than on

754   hit trials of the liberal condition. Thus, when the participant was induced to adopt a more

25

755 conservative decision bias, explicit detection of the stimulus was associated with more

756 pronounced oculomotor freezing.

DISCUSSION

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758 Detecting potentially relevant stimuli in the environment is a fundamental task of perceptual

759 systems. Our data suggest that although sensory input is continuous and noisy, the brain

760 switches into a qualitatively different state when there is sufficient evidence that a target is

761 present. Passing this threshold gives rise to a conscious percept *and* an involuntary pause of

762 saccadic eye movements (that is, oculomotor freezing). A pause in microsaccades can be

763 considered the oculomotor system's "report" that it detected a stimulus. The participant's

764 decision to respond voluntarily to the stimulus — for instance, by pressing a button —

765 depends on the conscious percept as well as potential rewards and expectations.

766 Visual stimulus detection therefore has three consequences that are of interest to the present

767 investigation: a conscious percept, a decision to report stimulus presence, and oculomotor

768 freezing. It is crucial that we understand how those three consequences relate in terms of

769 neural and cognitive mechanisms. Provided oculomotor freezing is indeed a proxy for

770 conscious perception (as we argue below), researchers would be equipped with a "no-report"

771 paradigm to investigate the neural correlates of consciousness (Tsuchiya et al. 2015) without

772 interference from explicit cognitive tasks.

773 In five independent experiments across this study and a previous one (White and Rolfs

774 2016), we consistently found that explicit reports and oculomotor freezing covary: the eyes

775 only freeze in response to stimuli that the person reports seeing. To explain that covariation,

776 here we manipulated the likelihood of explicit reports of stimulus presence. When rewards

777 and penalties were greater on target-present than target-absent trials (Experiment 1), or

778 when the target probability was known to be high (Experiment 2), participants adopted a

779 liberal decision criterion, reporting target presence much more often than in the opposite

780 (conservative) conditions (**Figure 1**).

781 In contrast, the magnitude of the drop in microsaccade rates just after stimulus onset showed

782 little to no effect of our bias manipulations (**Figure 2**). We need not rely only on that null

783 result, however, because we also found effects of the bias condition when splitting the trials

784 according to the explicit report (**Figure 3**). The difference in microsaccade rates between hit

785 and miss trials, which indexes the link between explicit reports and oculomotor freezing, was

786 larger in the conservative than the liberal condition. Our interpretation is that when

787 participants make conservative decisions, they only report sensations that are strong enough

788 to also trigger oculomotor freezing. In contrast, when participants make liberal decisions,

789 they often make strategic guesses that a stimulus was present, even when the sensory

790 signal was weak and oculomotor freezing was not triggered.

791 We therefore reject the shared-criterion hypothesis and support the distinct-criteria

792 hypothesis (described in the Introduction). The criteria in question specify the magnitude of

793 sensory evidence required to trigger a response. There is one criterion for explicitly reporting

794 stimulus presence, and it can be shifted to maximize rewards. There is also a distinct

795 criterion for inhibiting eye movements, which is relatively stable and not affected by shifts of

796 decision criterion.

797 This conclusion is consistent with studies that predicted individual perceptual contrast

798 thresholds based on microsaccade patterns that were measured while the participant did not

799 explicitly respond to the stimuli (Bonneh et al. 2015; Denniss et al. 2018; Scholes et al.

800 2015). These studies show that oculomotor freezing is not related to response preparation.

801 However, participants in those studies either had to silently count the stimuli (Bonneh et al.

802 2015), or prepare to respond on a random subset of trials (Denniss et al. 2018; Scholes et al.

803 2015), so they were likely making covert decisions about each stimulus. Therefore, decision-

804 making processes could have contributed to oculomotor freezing in those data. Our data help

805 isolate the link between perception and oculomotor freezing.

806 A key feature of our theory is that oculomotor freezing is all-or-none, not graded. In a prior

807 study (White and Rolfs 2016), we varied the visibility of a target grating by varying its

808 luminance contrast, or by adapting the observer to the same or different orientation.

809 Considering all target-present trials, the degree of oculomotor freezing scaled with explicit *d'*.

810 However, when considering only hit trials, oculomotor freezing was equivalently across all

811 contrast levels and adaptation states. Intense stimuli had no effect on eye movements if the

812 observer missed them, and faint stimuli were accompanied by full-fledged inhibition provided

813 they were detected. We found similar patterns in the new data reported above, providing

814 consistent support that oculomotor freezing is a discrete all-or-none reflex that occurs if and

815 only if a stimulus is consciously detected. Such a model is reminiscent of "high threshold

816 theory," which has been largely discredited (Swets 1961). Standard signal detection theory,

817 which has been more successful, assumes no threshold for detection other than the

27

818 observer's flexible decision criterion. In that regard, the data presented here are not fully

819 consistent with standard signal detection theory.

820 Our data are, at least in part, consistent with the "global neuronal workspace theory" of

821 consciousness. It proposes that a stimulus becomes reportable when "ignites" sustained

822 neural communication across the brain (Mashour et al. 2020). Recent electrophysiological

823 data suggest that ignition occurs when activity in frontal cortex, not sensory cortex, reaches a

824 threshold, roughly 200 ms after stimulus onset (Van Vugt et al. 2018). We might speculate

825 that such an 'ignition' is related to oculomotor freezing, but it occurs later than the initial drop

826 in microsaccade rates.

827 For now, we consider two possibilities for how oculomotor freezing relates to the conscious

828 experience of the stimulus that triggers it. Both are compatible with the distinct-criteria

829 hypothesis described in the Introduction. (1) Oculomotor freezing and conscious perception

830 are tightly coupled, because they are both triggered when the same sensory signal crosses

831 the same threshold. That threshold is not affected by bias manipulations, unlike the criterion

832 for explicit reports. (2) Oculomotor freezing and conscious perception can be dissociated,

833 because the threshold for oculomotor freezing is stable but the threshold for conscious

834 perception is affected by bias manipulations, along with the decision criterion. While our data

835 reveal that explicit reports and oculomotor freezing have distinct criteria, they are consistent

836 with both possibilities regarding conscious perception.

837 We nonetheless favor the first possibility: oculomotor freezing and conscious perception are

838 coupled. This hypothesis must also assume that the bias manipulations (payoffs and

839 probability cues) affect decisions at a post-perceptual stage. Specifically, in the liberal

840 conditions, observers reported "yes" more often because doing so maximized rewards, not

841 because they actually *saw* the target more often. That is why the difference in microsaccade

842 rates between hit and correct reject trials is weaker in the liberal than conservative condition.

843 The implication is that oculomotor freezing provides an implicit index of conscious perception

844 that is free of bias.

845 However, this conclusion fails if the bias manipulations do affect conscious perception (i.e.,

846 the second possibility). There is some neurophysiological evidence that expectations, as

847 manipulated by the probability cues in Experiment 2, can affect sensory processing (De

848 Lange et al. 2018; Pajani et al. 2015). One theory is that expecting a stimulus evokes a

849 "template" in neural populations that prefer the expected features (Kok et al. 2014, 2017). In

850 contrast, one fMRI study concluded that payoff and probability manipulations recruit frontal

851 and parietal brain regions involved in decision-making to shift the starting point of evidence

852 accumulation, similar to a criterion shift (Mulder et al. 2012). The existing behavioral

853 evidence is also ambiguous. One study argued that expectation improves detection by

854 elevating the baseline of "signal-selective units" (Wyart et al. 2012). Another found that

855 probability cues presented *after* the stimulus had similar effects as cues presented *before* the

856 stimulus, in favor of a post-perceptual criterion shift (Bang and Rahnev 2017). It remains a

857 matter of discussion, therefore, whether expectations affect conscious perception or decision

858 processes (Press et al. 2020; Rungratsameetaweemana et al. 2018;

859 Rungratsameetaweemana and Serences 2019; Summerfield and Egner 2016). The simplest

860 model that explains our data assume that they affect decision processes only.

861 We must also note that the results favoring the distinct-criteria hypothesis are clearer in

862 Experiment 2 (which manipulated expectations) than Experiment 1 (which manipulated

863 rewards). Indeed, other researchers have found that probability manipulations have stronger

864 effects on perceptual decisions than reward manipulations do (Leite and Ratcliff 2011;

865 Mulder et al. 2012; Simen et al. 2009). In our case there are several possible explanations:

866 first, there were greater individual differences in explicit report criteria in Experiment 1

867 (**Figure 1d**), perhaps due to variable interpretations of, or value placed in, the rewards. Such

868 individual differences may have added noise to the microsaccade data as well. Second,

869 overall *d'* levels were higher in Experiment 1 than 2 (**Figure 1c**). The bias manipulations are

870 likely to have greater effects when the target is difficult to detect. Third, it may be that

871 expected rewards affect decisions at a post-perceptual stage, whereas expectations affect

872 perception, as discussed above. In that case, the explicit reports in Experiment 1 were less

873 driven by the sensory signal, thus showing a less clear relationship with oculomotor freezing.

874 In contrast, Experiment 2 could be explained by a model in which expecting a stimulus

875 lowers the sensory threshold for conscious perception, but does not affect the threshold for

876 oculomotor freezing. While this model would explain the smaller difference in microsaccade

877 rates between hit and miss trials in the liberal condition (**Figure 3d**), it is comparably

878 complicated.

879 We may also consider the probability cues of Experiment 2 in light of the "predictive coding"

880 framework (De Lange et al. 2018). A target in the "conservative" condition is unexpected, and

29

881　thus should produce a larger prediction error. If oculomotor freezing is a "surprise" response,

882　then we would have predicted a larger drop in microsaccades in target-present trials of the

883　conservative condition than the liberal condition. We did observe that, but only on hit trials

884　(**Figure 3c**). The predictive coding framework may therefore help explain oculomotor

885　freezing.

886　Altogether, the most parsimonious explanation for our results is that oculomotor freezing and

887　conscious detection share a common sensory threshold. This threshold is distinct from the

888　decision criterion to report a stimulus, which is shifted by weighted payoffs and expectations.

889　The alternate explanation, that the threshold for conscious detection can diverge from the

890　threshold for oculomotor freezing, is more complicated. It must either postulate an additional

891　free parameter, for a total of three sensory thresholds/criteria, or it must assume that the

892　decision criterion is also the threshold for perception and thus bias manipulations truly affect

893　perception. To the extent that the more parsimonious explanation stands, oculomotor

894　freezing provides a valuable tool to measure conscious perception free of the influence of

895　decision bias, and without requiring explicit reports.

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Supplementary Data: Two supplementary data figures can be viewed here: https://osf.io/t9by7/ .

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