Decoupling sensory from decisional choice biases in perceptual decision making

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ABSTRACT

The contribution of sensory and decisional processes to perceptual decision making is still unclear, even in simple perceptual tasks. When a decision maker needs to select an action from a set of balanced alternatives, any tendency to choose one alternative more often—choice bias—is consistent with a bias in the sensory evidence, but also with a preference to select that alternative independently of the sensory evidence. To decouple sensory from decisional biases, here we asked humans to perform a simple perceptual discrimination task with two symmetric alternatives under two different task instructions. The instructions varied the response mapping between perception and the category of the alternatives. In two experiments, we found that 30 out of 32 participants exhibited sensory biases and 15 decisional biases. The decisional biases were consistent with a criterion change in a simple signal detection theory model. Perceptual decision making, thus, even in simple scenarios, is affected by sensory and decisional choice biases.

KEYWORDS

Decision making, perception, choice biases, discrimination, Signal Detection Theory.

INTRODUCTION

You ask a friend about the tilt of a canvas that is perfectly horizontal and she says that the top right corner is *up.* What causes her inaccuracy? One possibility is that her sensory representation is biased and she perceives the canvas tilted. Another possibility, however, is that under uncertainty about the orientation of the canvas, she prefers to choose *up* over *down*. This situation exemplifies a major problem in the study of perception: perceptual decisions not only depend on the sensory evidence, but also on decisional components (Green and Swets 1966; Gold and Ding 2013).

When a decision maker needs to select an action from a set of alternatives, the tendency to choose one alternative over the others is known as choice bias (Gold and Ding 2013). Choice biases occur in perceptual tasks even in simple scenarios like the one described above, in which the stimuli carry similar levels of signal relative to a neutral point (Newsome and Paré 1988; Mareschal and Clifford 2012; Jazayeri and Movshon 2007; Milner,

51 Brechmann, and Pagliarini 1992; Tadin et al. 2003). Choice biases are extensively studied in
52 relation to how current decisions are influenced by previous decisions, what is known as
53 choice history biases (Abrahamyan et al. 2016; Akaishi et al. 2014; Fründ, Wichmann, and
54 Macke 2014; Urai, Braun, and Donner 2017; Fischer and Whitney 2014; Braun, Urai, and
55 Donner 2018; St John-Saaltink et al. 2016; Fritsche, Mostert, and de Lange 2017).
56 Depending on the perceptual scenario, people tend to repeat their previous choice (Akaishi
57 et al. 2014; Braun, Urai, and Donner 2018), alternate between choices (Fritsche, Mostert,
58 and de Lange 2017) or idiosyncratically repeat or alternate (Urai, Braun, and Donner 2017;
59 Abrahamyan et al. 2016). Whether choice history biases reflect a bias in the sensory
60 evidence or in the decision process is under debate (Akaishi et al. 2014; Fischer and
61 Whitney 2014; St John-Saaltink et al. 2016; Fritsche, Mostert, and de Lange 2017).
62
63 Another form of choice bias refers to the overall tendency to choose one alternative over the
64 others—global choice biases. The existence of these biases is acknowledged (Gold and
65 Ding 2013; Kingdom and Prins 2016; Michael J. Morgan et al. 2012; García-Pérez and
66 Alcalá-Quintana 2013; Peters, Ro, and Lau 2016) and they are included in current models of
67 perceptual decision making (Abrahamyan et al. 2016; Akaishi et al. 2014; Urai, Braun, and
68 Donner 2017; Braun, Urai, and Donner 2018), but whether they reflect sensory or decisional
69 processes is unknown. The problem to identify their origin is that, in standard perceptual
70 paradigms, the tendency to choose one alternative more often is consistent with a biased
71 sensory representation, but also with a bias in the decision process (García-Pérez and
72 Alcalá-Quintana 2013; Gold and Ding 2013). Here, to disentangle the contribution of sensory
73 and decisional processes to global choice bias, we measured choice behavior in a simple
74 common perceptual discrimination task with two symmetric alternatives, but under two
75 different task instructions. The instructions varied the response mapping between perception
76 and the category of the alternatives.
77
78
79 **RESULTS**
80
81 In Experiment 1, the orientation of a grating centered on a fixation point was chosen
82 randomly on each trial from a range centered around the horizontal orientation. Seventeen
83 participants judged whether the grating was pointing down or up (by pressing the *down* or *up*
84 arrow keys on a keyboard) relative to a reference that we asked participants to imagine
85 placed on the right at the same height of the fixation point (Figure 1A). *Down* and *up* choices
86 correspond to clockwise and counterclockwise orientations relative to horizontal.
87
88 We first describe the results of four representative participants that illustrate the four types of
89 choice behaviors that we found (Figure 1C-F). The circles in Figure 1C-F show the
90 probability of clockwise responses (pressing the *down* key) as a function of the orientation of
91 the grating and the curves show the psychometric fits (see *Models;* figure supplement 1
92 shows the results for all participants). Participant 12 (Figure 1C) did not show asymmetries
93 in choice behavior—no global choice bias was present (to see how we assessed that the
94 bias was not significant, see *Materials and Methods*). Participant 2 (Figure 1D) and 4 (Figure
95 1F) had a tendency to give a response consistent with clockwise orientation (pressing the
96 *down* key)—that shifts the psychometric curve leftwards— and participant 9 (Figure 1F) had
97 a tendency to give a response consistent with counterclockwise orientation (pressing the *up*
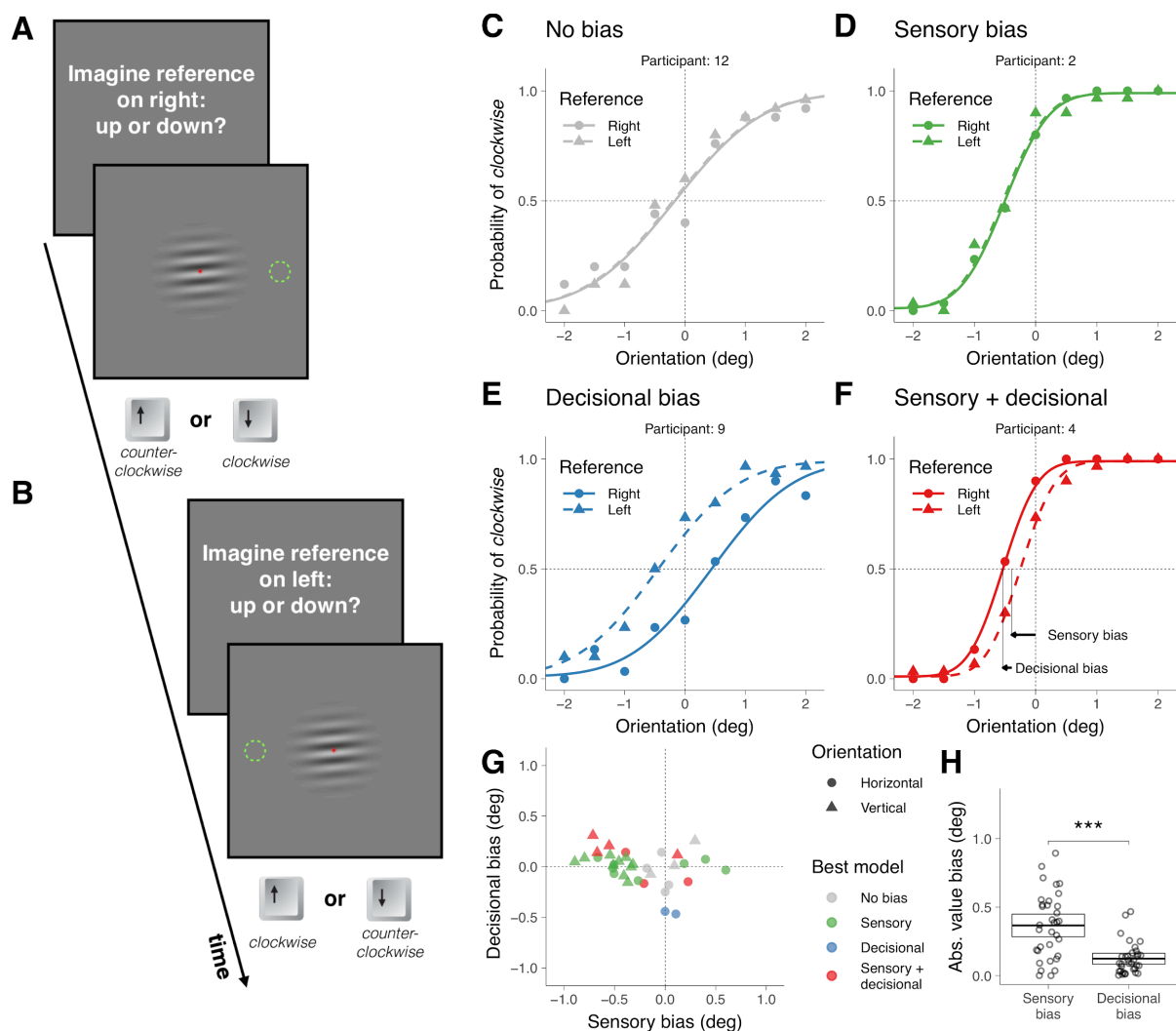98 key)—that shifts the psychometric curve rightwards.

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Figure 1. Symmetric task in Experiment 1. (A) Illustration of a trial in which the participant was asked to imagine a reference on the right (the green dotted circumference was not displayed during the experiment; in Materials and Methods we described the exact message displayed on the screen). (B) Illustration of a trial in which the participant was asked to imagine a reference on the left. (C-F) Choice behavior for 4 representative participants. (G) Decisional and sensory biases. For each participant, the circles correspond to the gratings presented around the horizontal orientation (Figure 1A-B) and the triangles to the gratings presented around the vertical orientation (not shown). The color indicates the best model assessed using likelihood ratio tests (see Materials and Methods). (H) Across participants, the absolute value of the sensory and the decisional biases was significantly different (t(33) = 4.8, p = 3.1 x 10^{-5}). The crossbars display the mean and the 95% t-test confidence intervals.

The biases could reflect that the perceived horizontality of the grating corresponds to different orientations for different participants (sensory bias) or that under uncertainty participants had a tendency to select either the down or up alternative (decisional bias). It could also be that biases include a sensory and a decisional component.

To decouple these possibilities, in other trials intermixed with the trials just described we presented the same stimuli but asked participants whether the grating was pointing down or up relative to a reference that now we asked them to imagine on the *left* (Figure 1B). This variation in the instructions was easy for the participants to understand and effectively reversed the mapping between perception and the category of the alternatives. We did not display the reference to keep the stimuli identical across locations of the reference. For the

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122   left reference, *down* choices correspond to counterclockwise orientations relative to
123   horizontal and *up* choices to clockwise. If the bias is of sensory origin, the probability of
124   choosing an alternative consistent with clockwise orientation (triangles in Figure C-F) should
125   not depend on where the reference was imagined (right or left). This is the choice behavior
126   that participant 2 exhibited (Figure 1D). Notice that the similar pattern of clockwise
127   responses for the two locations of the reference indicates that the participant reversed the
128   frequency of pressing the *down* and *up* keys. If the bias is decisional, the probability of
129   choosing an alternative consistent with clockwise orientation for the left reference should be
130   shifted symmetrically relative to 0 deg (see *Models*). This is the choice behavior of
131   participant 9 (Figure 1E). In this case, the participant had a tendency to press more often the
132   *up* key independently of the location of the reference. If sensorial and decisional biases
133   contribute, the probability of choosing an alternative consistent with clockwise orientation
134   should be shifted, but not symmetrically. This is the choice behavior of participant 4 (Figure
135   1F).

137   For each participant, we quantified the magnitude of the sensory and decisional biases
138   (illustrated for participant 4 using arrows, Figure 1F, see *Models*). Figure 1G shows, for each
139   participant, the magnitude of the decisional bias against the magnitude of the sensory bias
140   and which is the bias model that better describes the data (see *Models* and *Materials and*
141   *Methods*). For each participant, two data points are plotted. The circles correspond to the
142   trials just described, in which the grating was presented around the horizontal orientation.
143   The triangles correspond to other trials—intermixed with the previous ones—in which the
144   grating was presented around the vertical orientation (in this case, participants judged the
145   orientation using the *right* and *left* keys relative to a reference that we asked participants to
146   image on top or at the bottom). Most participants showed significant biases. About half of the
147   participants showed biases consistent with only a sensory origin and about half showed
148   decisional biases mostly combined with sensory biases (although two participants showed
149   biases consistent with only a decisional origin). Across participants, the absolute value of the
150   magnitude biases was larger for the sensory biases than for the decisional biases, indicating
151   that the sensory biases dominated (Figure 1H).

153   The task described could be considered symmetric because the evidence supporting
154   clockwise or counterclockwise choices should be similar when the stimulus has the same
155   magnitude but different sign relative to the neutral point. Given this symmetry, it could be
156   argued that what we have described as sensory biases might be a more complex form of
157   decisional biases than the one we tested: participants might not prefer the *down* or *up*
158   alternative (or *right* and *left*), but instead biased to choose the alternative consistent with
159   clockwise or counterclockwise orientation. In this case, the sensory biases that we found
160   should not remain when the same stimuli are presented, but the task has two choices
161   unrelated to the clockwise and counterclockwise alternatives. To assess this prediction, in
162   some other trials—intermixed with the previous trials—we asked participants to imagine a
163   reference on the right or on the left (or bottom and top) and perform a two-alternative
164   asymmetric choice task that consisted in indicating whether the grating was aligned or not
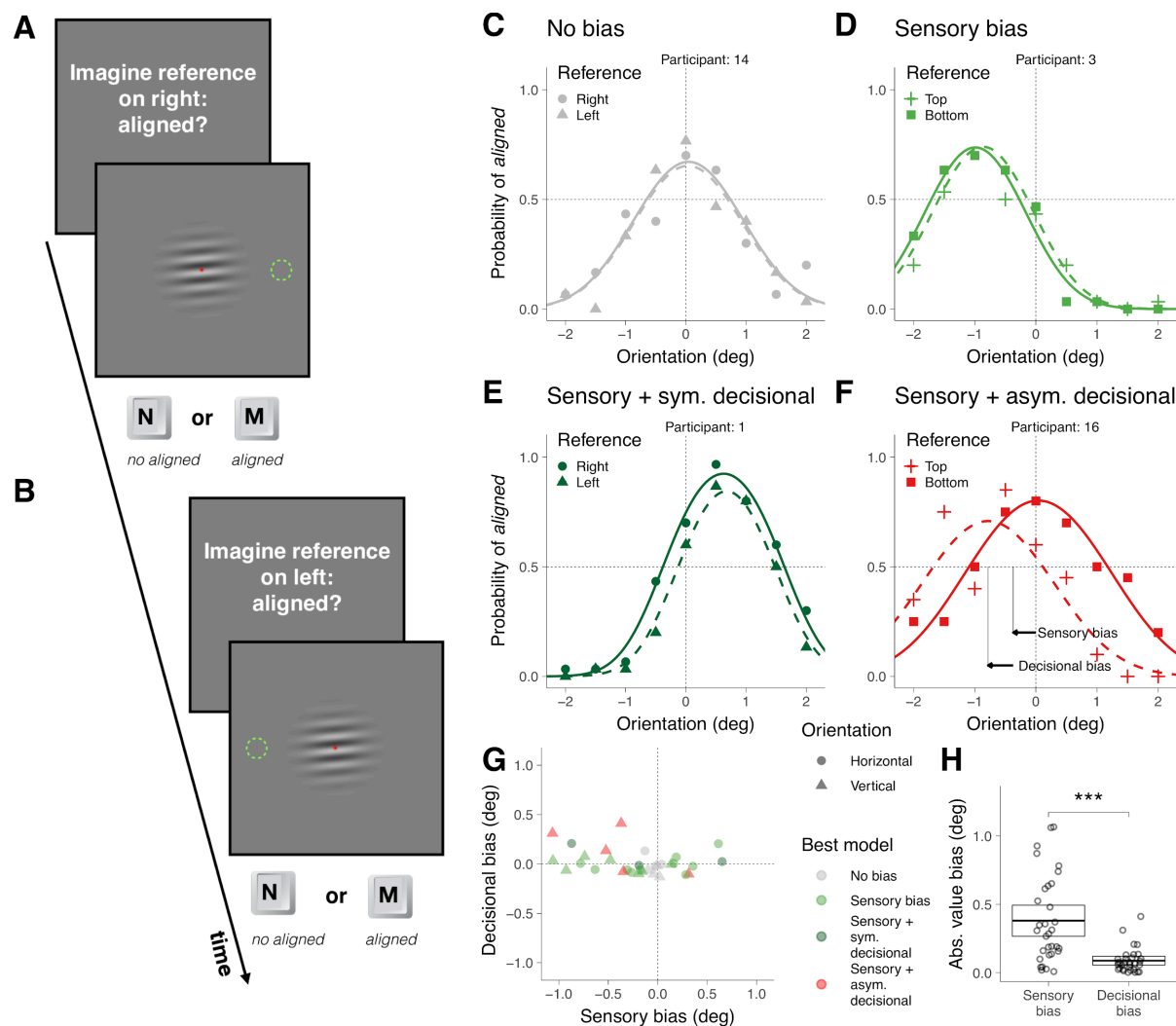165   with the imagined reference (Figure 2A-B).

Figure 2. Asymmetric task in Experiment 1. (A) Illustration of a trial in which the participant was asked to imagine a reference on the right. (B) Illustration of a trial in which the participant was asked to imagine a reference on the left. (C-F) Choice behavior for 4 representative participants. (G) Decisional and sensory biases. (H) Across participants, the absolute value of the sensory and the decisional biases was significantly different (t(31) = 5.4, p = 6.0 x 10^{-6}). The crossbars display the mean and the 95% t-test confidence intervals.

To illustrate the choice behaviors on this task, we first describe the results of four representative participants (Figure 2C-F). The symbols in Figure 2C-F show the probability of responding *aligned* as a function of the orientation of the grating and the curves show the psychometric fits for the two possible locations of the reference (see *Supplementary Models;* figure supplement 2 shows the results for all participants). The arrows in Figure 2F illustrates the estimation of the magnitude of the sensory and decisional bias (see *Supplementary Models*). For participant 14 (Figure 2C), the probability of responding *aligned* was centered around 0 and did not depend on the location of the reference (no bias). For participant 3 (Figure 2D), the probability of responding *aligned* was not centered around 0, but did not depend on the location of the reference (sensory bias). For participant 1 (Figure 1E), the probability of responding *aligned* was not centered around 0 and depended on the location of the reference, but the tendency to respond *aligned* more often for one location did not affect where the psychometric fit was centered (sensory bias with a symmetric decisional bias, see *Supplementary Models*). Finally, for participant 16, the probability of responding

189   *aligned* was not centered around 0 and depended on the location of the reference, but in this
190   case this tendency affected where the psychometric fits were centered (sensory bias with an
191   asymmetric decisional bias, see *Supplementary Models*).
192
193   Figure 2G shows, for each participant and overall orientation of the grating (horizontal or
194   vertical), the magnitude of the decisional bias against the magnitude of the sensory bias and
195   which is the bias model that better describes the data (see *Materials and Methods*). Most
196   participants showed significant biases that include sensory and decisional biases. It has
197   been suggested that asymmetric tasks are less prone to decisional biases than symmetric
198   tasks (Schneider and Komlos 2008; but see Anton-Erxleben, Abrams, and Carrasco 2010).
199   We did find less groups with significant decisional biases (the asymmetric ones, Figure 2F)
200   for the asymmetric task (5 fits; figure 2G and figure supplemental 2) than for the symmetric
201   task (8 fits; figure 1G and figure supplemental 1), but the difference was not significant (χ^2
202   (1) = 0.52, p = 0.47). Across participants, the absolute value of the magnitude biases was
203   larger for the sensory biases than for the decisional biases, indicating that the sensory
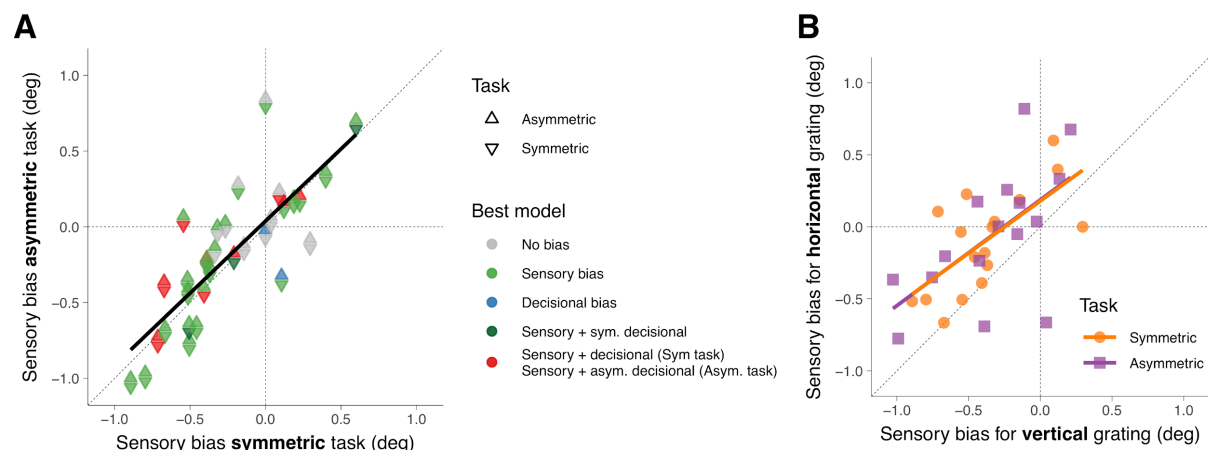204   biases dominated (Figure 1H).
205

Figure 3. (A) Across participants, the sensory biases estimated from the symmetric task correlated with the
sensory biases estimated from the asymmetric task ($r(30) = 0.81$, $p = 2.7 \times 10^{-8}$). The color of the triangles
indicates the model that best fit the data. The black line corresponds to a simple linear regression fit. To compare
the symmetric and the asymmetric task with the counterparts in the temporal domain (see Discussion), we also
calculated the correlation of the biases across tasks using only one reference for each pair of coupled references
(bottom or left; $r(30) = 0.77$, $p = 2.3 \times 10^{-7}$). In this case, we estimated the bias for the symmetric task as the
orientation for which the probability of clockwise responses was 50% and for the asymmetric task as the
orientation for which the probability was maximum. (B) Across participants, the sensory biases estimated using
the horizontal grating correlated with the sensory biases estimated using the vertical grating for the symmetric
($r(15) = 0.67$, $p = 0.0030$) and the asymmetric task ($r(15) = 0.60$, $p = 0.015$). The lines correspond to simple linear
regression fits.

218
219   Figure 3A shows that, within participants, the sensory biases estimated from the asymmetric
220   task are very similar to those estimated from the symmetric task. This shows that what we
221   described as sensory biases for the symmetric task had indeed a sensory origin, and not a
222   complex form of decisional biases. We also found a good agreement, within participants,
223   between the sensory biases for the horizontal grating and the vertical grating for the two
224   tasks (Figure 3B). This suggests that the sensory biases are consistent with a clockwise or
225   counterclockwise global perceptual rotation of the stimulus.
226

227 Across trials we intermixed four locations of the reference and two tasks (symmetric and
228 asymmetric) that required pressing different keys. These high demands on participants might
229 have minimized decisional biases. To test whether the task demands influenced the
230 proliferation of decisional biases, in Experiment 2, for 16 new participants, we repeated the
231 symmetric task using two references (Top and Bottom) that could be blocked in two ways. In
232 some blocks of trials the two references were mixed across trials and participants, thus,
233 needed to establish a mapping between perception and the category of the alternatives on
234 each trial. In some other blocks, only one reference was presented on each block (on
235 different blocks, the reference changed) and participants did not need to update the
236 response mapping on each trial. Consistent with Experiment 1, we found that participants
237 exhibited significant sensory and decisional biases, but we did not find significant differences
238 in decisional biases between the two blocking conditions (figure supplementary 3). We
239 found, however, that the decisional biases in Experiment 2 were larger than in Experiment 1
240 (figure supplementary 3), which suggests that very high demands on the task like those in
241 Experiment 1 can reduce the proliferation of decisional biases.
242
243 Taking into account Experiment 1 and 2, we have found that from the 32 participants, 30
244 (94%) had significant global choice biases. From these 30, the sensory contribution was
245 significant in all of them (that is, 94% of participants had sensory bias) and the decisional
246 contribution was significant in 15 (that is, 47% of participants had decisional biases).
247
248
249 **MODELS**
250
251 On a given trial of the symmetric task (the model for the asymmetric task is described in
252 *Supplementary Models*) a grating with orientation θ_i that could be clockwise or
253 counterclockwise, is presented and the participant decides whether its orientation is
254 consistent with clockwise a_{cw} or counterclockwise a_{ccw} orientation. A simple standard signal
255 detection theory (SDT) model assumes that: 1) the sensory evidence s associated to the
256 stimulus is a random variable normally distributed with variance σ^2 centered on μ_{cw} when θ_i
257 is clockwise and centered on μ_{ccw} when θ_i is counterclockwise; 2) to make choices, the
258 participant sets a criterion β, computes the log likelihood ratio $\log \Lambda$ of s under the hypothesis
259 that $\mu = \mu_{cw}$ and the hypothesis that $\mu = \mu_{ccw}$

$$\log \Lambda(s) = \log \left(\frac{p(s|\mu = \mu_{cw})}{p(s|\mu = \mu_{ccw})} \right) = \log \left(\frac{(2\pi\sigma^2)^{-1/2}e^{-\frac{(s-\mu_{cw})^2}{2\sigma^2}}}{(2\pi\sigma^2)^{-1/2}e^{-\frac{(s-\mu_{ccw})^2}{2\sigma^2}}} \right)$$

260 (1)

261 and chooses the action a_{cw} when $\log \Lambda(s) > \beta$.
262
263 In standard SDT models the origin and scale of the sensory evidence is arbitrary (Wickens
264 2001; Green and Swets 1966). A typical choice is (Wickens 2001; Green and Swets 1966)

$$\mu_{cw} = \frac{d'}{2} \qquad \mu_{ccw} = -\frac{d'}{2} \qquad \sigma = 1$$

265 (2)

266 which results in $\log \Lambda(s) = d's$. That is, one can use directly the evidence as a decision
267 variable and choose a_{cw} when $s > c = \beta/d'$ (Wickens 2001; Green and Swets 1966).
268
269 The probability of choosing clockwise when θ_i is clockwise is

$$P\left(a = a_{cw}; \mu = \mu_{cw}\right) = \frac{1}{\sqrt{2\pi}} \int_c^\infty e^{\frac{-(s-\mu_{cw})^2}{2}} \, ds = \Phi(\mu_{cw} - c) \tag{3}$$

where Φ is the standard cumulative normal function. To relate this probability to the magnitude of the stimulus, this standard SDT could be extended to include how the stimulus is transduced into sensory evidence (García-Pérez and Alcalá-Quintana 2013; Schneider and Bavelier 2003; García-Pérez and Peli 2014; Schneider and Komlos 2008). Adding the transduction provides a meaningful origin and scale to the sensory evidence. Assuming that the transduction is linear

$$\mu_{cw} = a\theta_i + b \tag{4}$$

the probability of choosing clockwise as a function of θ_i becomes

$$P\left(a = a_{cw}; \theta_i\right) = \Phi(a\theta_i + b - c) = \Phi\left(\frac{\theta_i - (\delta_D - \delta_S)}{\sigma}\right) \tag{5}$$

where

$$\delta_S = \frac{b}{a} = \text{sensory bias} \qquad \delta_D = \frac{c}{a} = \text{decisional bias} \qquad \sigma = \frac{1}{a} \tag{6}$$

which corresponds to a psychometric function centered on $\delta_D - \delta_S$ with slope given by σ.

Consider the trials in which the grating is presented in orientations around the horizontal orientation and the reference is on the right (the reasoning that follows also holds for vertical orientations). If the orientation of the grating can take M different values, each value is presented n times and k_i is the number of times that the participant pressed the *down* key (clockwise), then the probability density function that defines statistical model for these trials is

$$f(k_1, \ldots, k_M; \delta_S, \delta_D, \sigma) = \prod_{i=1}^M \binom{n}{k_i} \Phi\left(\frac{\theta_i - (\delta_D - \delta_S)}{\sigma}\right)^{k_i} \left(1 - \Phi\left(\frac{\theta_i - (\delta_D - \delta_S)}{\sigma}\right)\right)^{n-k_i} \tag{7}$$

Given that f depends on $\delta_D - \delta_S$, it is not possible to distinguish sensory from decisional biases.

Consider now the trials for the left reference. A criterion c associated to a bias to choose responses consistent with clockwise orientation for the right reference corresponds to a criterion $-c$ for the left reference. The statistical model that incorporates responses for the two locations of the reference is

$$f(k_1, \ldots, k_{2M}; \delta_S, \delta_D, \sigma) = \prod_{i=1}^M \binom{n}{k_i} \Phi_R^{k_i} (1 - \Phi_R)^{n-k_i} \prod_{i=M+1}^{2M} \binom{n}{k_i} \Phi_L^{k_i} (1 - \Phi_L)^{n-k_i} \tag{8}$$

where

$$\Phi_R = \Phi\left(\frac{\theta_i - (\delta_D - \delta_S)}{\sigma}\right) \qquad \Phi_L = \Phi\left(\frac{\theta_i - (-\delta_D - \delta_S)}{\sigma}\right) \tag{9}$$

and the index i larger than M refers to the trials for the left reference. Now, by fitting two psychometric functions conjointly, δ_D and δ_S are not degenerated and could be estimated. This is the exact model that we fitted for 17 of the 34 groups (17 participants that discriminate orientations around the horizontal and the vertical orientation in Experiment 1). For the rest of the groups, we also fitted this basic model, but adding some extra features that significantly improved the quality of the fit (using likelihood ratio tests, see *Materials and*

309   *Methods*).

310

311   The first feature is related to the variability of the sensory evidence σ. The basic model
312   considers that this variability does not depend on where the participants imagined the
313   reference, which results in the two psychometric functions having the same slope. We found
314   this to be the case in 28 of the 34 fits, but in 6 groups we found that considering different
315   variabilities (σ_1 and σ_2) for the two locations of the reference was better. It might be that
316   orienting attention to different parts of the visual field might change the uncertainty in the
317   sensory evidence for some participants.

318

319   The other feature that we added consisted in adding lapses, which are responses that are
320   incorrect independently of the sensory evidence (Kingdom and Prins 2016; Gold and Ding
321   2013). This might occur, for example, when the participant misses the stimulus because of
322   blinking or a loss of attention. To incorporate lapses into the basic model, Φ_R need to be
323   replaced by $\lambda_1 + (1 - \lambda_1 - \lambda_2)\Phi_R$ and Φ_L by $\lambda_1{}' + (1 - \lambda_1{}' - \lambda_2{}')\Phi_L$ (Kingdom and Prins
324   2016). From the 34 groups, adding lapses improved the fit in 14 cases. From those, 3 fits
325   required the 4 lapse parameters, 4 fits required 2 lapse parameters (one for each
326   psychometric function, $\lambda_1 = \lambda_2; \lambda_1' = \lambda_2'$) and 7 fits required 1 lapse rate ($\lambda_1 = \lambda_2 = \lambda_1' = \lambda_2'$
327   ). Importantly, including a lapse rate parameter λ^* placed on the right asymptote for the right
328   reference

329

330     $\lambda_1 + \lambda^* + (1 - \lambda_1 - \lambda_1 - \lambda^*)\Phi_R$ (10)

331

332   and placed on the left asymptote for the left reference

333

334     $\lambda_2 + (1 - \lambda_2 - \lambda_2 - \lambda^*)\Phi_L$ (11)

335

336   did not improve significantly the fit for any group, which indicates that decisional biases
337   cannot be explained by a tendency of participants to select one alternative completely
338   independently of the sensory evidence.

339

340   Perceptual tasks with two symmetric alternatives have been also modeled using a high
341   threshold model, called the indecision model (García-Pérez and Alcalá-Quintana 2013;
342   García-Pérez and Peli 2014). This model is similar to the SDT model described, but divides
343   the sensory axis in 3 regions delimited by c_1 and c_2. When the sensory evidence is lower
344   than c_1 the participant chooses a_{ccw} and when is larger than c_2, chooses a_{cw}. Critically, when
345   the sensory evidence lies between c_1 and c_2—called interval of uncertainty—the model
346   assumes that the observer is undecided and guesses the response (choosing a_{ccw} with
347   probability ξ). The probability of choosing clockwise when θ_i is clockwise and the reference
348   is on the right is

349

350     $$P\left(a = a_{cw}; \mu = \mu_{cw}\right) = \frac{1}{\sqrt{2\pi}} \int_{c_2}^{\infty} e^{\frac{-(s - \mu_{cw})^2}{2}} \, ds + \xi \frac{1}{\sqrt{2\pi}} \int_{c_1}^{c_2} e^{\frac{-(s - \mu_{cw})^2}{2}} \, ds$$

351

352     $$= \Phi(\mu_{cw} - c_2) + \xi \left(\Phi(c_2 - \mu_{cw}) - \Phi(c_1 - \mu_{cw})\right).$$ (12)

353

354   For the left reference, assuming that c_1 and c_2 do not change, ξ should be replaced by

9

355   $(1 - \xi)$. We fitted this model to the 19 groups with significant decisional biases and found
356   that for all of them (except for participant 8 for the vertical condition in Experiment 1) the
357   SDT model was better using the Akaike information criterion (Burnham and Anderson 2004).
358   Given that the indecision model has 2 parameters more than the SDT model (c is replaced
359   by c_1 and c_2 and ξ is introduced), we also compared the SDT model to a simplified version of
360   the indecision model with symmetric boundaries $c_1 = -c_2$ (García-Pérez and Alcalá-
361   Quintana 2013; García-Pérez and Peli 2014). In this case, the SDT model was better for all
362   the groups.

365   **DISCUSSION**

367   We showed that, in a simple discrimination task with two symmetric alternatives, most
368   people exhibit global choice biases. Changing the stimulus-response mapping and testing a
369   task with two asymmetric alternatives, we found that these biases reflect biases in the
370   sensory evidence and in the decisional process. Specifically, about half of the participants
371   showed biases consistent with only a sensory origin and about half of the participant biases
372   with a contribution of sensory and decisional biases. We also found that a very few
373   participants exhibited biases consistent with only a decisional origin.

375   A SDT model, in which the sensory biases were included as an intercept term in a linear
376   transduction of the stimuli (García-Pérez and Alcalá-Quintana 2013; Schneider and Bavelier
377   2003; García-Pérez and Peli 2014; Schneider and Komlos 2008) and decisional biases
378   correspond to a shift in the criterion, fitted well the choice behavior of the participants. A
379   model in which participants have a tendency to choose one alternative independently of the
380   magnitude of the sensory evidence did not fit well the data; it rather predicts an asymmetry
381   on the lapse rate across locations of the reference that was not observed. Finally, a model
382   (García-Pérez and Alcalá-Quintana 2013; García-Pérez and Peli 2014) in which participants
383   guess when the sensory evidence lies within some uncertainty range was not parsimonious:
384   first, to fit the data for the participants with pure sensory biases, the model needs that
385   participants, when uncertain, guess the two alternatives equally often; second, for the
386   participants with decisional biases, we found that the SDT model provided a better fit.

388   Perceptual discrimination tasks with two symmetric alternatives are often regarded as
389   performance tasks (Carandini and Churchland 2013; Dayan and Abbott 2001). If a stimulus
390   has positive signal (e.g. rightward motion) relative to a neutral point (no net motion), but the
391   decision--maker chooses the alternative consistent with negative signal (leftward motion),
392   the response is considered an error (false alarm). Our results, however, suggest that in
393   some cases a positive signal might be perceived consistently as a negative signal (sensory
394   bias). Consequently, it might be inappropriate to consider these responses as errors and, in
395   case feedback is given, provide a negative reward. Our results suggest that perceptual
396   discrimination tasks with two symmetric alternatives should be regarded as appearance
397   tasks (Kingdom and Prins 2016; Gold and Ding 2013).

399   Discrimination tasks with two symmetric alternatives are commonly used to assess how
400   perception is affected by contextual cues (Carrasco, Ling, and Read 2004; Schwartz, Hsu,
401   and Dayan 2007), but in some scenarios it is unclear whether the context influences

402 perception or biases decisions (Carrasco 2011; García-Pérez and Alcalá-Quintana 2013;
403 Michael J. Morgan et al. 2012; Störmer, McDonald, and Hillyard 2009; Schneider 2011;
404 Anton-Erxleben, Abrams, and Carrasco 2010; Jogan and Stocker 2012; Mather and
405 Sharman 2015). Our results indicate that, even when the symmetry of the task is not broken
406 by the context, half of the participants exhibit decisional biases. This suggests that to reliably
407 estimate sensory biases in the presence of contextual cues, it might be better to use
408 manipulations of the stimulus-response mapping like the one that we used or tasks for which
409 the potential contribution of decisional biases is reduced or eliminated (Jogan and Stocker
410 2012; Patten and Clifford 2015; M. J. Morgan 2014).

412 To facilitate that participants internalize two different associations between perception and
413 the responses, we asked them to compare the orientation of the stimulus to a reference
414 imagined in two different locations. Given that the reference was not physically present, we
415 think, however, that it is likely that participants were performing judgments of absolute
416 orientation relative to an internal point of horizontality (or verticality). As we found evidence
417 that the sensory biases were consistent with a global perceptual rotation, if participants were
418 performing judgments of relative orientation between the stimulus and the reference—
419 instead of judgments of absolute orientation—then sensory biases should not be expected,
420 as both the stimulus and the reference should be biased in the same direction.

422 We found a good agreement between the sensory biases estimated from the symmetric and
423 the asymmetric task. We also found a good agreement between tasks when the biases were
424 estimated taking into account only one localization of the reference, and thus for which it was
425 not possible to assess the contribution of sensory and decisional biases (see legend for
426 Figure 3A). This is expected given the large contribution of sensory biases to the total
427 magnitude of the biases. In the temporal domain, however, the biases estimated from
428 temporal order judgments (symmetric task) and simultaneity judgments (asymmetric task) do
429 not agree (Love et al. 2013; Linares and Holcombe 2014; van Eijk et al. 2008), which
430 suggests that decision making for time perception might be even more affected by decisional
431 biases (Linares and Holcombe 2014; Shore, Spence, and Klein 2001; Schneider and
432 Bavelier 2003).

435 **ACKNOWLEDGMENTS**

443 **MATERIALS AND METHODS**

445 **Participants**

447 The study was approved by the ethical committee of the University of Barcelona and
448 followed the requirements of the Helsinki convention. The participants, who did not know the
449 hypothesis of the experiments, provided written consent to perform the experiments. Twenty-

450   one participants were recruited for Experiment 1 and sixteen for Experiment 2.
451
452   **Stimuli and tasks**
453
454   Stimuli were generated using PsychoPy (Peirce 2007), displayed on a Sony G520 CRT
455   screen (40 cm width and 30 cm height; 60 Hz refresh rate) and viewed from a distance of 57
456   cm in a dark room. They consisted in a Gabor patch (standard deviation (sd) of the Gaussian
457   envelope: 1.33 degrees of visual angle (dva); maximum luminance: 79 cd/m^2) and a red
458   Gaussian blob (sd: 0.1 dva; maximum luminance: 19 cd/m^2) on top of it that participants
459   were asked to fixate during the experiment. Stimuli were presented against a uniform circular
460   grey background (diameter: 25 dva; luminance: 43 cd/m^2) that was displayed in a black
461   background (luminance: 0.2 cd/m^2). The verticality of the Gabor was calibrated using a
462   pendulum.
463
464   *Experiment 1:* Participants performed 6 blocks of 360 trials. In each block, 8 conditions were
465   randomly intermixed across trials. On each trial, before the Gabor was presented, a text
466   message informed participants about the condition. A *right: up or down?* message instructed
467   participants to imagine a reference on the right (at the same height of the fixation point) and
468   respond whether the Gabor was pointing down (clockwise) or up (counterclockwise) relative
469   to it. A *left: up or down?* message instructed participants to imagine a reference on the left
470   and respond whether the Gabor was pointing down (counter-clockwise) or up (clockwise).
471   For these conditions, the orientation of the Gabor was chosen randomly from a range
472   centred around horizontal orientation (from -2 to 2 deg in steps of 0.5 deg) according to the
473   method of constant stimuli (Kingdom and Prins 2016). The *up: right or left?* and the *down:
474   right or left?* messages provided parallel instructions for imaginary references on top and at
475   the bottom. For these conditions the orientation was centered around vertical orientation.
476   Participants used the arrow keys to respond. A *right?* message instructed participants to
477   imagine a reference on the right and respond whether the Gabor was aligned with it
478   (pressing *m* key) or not (pressing *n* key). A *left?*, *up?* and *down?* provided parallel
479   instructions for references in other locations. The messages were available until participants
480   pressed the spacebar. The Gabor was presented for 100 ms, 500 ms after the keypress.
481
482   *Experiment 2:* Experiment 2 was like Experiment 1, but included only the symmetric task and
483   orientations around vertical. Participants performed 4 blocks of 270 trials. Half of the
484   participants performed first two blocks in which they were asked to imagined the reference
485   always in the same location within a block and, then, two blocks in which they were asked to
486   imagine the reference at one location that changed randomly across trials. For the other half
487   of participants, the block order was inverted.
488
489   **Instructions**
490
491   Before the experiments, to facilitate the understanding of the instructions, a reference (a
492   green Gabor patch; sd: 0.1 dva; maximum luminance: 29 cd/m^2) was displayed for 5 to 10
493   trials at the corresponding cardinal location at a distance of 6 dva from the center of the
494   fixation point.
495
496
497

Analysis

The data and the code to do the statistical analysis and create the figures is available at https://github.com/danilinares/2018LinaresAguilarLopezmoliner. The model fitting, goodness of fit and model selection (likelihood ratio test and Akaike information criterion) was performed using the R package *quickspy* (Linares and López i Moliner 2016), which under the development version allows fitting several psychometric functions conjointly.

Experiment 1 (symmetric task): For four of the twenty-one participants, a preliminary analysis revealed that the responses were inverted or not modulated by the orientation of the grating and were not analyzed further. For each participant and condition of overall orientation (horizontal or vertical), we fitted the model in equation (8) with all the extra features (2 slopes and 4 lapses, see *Models*; parameters: δ_S, δ_D, σ_1, σ_2, λ_1, λ_2, λ_1', λ_2') using maximum likelihood estimation. Then, using consecutive likelihood ratio tests performed using the χ^2 distribution and a significance level of 0.05 (Prins and Kingdom 2018), we reduced model complexity to select for each participant and condition of orientation the simplest model that captured the data and incorporated at least the parameters δ_S, δ_D and σ. The first two parameters correspond to the sensory and decisional biases plotted in Figure 1G. To assess, for each participant and condition of orientation, which was the best bias model, we performed further likelihood ratio tests with simpler models. The best bias model was described as *Sensory bias* if a simpler model with $\delta_D = 0$ provided a better fit; *Decisional bias* if a model with $\delta_S = 0$ was better; *No bias* if a model with $\delta_D = \delta_S = 0$ was better; and *Sensory + decisional bias* if the complexity of the original model could not be further reduced. When we compared the models with lapse parameters with the models without lapses, we used a lapse rate of 0.01 instead of zero because this resulted in better fits (Prins 2012).

Experiment 1 (asymmetric task): For one of the participants that could perform the symmetric task, the responses were not modulated by the orientation of the grating for the asymmetric task and the data was not analyzed. To estimate sensory and decisional biases and assess which bias model was better, we used the same procedure described for the symmetric task.

Experiment 2: The data were analyzed as it is described for the symmetric task in Experiment 1.

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SUPPLEMENTARY MODELS

A simple SDT model for the asymmetric task divides the sensory axis in 3 regions delimited by c_1 and c_2. When the sensory evidence is lower than c_1 or larger than c_2, the participant responds *no aligned*. When the sensory evidence lies between c_1 and c_2, the participant responds *aligned*—in contrast to the indecision model (García-Pérez and Alcalá-Quintana 2013; García-Pérez and Peli 2014), there is not guesses in this case. The probability of choosing *aligned* when θ_i is clockwise is

$$P\left(a = \text{aligned}; \mu = \mu_{cw}\right) = \frac{1}{\sqrt{2\pi}} \int_{c_1}^{c_2} e^{\frac{-(s-\mu_{cw})^2}{2}} \, ds =$$

$$= \Phi(c_2 - \mu_{cw}) - \Phi(c_1 - \mu_{cw}) = \Phi\left(\frac{-\theta_i - (\delta_S + \delta_{D2})}{\sigma}\right) - \Phi\left(\frac{-\theta_i - (\delta_S + \delta_{D1})}{\sigma}\right) \quad (13)$$

where

$$\delta_S = \frac{b}{a} \qquad \delta_{D1} = \frac{c_1}{a} \qquad \delta_{D2} = \frac{c_2}{a} \qquad \sigma = \frac{1}{a} \quad (14)$$

The model assumes that for one of the references (right) the criteria are symmetric $\delta_{D2} = -\delta_{D1}$, but not for the other reference (left). The statistical model that incorporates the two locations of the reference is thus

$$g(k_1, \ldots, k_{2M}; \delta_S, \delta_D, \sigma) = \prod_{i=1}^{M} \binom{n}{k_i} \Psi_R^{k_i} \left(1 - \Psi_R\right)^{n-k_i} \prod_{i=M+1}^{2M} \binom{n}{k_i} \Psi_L^{k_i} \left(1 - \Psi_L\right)^{n-k_i} \quad (15)$$

where k_i is the number of times that the participant responds *aligned* and

$$\Psi_R = \Phi\left(\frac{-\theta_i - (\delta_S - \delta_{D1})}{\sigma}\right) - \Phi\left(\frac{-\theta_i - (\delta_S + \delta_{D1})}{\sigma}\right)$$

$$\Psi_L = \Phi\left(\frac{-\theta_i - (\delta_S + \delta'_{D2})}{\sigma}\right) - \Phi\left(\frac{-\theta_i - (\delta_S + \delta'_{D1})}{\sigma}\right) \quad (16)$$

This was the best model for 5 or the 32 groups (likelihood ratio tests, see *Materials and Methods*). For 2 groups, assuming symmetric criteria also for the left reference $\delta'_2 = -\delta'_1$ provided a better fit. For 24 groups, assuming the same symmetric criteria for the two locations of the reference $\delta'_2 = \delta_2 = -\delta'_1 = \delta_1$ was better. Finally, for 1 group, the best fit resulted from replacing σ by σ_1 and σ_2.

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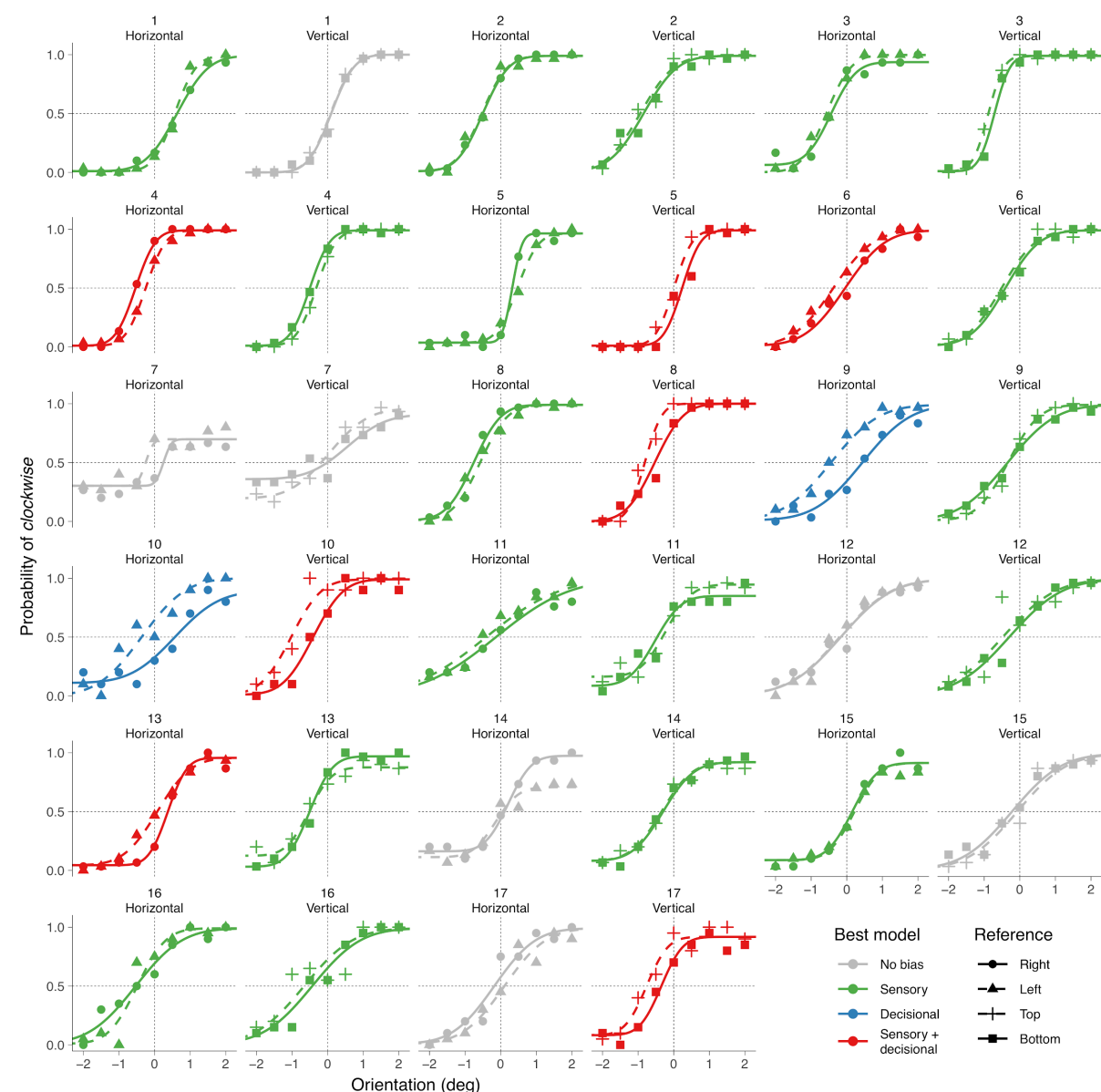
SUPPLEMENTARY FIGURES

Figure supplementary 1. Choice behavior in the symmetric task for all participants in Experiment 1. The psychometric curves (see Models and Materials and Methods) provided a good fit of the data; only for participant 16, the deviance (Kingdom and Prins 2016; Wichmann and Hill 2001) was significant taking into account a χ^2 distribution for the deviance (horizontal orientation: D(14) = 29 , p = 0.098; vertical orientation: D(15) = 28 , p = 0.022).
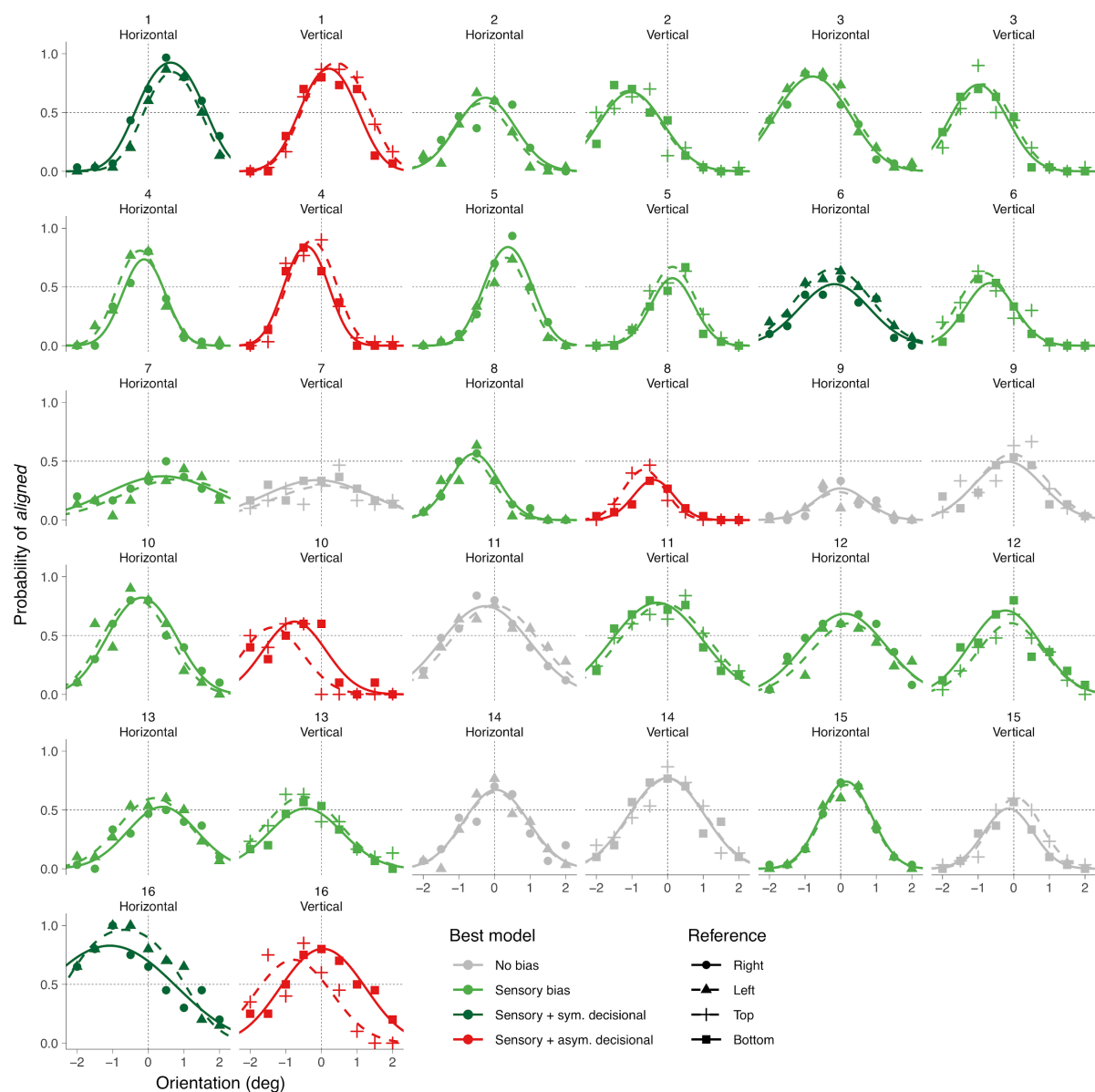
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711 *Figure supplementary 2. Choice behavior in the asymmetric task for all participants in Experiment 1. The*
712 *goodness of fit showed significant deviances for 6 of the 32 groups (participant 2 for vertical and horizontal,*
713 *participant 4 for vertical, participant 9 for vertical, participant 14 for horizontal and participant 16 for horizontal).*
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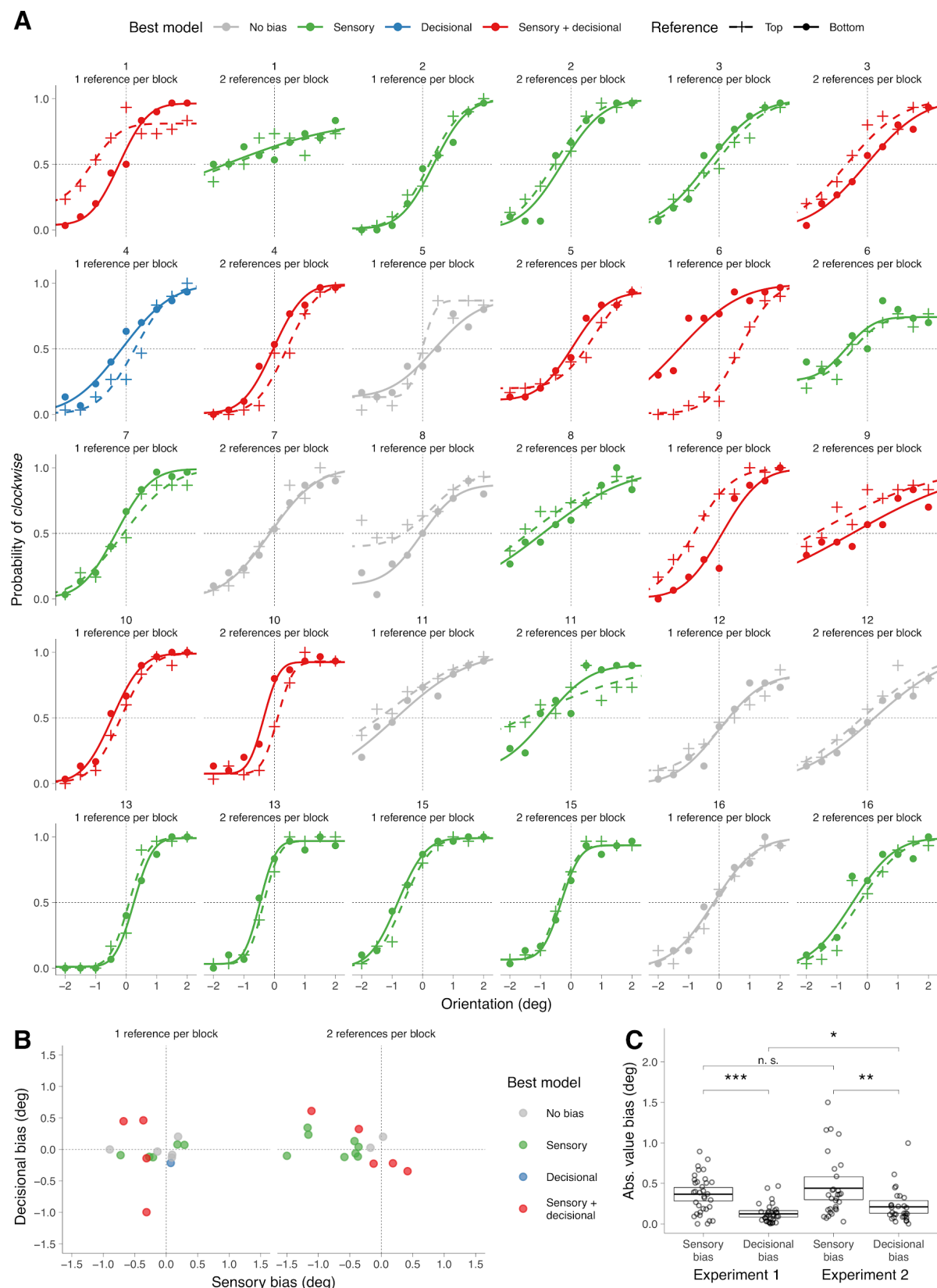719
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Figure supplementary 3. (A) Choice behavior for the 1 reference per block and 2 references per block conditions for all participants in Experiment 2. (B) Decisional and sensory biases for each participant. The color indicates the best model. (C) Across the participants of Experiment 2, a two-way repeated measures ANOVA for the absolute value of the biases indicated no significant effect of number of references per block (1 reference per block or 2 references per block; (F(1,14) = 3.7 ; p = 0.073), a significant effect of the type of biases (sensory or decisional; F(1,14) = 8.7 ; p = 0.010) and no significant interaction (F(1,14) = 3.6 ; p = 0.078). The graph shows the absolute

734   *value of the biases from Experiment 1 (also showed in Figure 1H) and Experiment 2 (collapsed across number of*
735   *references per block). The crossbars display the mean and the 95% t-test confidence intervals. For Experiment 2,*
736   *the absolute value of the sensory and the decisional biases is significantly different (t(29) = 3.13, p = 0.0040).*
737   *Across experiments, the absolute value of the sensory biases is not significantly different (t(47) = 0.92, p =*
738   *0.3619), but the absolute value of the decisional biases is significantly different (t(44) = 2.0, p= 0.048).*
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