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Mind over matter: A perceptual decision bias toward filled-in stimuli in

the blind spot

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Author Contributions

BE, JO and PK designed the study. BE and KH recorded and analyzed the data. BE, JO and PK

wrote and revised the manuscript.

18

19   **ABSTRACT**

20   Although there are no photoreceptors corresponding to the physiological blind spots, we

21   experience visual content there as if it were veridical, when it is in fact only "filled in" based on the

22   surroundings. Given that we have at least implicit knowledge that a stimulus is being filled in,

23   could this knowledge bias our behavior? We asked subjects to choose between a stimulus

24   partially presented in the blind spot that elicits filling in and another at the same eccentricity

25   outside of the blind spot. Subjects displayed a bias toward the blind spot stimulus, where the filled-

26   in part could have actually concealed a non-target (15.01%, CDI_{95}: 8.49%-21.08%). Two control

27   experiments confirmed this finding. The preference for inferred versus veridical content suggests

28   that the locally inferred percept is favored due to reduced external noise in concordance with

29   predictive coding models of visual processing.

30

31 **INTRODUCTION**

32 In order to make optimal and adaptive decisions, animals integrate multiple sources of sensory

33 information. This is especially important in conditions of uncertainty when information from a

34 single sensory modality would be otherwise insufficient. For example, when animals are

35 confronted with weakly coherent stimuli during random-dot motion experiments, their

36 performance and corresponding neural activity vary proportionally to signal strength in a way that

37 is consistent with the progressive integration of evidence over time [1,2]. Crucially, sensory

38 integration does not only operate as a temporal accumulator because it is also possible to

39 combine information from multiple sensory sources [3–8].

40 In the case of multisensory perception, several experiments have shown that integration

41 often occurs in a statistically optimal way. This has been best demonstrated in cue-integration

42 experiments in which humans perform as if they were weighting the different sources of

43 information according to their respective reliabilities [9–12]. This form of statistical inference has also

44 been demonstrated for cortical neurons of the monkey brain, with patterns of activity at the

45 population level that are consistent with the implementation of a probabilistic population code [13,14].

46 In many of these sensory integration experiments, the perceptual reliability of different

47 inputs is probed through quantitative manipulations of the inputs' signal-to-noise ratios [15–17].

48 However, some percepts are unreliable not because they are corrupted by noise but because

49 they are internally inferred and thus intrinsically uncertain. This occurs naturally in the monocular

50 visual field at the physiological blind spot, where content is "filled in" based on information from

51 the surroundings. In this case, no veridical percept is possible at the blind spot location. Though

52 changes in reliability due to noise directly result in behavioral consequences, the effects of the

53 qualitative difference between veridical and inferred percepts that are otherwise apparently

54 identical is unknown.

55 We recently reported differences in the processing of veridical and inferred information at

56 the level of EEG responses[18]. In the present experiment, we address whether such an

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57   assessment of a dichotomous, qualitative difference in reliability is available for perceptual

58   decision-making. Using 3D shutter glasses, we presented one stimulus partially in the

59   participant's blind spot to elicit filling in and a second stimulus at the same eccentricity in the nasal

60   field of view outside of the blind spot. The subject's task was to indicate which of the two stimuli

61   was continuously striped and did not present a small orthogonal inset (see Fig. 1A). Crucially,

62   stimuli within the blind spot are filled in and thus perceived as continuous, even when they present

63   an inset. In the diagnostic trials, both stimuli were physically identical and continuous, and

64   subjects were confronted with an ambiguous decision between veridical and partially inferred

65   stimuli.

66   We evaluated two mutually exclusive hypotheses in which perceptual decision-making

67   could proceed when confronted with an ambiguous decision between veridical and inferred

68   percepts. In the first case, agents are unable to make perceptual decisions based on an implicit

69   assessment of differences in reliability between stimuli that otherwise look identical. Therefore,

70   subjects would have an equal chance of selecting stimuli presented inside or outside the blind

71   spot. Alternatively, it might be possible to use the information about the reduced reliability of filled-

72   in information. Therefore, we expect subjects to follow an optimal strategy and trust a stimulus

73   presented outside the blind spot, where the complete stimulus is seen, more often than when the

74   stimulus is presented inside the blind spot, where it is impossible to know the actual content of

75   the filled-in part.

76

77   **RESULTS**

78   We conducted three experiments (see Fig. 1 and the methods for a detailed task description).

79   The first experiment tested the presence of a bias against the blind spot location; the other two

80   experiments were replications of the first experiment with additional control conditions to test the

81   existence of biases between the nasal and temporal fields of view at locations that do not

82   correspond with the blind spot.

83   In the first experiment, 24 subjects performed a sometimes ambiguous 2-AFC task in

84   which they had to indicate which of the two stimuli was continuously striped instead of presenting

85   a small orthogonal inset (Fig. 1A). The stimuli were presented simultaneously in the periphery at

86   external locations corresponding to the blind spots (Fig. 1B, C). We used a 3D monitor and shutter

87   glasses that allowed for controlled monocular display of the stimuli. The first experiment consisted

88   of mixed perceptually ambiguous and unambiguous trials that we used to test the two competing

89   hypotheses on whether the reliability assessments of these conditions differed for decision-

90   making.

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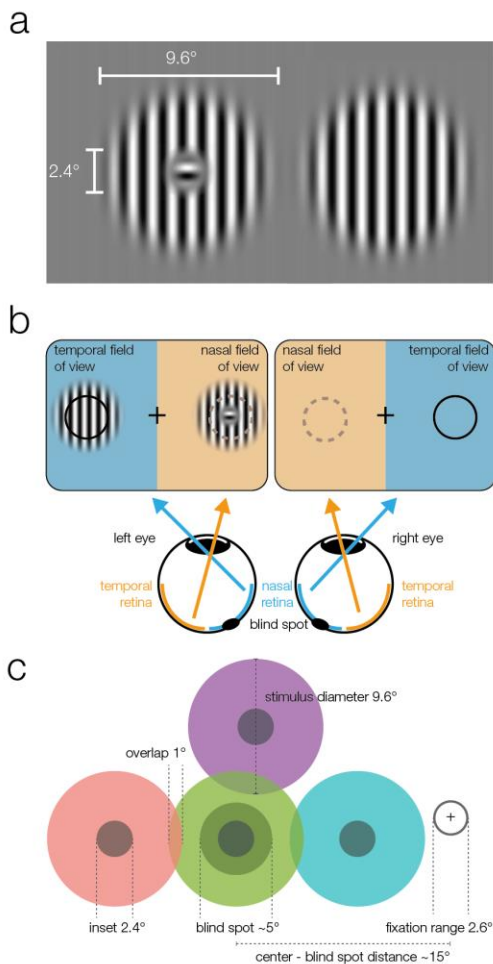
Figure 1: Stimuli and stimulation

a) Striped stimuli used in the study. The inset was set to ~50% of the average blind spot size. The global orientation of both stimuli was the same, but in different trials it could be either vertical (as shown here) or horizontal (not shown).

b) Two images were displayed using shutter glasses. For example, the left stimulus could be shown either in the temporal field of view (nasal retina) of the left eye (as in the plot) or in the nasal field of view (temporal retina) of the right eye (not shown). This example trial is unambiguous: The stimulus with an inset can be seen veridically and, therefore, the correct answer in this trial is to select the left stimulus.

c) The locations of stimulus presentation in the three experiments. All stimuli were presented relative to the individual blind spot, and the average blind spot location is shown here. All three experiments included the blind spot location (green). In the second experiment, effects at the blind spot were contrasted with a location above it (purple). In the third experiment, the contrasts were in positions located to the left or the right of the blind spot. Please note that the contrast between locations is across trials, and stimuli are presented at symmetrical positions in any given trial.

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111   In the unambiguous trials, an orthogonal inset was present in one of the stimuli.

112   Importantly, in these trials, the stimulus with the inset was outside the blind spot and therefore

113   clearly visible. As expected, subjects performed with near perfect accuracy (Fig. 2, unambiguous

114   trials), choosing the continuous stimulus in an average of 98.8% of trials (95%-quantile [96.4%–

115   100%]).

116

117   There were two types of ambiguous trials. In the first type (Fig. 2, ambiguous control), one

118   of the following applied: both stimuli were continuous and appeared outside the blind spots in the

119   nasal visual fields (Fig. 2, line 3); both were continuous and appeared inside the blind spots (Fig.

120   2, line 4); or one was continuous, the other had an inset, and both appeared inside the blind spots

121   either in the left/right and right/left ones (Fig. 2, lines 5 and 6). The central parts of the stimuli,

122   where the insets could appear, were perfectly centered inside the blind spot when presented (Fig.

123   1A). These stimuli were thus perceived as continuous due to filling in of the surrounding visible

124   part of the stimuli. Thus, in all four versions, subjects perceived two identical stimuli, and there

125   was no single correct answer. In this type of ambiguous trial, subjects showed a small global

126   leftward bias and chose the left stimulus in 53.6% of trials (Fig. 2, dashed line). In addition, no

127   difference can be seen between the perception of pairs of filled-in stimuli and pairs of veridical

128   continuous stimuli (Fig. 2, line 3 vs. 4-6). This type of ambiguous control trial clearly shows that

129   fill-in is perfect in our experiment.

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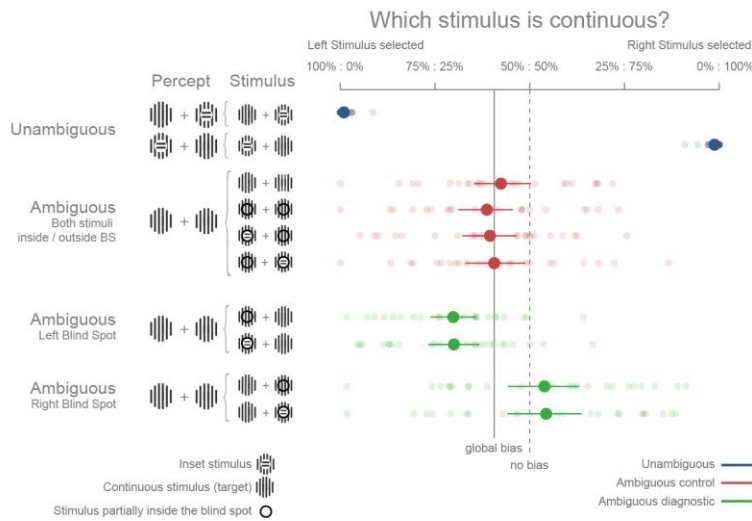
Figure 2: First experiment

In the first column, the percept of the subjects and the actual stimulation is contrasted. Stimuli containing a dark-line circle were presented in the blind spot, and thus an inset stimulus is perceived as a continuous stimulus. In the graph, the average response of each subject (n=24), and the group average with 95% bootstrapped CI are shown. The unambiguous trials show that the subjects were almost perfect in their selection of the continuous stimulus (blue). For the ambiguous control trials (red), both stimuli were presented either outside or inside the blind spot. Here only a global bias toward the left stimulus can be observed (solid line, the mean across all observed conditions). Note that the performance of presenting an inset in the blind spot is identical to presenting a continuous stimulus in the blind spot. The ambiguous diagnostic conditions (green) show the bias toward the blind spot for either side.

The second type of perceptually ambiguous trial allowed us to directly address our

hypotheses. Here, the important manipulation is that we can show stimuli at symmetrical

locations, with one inside and the other outside the blind spot (Fig. 2, ambiguous diagnostic). This

allowed us to test whether subjects show a bias against the stimulus that is partially inferred (inset

area inside the blind spot) and in favor of the veridical stimulus (in the opposite visual field). Note

here, that selecting the filled-in stimulus is a sub-optimal decision: the stimulus presented partially

in the blind spot is the only one who could possibly contain the inset. This is explicit in the cases

where an inset is shown in the blind spot but rendered invisible by fill-in (Fig.2, line 8 and 10). For

analyzis, we modeled the probability increase of choosing the right stimulus with predictors if the

right stimulus was presented in either the temporal visual field of the right eye (blind spot) or the

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153   nasal visual field of the left eye (non-blind spot), a similar factor was used for the left stimulus.

154   Consequently, the two one-sided model estimates were collapsed to a single measure.

155   Figure 2 (ambiguous diagnostic) shows that subjects indeed presented a bias. However,

156   in contrast to our expectations, subjects were more likely to choose the filled-in percept (15.01%,

157   CDI_{95} 8.49%–21.08%). In other words, when subjects had to decide which of the two stimuli (both

158   perceived as being continuous, and in most cases actually physically identical) was less likely to

159   contain an inset, they showed a bias for the one in which the critical information was not sensed

160   but inferred. Remarkably, this result is at odds with both of the experimental predictions that

161   postulated a bias in favor of the veridical stimulus or no bias.

162   In the second experiment, we focused on replicating the unexpected result of experiment

163   1 and evaluating whether the blind spot bias observed was due to systematic differences between

164   nasal and temporal retinae. In experiment 1, we presented stimuli at mirror eccentricities inside

165   and outside the blind spot. Therefore, we had to present them to opposite sides of one eye's

166   retina (temporal and nasal respectively; see Fig. 1B). Otherwise, the stimuli would have appeared

167   at the same external coordinates and led to binocular rivalry[19]. In experiment 2, we tested whether

168   the bias in experiment 1 was unspecific to the blind spot location but related to known differences

169   between the temporal and nasal retina (for a review, see [20]). There is higher photoreceptor

170   density[21], spatial resolution[22], luminance discrimination[23] and orientation discrimination[24] at

171   locations that project to the nasal retina (the temporal visual field where the blind spots are

172   located). Thus, we repeated our experiment with a new group of subjects (n=27) and an additional

173   condition. In this new condition, the two stimuli were displayed at symmetrical locations above the

174   blind spot (25° above the horizontal meridian; see Fig. 1C). The results of this second experiment

175   (Fig. 3A triangles, Fig. 3B for model parameters) replicate the previous observations of

176   experiment 1. Subjects showed a bias for selecting the stimulus presented inside the blind spot

177   (12.5%, CDI_{95}7.35%–17.49%). However, we also found a bias in the control condition toward the

178   stimuli presented in the temporal visual field above the blind spot (6.63%, CDI_{95}0.77%–12.3%). The

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179   bias was nevertheless stronger inside the blind spot (paired-diff: 6.11%, CDI_{95} 1.16%–10.78%). In

180   summary, on top of the bias inside of the blind spot area, we observed that subjects also showed

181   an additional, smaller bias for stimuli presented to the nasal retina (temporal visual field).

182   We performed an additional third experiment on a new group of subjects (n=24). Here, we

183   compared biases in the blind spot to two other control conditions flanking the blind spot region

184   from either left or right (Fig. 3A squares). The blind spot location again revealed the strongest effect

185   (13.18% CDI_{95} 6.47%–19.64%), while the locations inwards and outwards resulted in a 2.85% and

186   4.8% bias, respectively, for the temporal visual field (CDI_{95} -1.1%–6.65%; CDI_{95} 0.58%–8.89%). The

187   bias of both control locations was different from the bias of the blind spot location (inward vs. BS:

188   10.51%, CDI_{95} 3.55%–17.29%; outward vs. BS: 8.61%, CDI_{95} 0.98%–16.04%). In this experiment, as

189   in experiments 1 and 2, we observed a bias specific to the blind spot region.

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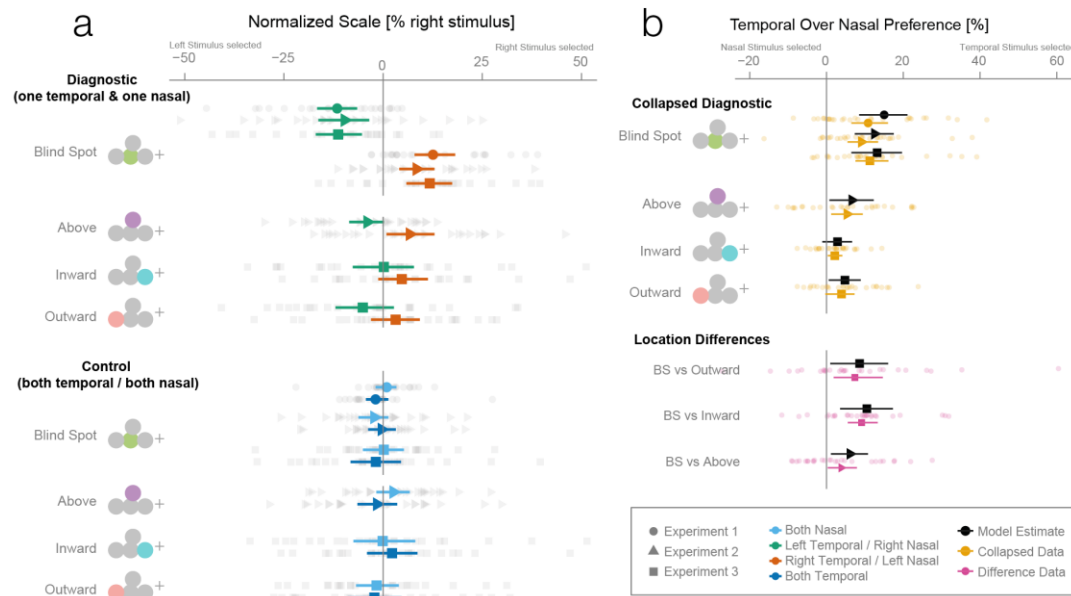
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193 **Figure 3: All experiments**

194 **a)** Fraction of choosing the right stimulus dependent on location (indicated by icon) and
195 experiment (Exp. 1: n=24, Exp. 2: n=27, Exp. 3: n=24). For plotting purposes we preprocessed
196 the data by subtracting the global bias. Each gray dot depicts one subject. The error bars depict
197 mean and 95% bootstrapped CI. A bias for the blind spot was visible in the form of "left" responses
198 when the left stimulus was presented in the temporal visual field of the left eye (green, nasal /
199 blind spot retina of the left eye) and of more "right" responses when the right stimulus was
200 presented in the temporal visual field of the right eye (green, nasal / blind spot of the right eye) in
201 all experiments. A bias was visible in the other tested locations, but it was much smaller. Control
202 conditions show that there was no bias if the stimuli were shown either both inside the temporal
203 fields (dark blue) or both inside the nasal fields (light blue).
204
205 **b)** Yellow color indicates combined data over the left and right side. Black color indicates the
206 posterior 95% credibility interval of a logistic mixed linear model. A bias for the blind spot stimulus
207 was clearly evident in all experiments. A much weaker effect was present in the other tested
208 locations. The within-subject differences between the blind spot and the other locations are
209 depicted in purple, and the respective modeled difference is shown in black.
210

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212 A bias for the temporal visual field, especially the blind spot, can also be reflected in the

213 distribution of reaction times. We compared the reaction times of trials where subjects selected a

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214   stimulus in the temporal visual field against trials where the stimulus in the nasal visual field was

215   selected. No prior hypotheses were formulated for the reaction time. Thus, in contrast to the other

216   analyses presented here, these are explorative. We observed an average reaction time of 637

217   ms (minimum subject average: 394 ms, maximum 964 ms) in the first experiment (Fig. 4A). We

218   used a linear mixed model to estimate the reaction time difference for selecting a stimulus

219   presented inside the blind spot (temporally) against one outside the blind spot (nasally). In the

220   first experiment (Fig. 4B), after excluding three outliers, we observed this effect with a median

221   posterior effect size of 13 ms ($CDI_{95\%}$ 2–42 ms) faster reaction times when selecting the blind

222   spot region. The three outliers (marked red in Fig. 4) were identified visually and removed because

223   they were distinctively different from the rest of the population. The mean of the outliers was 5.2

224   SD away from the remaining subjects. The outliers were nevertheless in the direction of the

225   reaction time effect and did not change its significance (with outliers, 63 ms, CDI_{95}7–124 ms).

226   However, faster reaction times while selecting the blind spot stimulus were not present in the

227   other two experiments. The nominal differences were in the same direction as experiment 1 but

228   comparably small and insignificant (4 ms, CDI_{95} -14–23 ms; and 22 ms. CDI_{95} -13–57 ms). Similar

229   results were obtained for the other locations tested (above: 8 ms, CDI_{95} -38–53 ms; outward: 2

230   ms CDI_{95} -13–16 ms; inward: 4 ms, CDI_{95} -29–37 ms). Furthermore, an analysis of the combined

231   data shows no evidence for a reaction time effect in any location, and the blind spot estimate

232   changes here to 12 ms (CDI_{95} -23–47 ms). Even though the signs of all three experiments indicate

233   that the reaction time for nasal stimuli is slower than for temporal ones despite the large total

234   number of subjects (n=75), the results of our experiments remain inconclusive on this issue.

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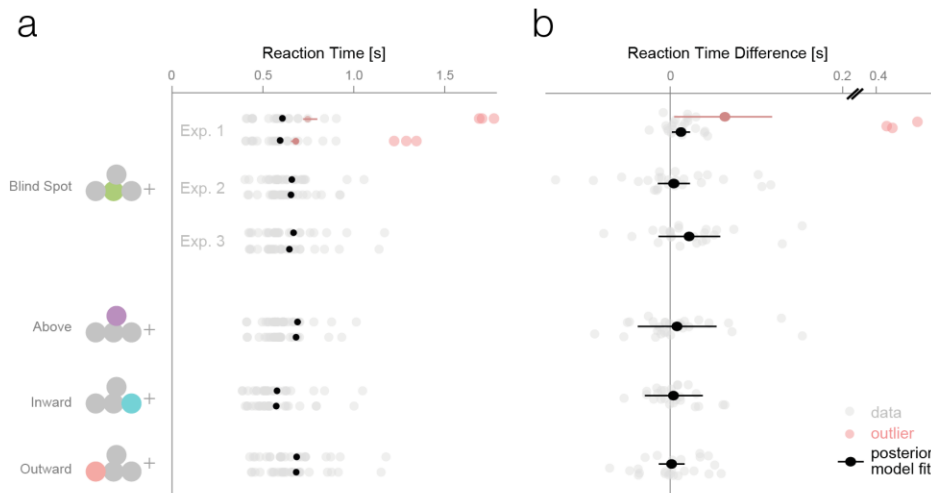
Figure 4: Reaction Times

a) Reaction times of nasal chosen trials (upper row of each pair) and temporal chosen trials (lower row of each pair). Black dots indicate the average reaction time across subjects with 95% bootstrapped CI (in A too small to display). Red circles depict the removed outliers and the mean with the outliers included.

b) Nasal chosen minus temporal chosen reaction times. The summary statistics depict the 95% CDI of the posterior effect estimate. We observe a bias in the first experiment and the blind spot with and without the outlier, but not in the other experiments or conditions.

For an overview of all experiments and the results of a logistic model that combines all selection-bias experiments, see Table 1 of the Appendix. In the combined model, we did not find any differences between the temporal field effects at locations other than the blind spots. In other words, the temporal field effects of the locations inwards, outwards and above were not different from each other. For the sake of clarity, we combined these location levels. Keeping everything else constant, we expect that if we present one stimulus in the blind spot against the equidistant nasal location, we are 13.44% CDI_{95} 9.94%–16.70% more likely to choose the stimulus in the blind spot. This bias is stronger than the effect observed elsewhere in the temporal field by 8.89% CDI_{95} 5.01%–12.53. In summary, subjects showed a robust bias for the blind spot locations that could not be explained by a non-specific bias for the temporal visual field. In the case of this task,

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257   when confronted with an ambiguous choice between veridical and inferred sensory information,

258   human subjects showed a suboptimal bias for inferred information.

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260 **DISCUSSION**

261 In three experiments, we showed that when confronted with identical physical stimulation in a

262 simple decision task, subjects biased their decisions toward stimuli in the temporal field of view.

263 Importantly, subjects showed a consistent bias for blind spot inferred percepts, which was

264 stronger than the bias at any other location in the temporal visual field.

265 Why do subjects choose the blind spot location when it is objectively the least reliable?

266 Our interpretation takes the results at face value: subjects must possess at least implicit

267 information about whether a percept originates from the blind spot in order to show a bias for it.

268 At the same time, the veridical information from the other stimulus is also available. This indicates,

269 that at least for the task presented here, perceptual decision-making can rely more on inferred

270 than veridical information, even when there is knowledge in the system about the nature of this

271 signal and its reduced reliability as a consequence. Thus, a suboptimal decision is made.

272 In the following, we propose two possible explanations for this effect. The first explains the

273 effect simply by stating that the blind spot is 'special' because the information around the optic

274 disc is sampled differently. The second explanation is based on the general notion of predictive

275 coding: the reduced noise in the inferred percept reduces the bottom-up prediction error.

276 In the results section, we introduced the evidence for psychophysical differences between

277 the nasal and temporal visual field, which motivated the control experiments. In the same vein,

278 the parts of the retina surrounding the optic disc might present further enhancements for

279 perception that are useful for a better estimation of the contents of the blind spot area. That means

280 that subjects could perceive the stimulus as more veridical due to enhanced sensory perception

281 at the boundary of the blind spot. Some weak evidence for this has been reported that indicates

282 better disparity estimates (Vernier task) in the peri-blind spot area compared to equally eccentric

283 locations in the nasal visual field. This effect seems to happen only when the element extends

284 into the blind spot and thus produces filling in and not for other filling in processes derived from

15

285   pathological scotomas [25]. This would indicate that the low-level, bottom-up information gained

286   from the blind spot is superior to the veridical input of other retinal origin.

287   Our alternative explanation is based on the framework of predictive coding. For this task,

288   we assume that predictive coding could work both as a way of predicting future sensory input

289   (task context) and static predictions based on spatial context (the filling-in). In our task, this would

290   mean that subjects generated predictions of continuous stimuli in the ambiguous trials. The

291   predicted sensory input was then compared to the incoming sensory input, and an error signal

292   representing the mismatch was returned. The filled-in signal might have had less perceptual

293   noise. This was partially explained by the hypothesized integration process over boundary

294   neurons [26] that act as smoothers and further explained by the fact that no unique perceptual noise

295   from the senses reached the low-level visual areas near the blind spot (as there are no sensory

296   inputs from the stimulus in the blind spot). Thus, with less noise, the inferred sensory input at the

297   V1 blind spot location has a higher signal-to-noise ratio and will match the predicted stimulus

298   signal better. A better match results in a smaller prediction error and thus a higher credibility at

299   later stages. A faster reaction time to the filled-in stimulus compared to the veridical stimulus could

300   be taken as further evidence that the integration process is indeed biased with less noise. With

301   respect to reaction times, our experiments remain inconclusive, and further research is needed

302   to fully support this assumption. In conclusion, predictive coding can best explain our results with

303   the additional assumptions that the signal-to-noise ratio of the blind spot percept is higher due to

304   the fill-in process and/or the blind spot lacking unique noise from the eye.

305   In a recent EEG study with human subjects, we demonstrated that a qualitative reliability

306   assessment exists at the neural level in the form of low- and high-level trans-saccadic predictions

307   of visual content [18]. Notably, active predictions of visual content differed between inferred and

308   veridical visual information presented inside or outside the blind spot, respectively. We could not

309   find differences between low-level error signals, but high-level error signals differed markedly. We

310   concluded that the inferred content is processed *as if* it were veridical for the visual system, but

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311   knowledge of its reduced precision is nevertheless preserved at later processing stages. Thus,

312   only an absence of a bias for the veridical peripheral stimulus could have been explained by this

313   finding of early *as if* veridical processing. The participants in the EEG study were a subset of the

314   subjects of experiment 1 and thus the same subjects who showed activity congruent with a

315   differential processing of filled-in and veridical inputs. They nevertheless choose the unreliable,

316   filled-in stimulus in this perceptual decision-making task. In other words, the implicit knowledge

317   that a filled-in stimulus is less reliable seems to be unavailable for perceptual decision-making.

318   In conclusion, we find a new behavioral effect where subjects reliably prefer a partially

319   inferred stimulus over a veridical one. Though both appear to be continuous, the filled-in one could

320   hide an inset and is therefore less reliable. In this perceptual decision-making task, in contrast to

321   predictions about future content over saccades, subjects do not make use of high-level

322   assessments about the reliability of the filled-in stimulus. Even more so, they prefer the unreliable

323   percept, possibly due to physiologically superior signal extraction, less noise accumulation or

324   both.

325

326   **METHODS**

327   Many of the methods are taken from Ehinger et al. 2015. All data and analyses are available at

328   https://osf.io/wphbd/.

329

330   **Subjects**:

331   Overall, 136 subjects took part in the experiments. Of the subjects, 33% (n=45) were removed due to

332   the screening experiments described below. An additional 4% (n=6) were removed due to low

333   performance ([n=2, <75%] in at least two conditions with a visible unique inset) or because they

334   responded to the stimuli with the inset stimulus instead of the continuous stimulus (n=4). The

335   experimental data were not recorded in 7% (n=10) due to eye tracking calibration problems (n=3) and

336   other issues during data collection (n=7). The remaining 75 subjects were recorded and analyzed in

337   the following experiments.

338   For the first experiment, we analyzed the data of 24 subjects (average age 21.9 years, age

339   range 18–28 years, 12 female, 20 right-handed, 16 right-eye dominant) with a subset of 15 taking part

340   in the EEG study of Ehinger et al. In the second experiment, we analyzed the data of 27 subjects

341   (average age 22.4 years, age range 19–33 years, 15 female, 25 right-handed, 19 right-eye dominant).

342   In the third, 24 subjects (average age 21.9 years, range 19–27 years, 19 female, 23 right-handed, 16

343   right-eye dominant).

344   All subjects gave written informed consent, and the experiment was approved by the local

345   ethics committee. We disclose that in the second experiment, we planned to record 18 subjects,

346   but the results of the initial analysis with this first group were not conclusive about differences

347   between the location inside and the location above the blind spot. Therefore, we decided to

348   increase the number of subjects by 50% (n=9).

349   **Screening**:

350   As described above, many subjects failed a simple screening test. In this pre-experiment,

351   we showed a single stimulus in the periphery either inside or outside the blind spot in the left or

352   right visual field. In two blocks of 48 trials, subjects indicated which stimulus (no inset vs. inset)

353   had been perceived. We thought of this simple experiment to evaluate our blind spot calibration

354   method, as an inset stimulus inside the blind spot should have been reported as no inset. The

355   first block was used as a training block. In the second block, we evaluated the performance in a

356   conservative way. If the performance was below 95% (three errors or more), we aborted the

357   session because the participant was deemed to be too unreliable to proceed further with our

358   experiment. Later analysis suggested that the errors of those subjects were unrelated to the blind

359   spot. There was no clear pattern among subjects in terms of eye-lateralization or location (i.e.,

360   inside vs. outside). In most cases the low performance was probably due to inattention. Overall,

361   about 66% (n=75) of recruited subjects passed this test and were admitted to subsequent

362   experiments.

363

364   **Eye Tracking, Screen, Shutter Glasses**

365   A remote, infrared eye-tracking device (Eyelink 1000, SR Research) with a 500 Hz sampling rate

366   was used. The average calibration error was kept below 0.5° with a maximal calibration error of

367   1.0°. Trials with a fixation deviation of 2.6° from the fixation point were aborted. We used a 24-

368   inch, 120 Hz monitor (XL2420t, BenQ) with a resolution of 1920x1080 pixels in combination with

369   consumer-grade shutter glasses for monocular stimulus presentation (3D Vision, Nvidia, wired

370   version). The shutter glasses were evaluated for appropriate crosstalk/ghosting using a custom-

371   manufactured luminance sensor sampling at 20 kHz. The measured crosstalk at full luminance

372   was 3.94%. The subject screen distance was 60cm in the first two experiments and 50cm in the

373   third experiment.

374

375   **Stimuli**

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376 Modified Gabor patches with a frequency of 0.89 cycles/° and a diameter of 9.6° were generated.

377 Two kinds of patterns were used (Fig. 1A): one completely continuous and one with a small

378 perpendicular inset of 2.4°. For comparison, the blind spot typically has a diameter of 4°–5°. The

379 Gabor had constant contrast in a radius of 6.3° around the center. This ensured the same

380 perception of the continuous stimulus outside the blind spot in comparison to a filled-in stimulus,

381 where the inner part is inside the blind spot. To account for possible adaptation effects, horizontal

382 and vertical stimuli were used in a balanced and randomized way across the trials. Stimuli were

383 displayed using the Psychophysics Toolbox [27] and Eyelink Toolbox [28]. The stimuli were displayed

384 centered at the individually calibrated blind spot location. The stimulus at the location above the

385 blind spot in experiment 2 was at the same distance as the blind spot but was rotated by 25° to

386 the horizon around the fixation cross. For the inward and outward condition of experiment 3,

387 stimuli were moved nasally or temporally by 8.6°, thus the stimuli had an overlap of only 1°. Less

388 overlap is not possible without either cutting the border of the screen or overlapping with the

389 fixation cross.

390

391 **Task**

392 After a fixation period of 500 ms, we presented two stimuli simultaneously in the left and right

393 peripheries. Subjects were instructed to indicate via button press (left or right) which stimulus was

394 continuous. Each stimulus was presented either in the temporal or nasal field of view. In some

395 trials, the required response was unambiguous, when one of the stimuli showed an inset and the

396 other did not (and at least the inset stimulus was presented outside the blind spot). In many trials

397 (80% of all experiments and locations, 46% when the stimulus was shown above the blind spot

398 in experiment 2), both stimuli were continuous and no unique correct answer existed. All trials

399 were presented in a randomized order. If the subject had not given an answer after 10 seconds,

400 the trial was discarded and the next trial started. All in all, subjects answered 720 trials over 6

401 blocks; in experiment 1 the trials were split up into two sessions. After each block the eye tracker

402   and the blind spot were re-calibrated. After cleaning trials for fixation deviation and blinks, an average

403   of 498 trials (90%-quantile: 402, 567) remained. For two subjects, only 360 trials could be recorded.

404

405   **Blind Spots**

406   In order to calibrate their blind spots, subjects were instructed to use the keyboard to move a

407   circular monocular probe on the monitor and to adjust the size and location to fill the blind spot

408   with the maximal size. They were explicitly instructed to calibrate it as small as necessary to

409   preclude any residual flickering. The circular probe flickered from dark gray to light gray to be

410   more salient than a probe with constant color [29]. All stimuli were presented centered at the

411   respective calibrated blind spot location. In total, each subject calibrated the blind spot six times.

412   For the following comparisons of blind spot characteristics we evaluated one-sample tests with

413   the percentile bootstrap method (10,000 resamples) of trimmed means (20%) with alpha = 0.05

414   [30]. For paired two-sample data, we used the same procedure on the difference scores. We used

415   bias-corrected, accelerated 95% bootstrapped confidence intervals of the trimmed mean (20%).

416   In line with previous studies [18,31], the left and right blind spots were located horizontally at -15.48°

417   (SD=0.49° CI:[-15.68°,-15.30°]) and 15.8° (SD=0.56° CI:[15.59°,16.02°]) from the fixation cross. The

418   mean calibrated diameter was 4.92° (SD=0.43° CI:[4.76°,5.08°]) for the left and 5.13° (SD=0.4°

419   CI:[4.98°,5.29°]) for the right blind spot. Blind spots did significantly differ in size (p<0.001, CI:[-0.26°,-

420   0.08°]) and in absolute horizontal position (in relation to the fixation cross; p<0.001, CI:[0.21°,0.43°]);

421   on average, the right blind spot was 0.32° further outside of the fixation cross. No significant difference

422   was found in the vertical direction (p=0.86), but this is likely due to the oval shape of the blind spot in

423   this dimension and the usage of a circle to probe the blind spot. These effects seem small, did not

424   affect the purpose of the experiments and will not be discussed further.

425

426   **GLMM Analysis**

427   We fitted a Bayesian logistic mixed-effects model predicting the probability of responding "right"

428   with multiple factors that represent the temporal over nasal bias and several other covariates

429   described below. Because we were interested in the bias between the nasal fields and the

430   temporal fields of view, we combined both predictors for the left and right temporal (and nasal,

431   respectively) locations and reported the combined value.

432   Data were analyzed using a hierarchical logistic mixed effects models fitted by the No-U-

433   Turn Sampler (NUTS, STAN Development Team). The model specification was based on an

434   implementation by Sorensen and Vasisth [32]. In the results section we report estimates of linear

435   models with the appropriate parameters fitted on data of each experiment independently. We also

436   analyzed all data in one combined model: there were no substantial differences between the

437   results from the combined model and the respective submodels (Appendix table 1). The models

438   are defined as follows using the Wilkinson notation:

439

440 $answer_{right} \sim 1 + Temporal_{Left} * Location + Temporal_{Right} * Location + Answer_{right}(t-1) +$

441 $Handedness_{Right} + DominantEye_{right} +$

442 $(1 + Temporal_{Left} * Location + Temporal_{Right} * Location + Answer_{right}(t-1) \ |Subject)$

443 $Answer_{i\ right} \sim Bernoulli(\theta_i)$

444 $\theta_i = logit^{-1}(X_{within}\beta_{within} + X_{between}\beta_{between} + N(0, \tau X_{within}) + N(0, e)$

445   Two factors were between subjects: *handedness* and *dominant eye*. In total, we have four

446   within-subject factors, resulting in eight parameters: There are two main factors representing

447   whether the left, and respectively the right, stimulus was inside or outside the *temporal* field.

448   Depending on the experiment, the main factor *location* had up to three levels: the stimuli were

449   presented outwards (3rd experiment), inwards (3rd), above (2nd) or on (1st, 2nd, 3rd) the blind

450   spot. In addition, we modeled the interactions between location and whether the left stimulus (and

451   the right stimulus, respectively) was shown temporally. In order to assure independence of

452   observation, an additional within-subject main factor *answer(t-1)* was introduced, which models

22

453   the current answer based on the previous one. In frequentist linear modeling terms, all within-

454   subject effects were modeled using random slopes clustered by subject and a random intercept

455   for the subjects. We used treatment coding for all factors and interpreted the coefficients

456   accordingly.

457   In the model we estimated the left and right temporal field effects separately. For the

458   statistical analysis, we combined these estimates by inverting the left temporal effect and

459   averaging with the right temporal effect. We did this for all samples of the mcmc-chain and then

460   took the median value. We then transformed these values to the probability domain using the

461   invlogit function, subtracting the values from 0.5 and multiplying by 100. All results were still in

462   the linear range of the logit function. We calculated 95% credible intervals the same way and

463   reported them as parameter estimates (CDI_{95} lower-upper) in the text. These transformed values

464   represent the additive probability (in %) of choosing a left (right) stimulus that is shown in the left

465   (right) temporal field of view compared to presenting the left (right) stimulus in the nasal field of

466   view, keeping all other factors constant.

467

468   **Reaction Times**

469   Initially, we did not plan to analyze the reaction time data. These analyses are purely explorative.

470   Our setup consisted of a consumer keyboard, thus delays and jitters are to be expected. But with

471   an average of 498 trials per subject, we did not expect a bias between conditions from jitter in our

472   analyses. Our reaction time data were analyzed with a simple Bayesian mixed linear model:

473

474        $$RT \sim 1 + Temporal_{Selected} * Location + (1 + Temporal_{Selected} * Location \,|\, subject)$$

475

476   Only trials without a visible inset stimulus were used. *Temporal selected* consists of all trials where

477   a temporal stimulus was selected. Because of the bias described in the results, there is a slight

23

478   imbalance in the number of trials between the two conditions: 234.9 CI:[228.5, 241.3] for the nasal

479   selection and 263.1 CI:[257.5, 269.4] for the temporal selection.

480

481   **Bayesian Fit**:

482   We did not make use of prior information in the analysis of our data. We placed implicit, improper,

483   uniform priors from negative to positive infinity on the mean and 0 to infinity for the standard

484   deviations of our parameters, the default priors of STAN. An uninformative lkj-prior ($\nu = 2$) was

485   used for the correlation matrix, slightly emphasizing the diagonal over the off-diagonal of the

486   correlation matrix [32,33].

487   We used six mcmc-chains using 2000 iterations each, with 50% used for the warm-up

488   period. We visually confirmed convergence through autocorrelation functions and trace plots, then

489   calculated the scale reduction factors [34], which indicated convergence as well (Rhat < 1.1).

490

491   **Effects not reported in the result section**

492   We report other effects based on a combined model over all experiments. We did not find

493   evidence for a different global bias (main effect location) in any of the four stimulation positions

494   tested here. Dominant eye has a 12.3% effect (CDI_{95} 2.78%-21.04%) on global bias; thus subjects

495   with a dominant right eye also preferred the right stimulus over the left one (irrespective of whether

496   the stimulus was visible through the left or the right eye). We find a global bias (in the intercept of

497   -27.6% CDI_{95} -40.08% - -9.66%, with treatment coding) toward choosing the left stimulus; this

498   might reflect that in the first two experiments we instructed subjects to use the right hand, thus

499   they used their index and middle fingers. In the third experiment we instructed subjects to use

500   both index fingers, resulting in a decreased bias to the left, with a shift more to the right (and thus

501   more to balanced answers) of 12.24% (CDI_{95} -1.98-24.16%]).

502   We did not find evidence for a bias due to handedness (5.22%, CDI_{95} -13.12%-23.46%).

24

503   There was a strong influence of the previous answer on the current answer. We observe a global

504   effect of 9.57% (CDI_{95} 1.7%-17.03%), and the coding suggests that subjects are more likely to

505   choose the right stimulus again when they have just chosen "right" in the previous trial. For this

506   effect it is more important to look at random effect variance, which is quite high with a standard

507   deviation of 29.9% (CDI_{95} 26.28%-33.7%), suggesting that there is large variation between

508   subjects. Indeed, a closer look at the random slopes of the effect reveals three different strategies:

509   Some subjects tend to stick the same answer, some subjects are balanced in their answers

510   without any trend and some subjects tend to regularly alternate their answers in each trial.

511

512   Other models we considered showed no effect when both stimuli were in the temporal field, nor

513   any three-way interaction. In order to simplify the final model, we removed these effects from

514   future fits.

515

516

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596

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603

604 **SUPPLEMENTARY**

605

606

Parameter	Experiment 1 (95% CDI)	Experiment 2 (95% CDI)	Experiment 3 (95% CDI)	All Experiments (95% CDI)
Location BS	15.01% [8.49%,21.08%]	12.50% [7.35%,17.49%]	13.18% [6.47%,19.64%]	13.44% [9.94%,16.70%]
Location above		6.63% [0.77%,12.30%]		6.73% [1.91%,11.31%]
Location outward			4.80% [0.58%,8.89%]	4.84% [0.75%,8.79%]
Location inward			2.85% [-1.10%,6.65%]	2.89% [-1.03%,6.63%]
BS - above		6.11% [1.16%,10.78%]		6.97% [1.69%,12.24%]
BS - outward			8.61% [0.98%,16.04%]	8.86% [3.73%,13.52%]
BS - inward			10.51% [3.55%,17.29%]	10.74% [6.15%,15.09%]

607 **Table 1:** Overview of the results of all experiments individually and the combined estimates.

608 Empty cells indicate that the condition was not measured in this study.

31