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

Benedikt V. Ehinger[1], Katja Häusser[1], José Ossandón*[1,2], Peter König*[1,3]

[1] Neurobiopsychology, Institute of Cognitive Science, University of Osnabrück, Osnabrück, Germany

[2] Biological Psychology and Neuropsychology, University of Hamburg, Hamburg, Germany.

[3] Department of Neurophysiology and Pathophysiology, University Medical Center Hamburg-Eppendorf, Hamburg, Germany

* Contributed equally

Correspondence: Benedikt V. Ehinger, Neurobiopsychology, Institute of Cognitive Science, University of Osnabrück, Albrechtstraße 28, Osnabrück, 49069, Germany - behinger@uos.de

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.

ABSTRACT

Modern theories of cognition place an emphasis on the (un)certainty of available information. This raises the question whether we trust more external sampled information or internal inference processes. The specific properties of visual processing around the blind spot region allow us to address this. Although there are no photoreceptors corresponding to the physiological blind spots, we experience visual content there as if it were veridical, when it is in fact only “filled in” based on the surroundings. We asked subjects to choose between a stimulus partially presented in the blind spot that elicits fill-in and another at the same eccentricity outside of the blind spot. Subjects displayed a systematic bias toward the blind spot stimulus, where the filled-in part could have actually concealed a non-target. Two control experiments confirmed this finding and demonstrate that this is not an effect of eccentricity, but a property of the filling in process. This intuitively puzzling effect finds a straightforward explanation within the context of predictive coding. The filled-in signals are produced by the brain’s generative model based on spatial-context priors. In contrast to other locations, predictions at the blind spot cannot be compared to feed-forwards inputs and therefore no error signal is generated. As a consequence, the error measure for the inferred percepts reaches the lower bound and are estimated as more reliable than actually seen contents. This experiment gives credibility to the interpretation of bottom-up signals not as conveying independent information about the world, but information relating to deviations of internal expectations.

SIGNIFICANCE

The common view treats visual processing as a hierarchy of increasingly refined representations of external stimuli. In contrast, predictive coding interprets bottom-up relayed information as error signals, indicating deviations from internal predictions. The validity of this view is not easy to test. Here we utilize the phenomenon of fill-in in physiological blind spot region to compare internally generated against veridical percepts. We demonstrate, that in the absence of bottom-up signals an internally constructed percept is assigned a reduced uncertainty compared to an identical percept based on actual external input. This finding supports the framework of predictive coding: the filled in percept has smaller prediction errors and therefore is selected as the more reliable stimulus.

INTRODUCTION

In order to make optimal and adaptive decisions, animals integrate multiple sources of sensory information. This is especially important in conditions of uncertainty when information from a single sensory modality would be otherwise insufficient. For example, when animals are confronted with weakly coherent stimuli during random-dot motion experiments, their performance and corresponding neural activity vary proportionally to signal strength in a way that is consistent with the progressive integration of evidence over time (1, 2). Crucially, sensory integration does not only operate as a temporal accumulator because it is also possible to combine information from multiple sensory sources (3–8).

In the case of multisensory perception, several experiments have shown that integration often occurs in a statistically optimal way. This has been best demonstrated in cue-integration experiments in which humans perform as if they were weighting the different sources of information according to their respective reliabilities (9–12). This form of statistical inference has also been demonstrated for cortical neurons of the monkey brain, with patterns of activity at the population level that are consistent with the implementation of a probabilistic population code (13, 14).

In many of these sensory integration experiments, the perceptual reliability of different inputs is probed through quantitative manipulations of the inputs' signal-to-noise ratios (15–17). However, some percepts are unreliable not because they are corrupted by noise but because they are internally inferred and thus intrinsically uncertain. This occurs naturally in the monocular visual field at the physiological blind spot, where content is "filled in" based on information from the surroundings. In this case, no veridical percept is possible at the blind spot location. Though changes in reliability due to noise directly result in behavioral consequences, the effects of the qualitative difference between veridical and inferred percepts that are otherwise apparently identical is unknown.

We recently reported differences in the processing of veridical and inferred information at the level of EEG responses(18). In the present experiment, we address whether such an assessment of a dichotomous, qualitative difference in reliability is available for perceptual decision-making. Using 3D shutter glasses, we presented one stimulus partially in the participant's blind spot to elicit filling in and a second stimulus at the same eccentricity in the nasal field of view outside of the blind spot. The subject's task was to indicate which of the two stimuli was continuously striped and did not present a small orthogonal inset (see Fig. 1A). Crucially, stimuli within the blind spot are filled in and thus perceived as continuous, even when they present an inset. In the diagnostic trials, both stimuli were physically identical and continuous, and subjects were confronted with an ambiguous decision between veridical and partially inferred stimuli.

We evaluated two mutually exclusive hypotheses in which perceptual decision-making could proceed when confronted with an ambiguous decision between veridical and inferred percepts. In the first case, agents are unable to make perceptual decisions based on an implicit assessment of differences in reliability between stimuli that otherwise look identical. Therefore, subjects would have an equal chance of selecting stimuli presented inside or outside the blind spot. Alternatively, it might be possible to use the information about the reduced reliability of filled-in information. Therefore, we expect subjects to follow an optimal strategy and trust a stimulus presented outside the blind spot, where the complete stimulus is seen, more often than when the stimulus is presented inside the blind spot, where it is impossible to know the actual content of the filled-in part.

RESULTS

We conducted three experiments (see Fig. 1 and the methods for a detailed task description). The first experiment tested the presence of a bias against the blind spot location; the other two experiments were replications of the first experiment with additional control conditions to test the existence of biases between the nasal and temporal fields of view at locations that do not correspond with the blind spot.

In the first experiment, 24 subjects performed a sometimes ambiguous 2-AFC task in which they had to indicate which of the two stimuli was continuously striped instead of presenting a small orthogonal inset (Fig. 1A). The stimuli were presented simultaneously in the periphery at external locations corresponding to the blind spots (Fig. 1B, C). We used a 3D monitor and shutter glasses that allowed for controlled monocular display of the stimuli. The first experiment consisted of mixed perceptually ambiguous and unambiguous trials that we used to test the two competing hypotheses on whether the reliability assessments of these conditions differed for decision-making.

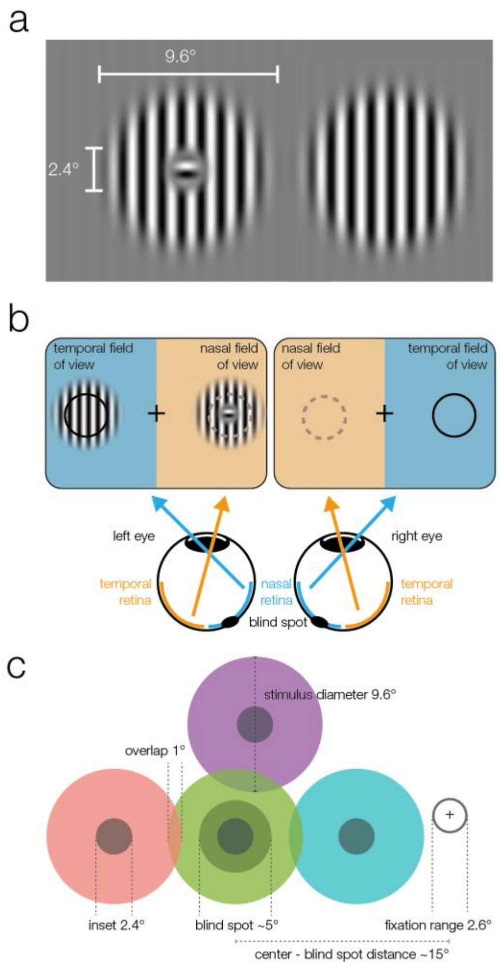

Figure 1: Stimuli and stimulation

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.

In the unambiguous trials, an orthogonal inset was present in one of the stimuli. Importantly, in these trials, the stimulus with the inset was outside the blind spot and therefore clearly visible. As expected, subjects performed with near perfect accuracy (Fig. 2, unambiguous trials), choosing the continuous stimulus in an average of 98.8% of trials (95%-quantile [96.4%–100%]).

There were two types of ambiguous trials. In the first type (Fig. 2, ambiguous control), one of the following applied: both stimuli were continuous and appeared outside the blind spots in the nasal visual fields (Fig. 2, line 3); both were continuous and appeared inside the blind spots (Fig. 2, line 4); or one was continuous, the other had an inset, and both appeared inside the blind spots either in the left/right and right/left ones (Fig. 2, lines 5 and 6). The central parts of the stimuli, where the insets could appear, were perfectly centered inside the blind spot when presented (Fig. 1A). These stimuli were thus perceived as continuous due to filling in of the surrounding visible part of the stimuli. Thus, in all four versions, subjects perceived two identical stimuli, and there was no single correct answer. In this type of ambiguous trial, subjects showed a small global leftward bias and chose the left stimulus in 53.6% of trials (Fig. 2, dashed line). In addition, no difference can be seen between the perception of pairs of filled-in stimuli and pairs of veridical continuous stimuli (Fig. 2, line 3 vs. 4-6). This type of ambiguous control trial clearly shows that fill-in is perfect in our experiment.

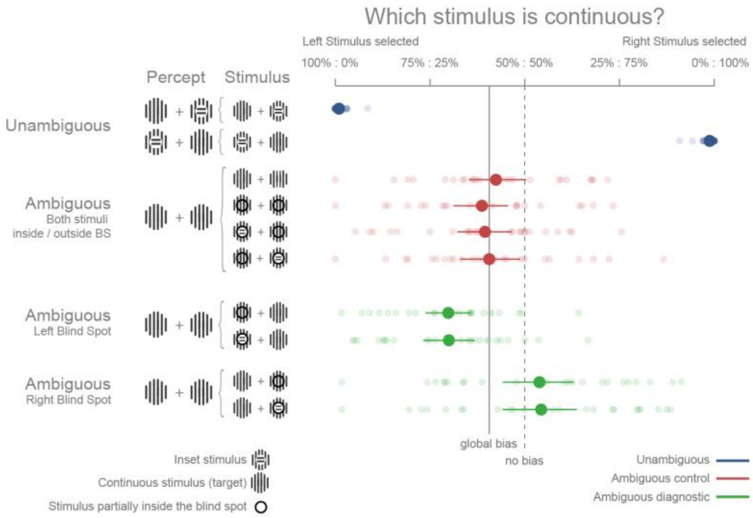

Figure 2: First experiment

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 analysis, 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 nasal visual field of the left eye (non-blind spot), a similar factor was used for the left stimulus. Consequently, the two one-sided model estimates were collapsed to a single measure.

Figure 2 (ambiguous diagnostic) shows that subjects indeed presented a bias. However, in contrast to our expectations, subjects were more likely to choose the filled-in percept (15.01%, CDI_{95} 8.49%–21.08%). In other words, when subjects had to decide which of the two stimuli (both perceived as being continuous, and in most cases actually physically identical) was less likely to contain an inset, they showed a bias for the one in which the critical information was not sensed but inferred. Remarkably, this result is at odds with both of the experimental predictions that postulated a bias in favor of the veridical stimulus or no bias.

In the second experiment, we focused on replicating the unexpected result of experiment 1 and evaluating whether the blind spot bias observed was due to systematic differences between nasal and temporal retinae. In experiment 1, we presented stimuli at mirror eccentricities inside and outside the blind spot. Therefore, we had to present them to opposite sides of one eye's retina (temporal and nasal respectively; see Fig. 1B). Otherwise, the stimuli would have appeared at the same external coordinates and led to binocular rivalry(19). In experiment 2, we tested whether the bias in experiment 1 was unspecific to the blind spot location but related to known differences between the temporal and nasal retina (for a review, see (20)). There is higher photoreceptor density(21), spatial resolution(22), luminance discrimination(23) and orientation discrimination(24) at locations that project to the nasal retina (the temporal visual field where the blind spots are located). Thus, we repeated our experiment with a new group of subjects (n=27) and an additional condition. In this new condition, the two stimuli were displayed at symmetrical locations above the blind spot (25° above the horizontal meridian; see Fig. 1C). The results of this second experiment (Fig. 3A triangles, Fig. 3B for model parameters) replicate the previous observations of experiment 1. Subjects showed a bias for selecting the stimulus presented inside the blind spot (12.5%, CDI_{95}7.35%–17.49%). However, we also found a bias in the control condition toward the stimuli presented in the temporal visual field above the blind spot (6.63%, CDI_{95}0.77%–

12.3%). The bias was nevertheless stronger inside the blind spot (paired-diff: 6.11%, CDI_{95}1.16%–10.78%). In summary, on top of the bias inside of the blind spot area, we observed that subjects also showed an additional, smaller bias for stimuli presented to the nasal retina (temporal visual field).

We performed an additional third experiment on a new group of subjects (n=24). Here, we compared biases in the blind spot to two other control conditions flanking the blind spot region from either left or right (Fig. 3A squares). The blind spot location again revealed the strongest effect (13.18% CDI_{95} 6.47%–19.64%), while the locations inwards and outwards resulted in a 2.85% and 4.8% bias, respectively, for the temporal visual field (CDI_{95} -1.1%–6.65%; CDI_{95} 0.58%–8.89%). The bias of both control locations was different from the bias of the blind spot location (inward vs. BS: 10.51%, CDI_{95} 3.55%–17.29%; outward vs. BS: 8.61%, CDI_{95} 0.98%–16.04%). In this experiment, as in experiments 1 and 2, we observed a bias specific to the blind spot region.

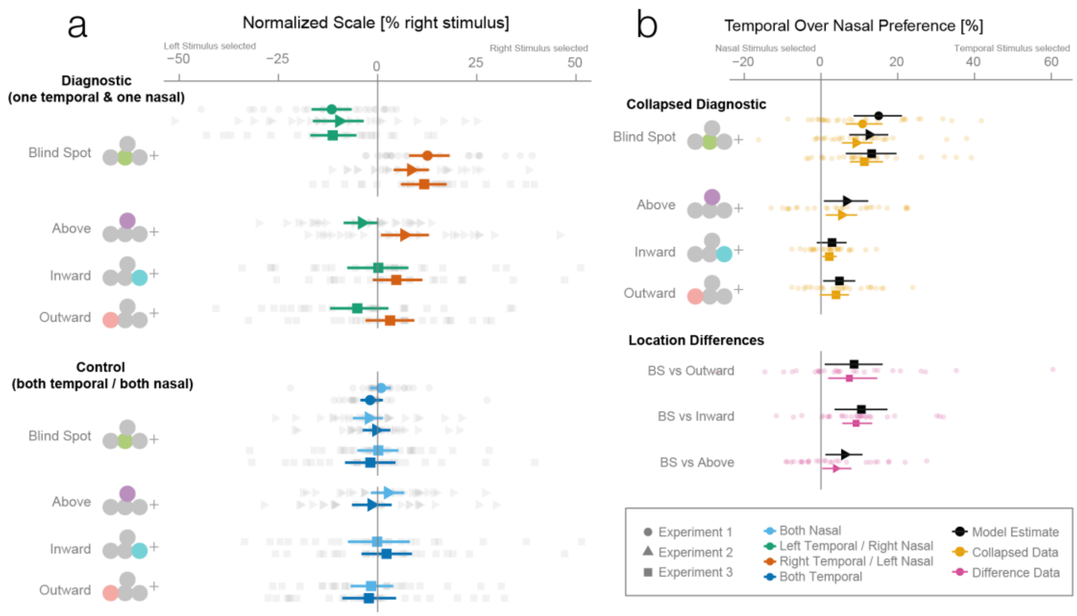

Figure 3: All experiments

a) Fraction of choosing the right stimulus dependent on location (indicated by icon) and experiment (Exp. 1: n=24, Exp. 2: n=27, Exp. 3: n=24). For plotting purposes we preprocessed the data by subtracting the global bias. Each gray dot depicts one subject. The error bars depict mean and 95% bootstrapped CI. A bias for the blind spot was visible in the form of “left” responses when the left stimulus was presented in the temporal visual field of the left eye (green, nasal / blind spot retina of the left eye) and of more “right” responses when the right stimulus was presented in the temporal visual field of the right eye (green, nasal / blind spot of the right eye) in all experiments. A bias was visible in the other tested locations, but it was much smaller. Control conditions show that there was no bias if the stimuli were shown either both inside the temporal fields (dark blue) or both inside the nasal fields (light blue).

b) Yellow color indicates combined data over the left and right side. Black color indicates the posterior 95% credibility interval of a logistic mixed linear model. A bias for the blind spot stimulus was clearly evident in all experiments. A much weaker effect was present in the other tested locations. The within-subject differences between the blind spot and the other locations are depicted in purple, and the respective modeled difference is shown in black.

A bias for the temporal visual field, especially the blind spot, can also be reflected in the distribution of reaction times. We compared the reaction times of trials where subjects selected a stimulus in the temporal visual field against trials where the stimulus in the nasal visual field was selected. No prior hypotheses were formulated for the reaction time. Thus, in contrast to the other analyses presented here, these are explorative. We observed an average reaction time of 637 ms (minimum subject average: 394 ms, maximum 964 ms) in the first experiment (Fig. 4A). We used a linear mixed model to estimate the reaction time difference for selecting a stimulus presented inside the blind spot (temporally) against one outside the blind spot (nasally). In the first experiment (Fig. 4B), after excluding three outliers, we observed this effect with a median posterior effect size of 13 ms ($CDI_{95\%}$ 2–42 ms) faster reaction times when selecting the blind spot region. The three outliers (marked red in Fig. 4) were identified visually and removed because they were distinctively different from the rest of the population. The mean of the outliers was 5.2 SD away from the remaining subjects. The outliers were nevertheless in the direction of the reaction time effect and did not change its significance (with outliers, 63 ms, CDI_{95}7–124 ms). However, faster reaction times while selecting the blind spot stimulus were not present in the other two experiments. The nominal differences were in the same direction as experiment 1 but comparably small and insignificant (4 ms, CDI_{95} -14–23 ms; and 22 ms. CDI_{95} -13–57 ms). Similar results were obtained for the other locations tested (above: 8 ms, CDI_{95} -38–53 ms; outward: 2 ms CDI_{95} -13–16 ms; inward: 4 ms, CDI_{95} -29–37 ms). Furthermore, an analysis of the combined data shows no evidence for a reaction time effect in any location, and the blind spot estimate changes here to 12 ms (CDI_{95} -23–47 ms). Even though the signs of all three experiments indicate that the reaction time for nasal stimuli is slower than for temporal ones despite the large total number of subjects (n=75), the results of our experiments remain inconclusive on this issue.

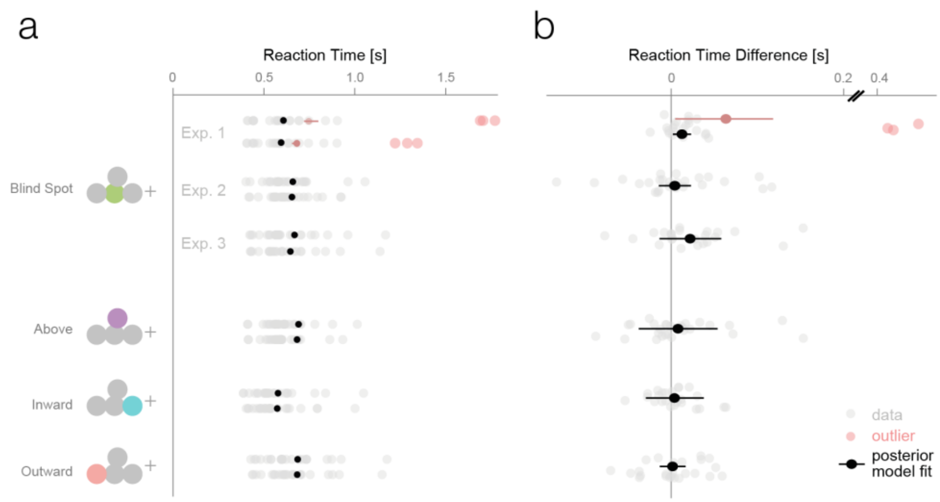

Figure 4: Reaction Times

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, when confronted with an ambiguous choice between veridical and inferred sensory information, human subjects showed a suboptimal bias for inferred information.

DISCUSSION

In three experiments, we showed that when confronted with identical physical stimulation in a simple decision task, subjects biased their decisions toward stimuli in the temporal field of view. Importantly, subjects showed a consistent bias for blind spot inferred percepts, which was stronger than the bias at any other location in the temporal visual field.

Why do subjects choose the blind spot location when it is objectively the least reliable? Our interpretation takes the results at face value: subjects must possess at least implicit information about whether a percept originates from the blind spot in order to show a bias for it. At the same time, the veridical information from the other stimulus is also available. This indicates, that at least for the task presented here, perceptual decision-making can rely more on inferred than veridical information, even when there is knowledge in the system about the nature of this signal and its reduced reliability as a consequence. Thus, a suboptimal decision is made.

In the following, we propose two possible explanations for this effect. The first explains the effect simply by stating that the blind spot is 'special' because the information around the optic disc is sampled differently. The second explanation is based on the general notion of predictive coding: the reduced noise in the inferred percept reduces the bottom-up prediction error.

In the results section, we introduced the evidence for psychophysical differences between the nasal and temporal visual field, which motivated the control experiments. In the same vein, the parts of the retina surrounding the optic disc might present further enhancements for perception that are useful for a better estimation of the contents of the blind spot area. That means that subjects could perceive the stimulus as more veridical due to enhanced sensory perception at the boundary of the blind spot. Some weak evidence for this has been reported that indicates better disparity estimates (Vernier task) in the peri-blind spot area compared to equally eccentric locations in the nasal visual field. This effect seems to happen only when the element extends into the blind spot and thus produces filling in and not for other filling in processes derived from pathological scotomas (25). This would indicate that the low-level, bottom-up information gained from the blind spot is superior to the veridical input of other retinal origin.

Our alternative explanation is based on the framework of predictive coding (26–28). For this task, we assume that predictive coding could work both as a way of predicting future sensory input (task context) and static predictions based on spatial context (the filling-in). Similar spatial context predictions have recently be found for illusionary figures in human V1 using high-field fMRI (29). In our task, this would mean that subjects generated predictions of continuous stimuli in the ambiguous trials. The predicted sensory input was then compared to the incoming sensory input, and an error signal representing the mismatch was returned. The filled-in signal might have had less perceptual noise. This was partially explained by the hypothesized integration process over boundary neurons (30) that act as smoothers and further explained by the fact that no unique perceptual noise from the senses reached the low-level visual areas near the blind spot (as there are no sensory inputs from the stimulus in the blind spot). Thus, with less noise, the inferred sensory input at the V1 blind spot location has a higher signal-to-noise ratio and will match the predicted stimulus signal better. A better match results in a smaller prediction error and thus a higher credibility at later stages. A faster reaction time to the filled-in stimulus compared to the veridical stimulus could be taken as further evidence that the integration process is indeed biased with less noise. With respect to reaction times, our experiments remain inconclusive, and further research is needed to fully support this assumption. In conclusion, predictive coding can best explain our results with the additional assumptions that the signal-to-noise ratio of the blind spot percept is higher due to the fill-in process and/or the blind spot lacking unique noise from the eye.

In a recent EEG study with human subjects, we demonstrated that a qualitative reliability assessment exists at the neural level in the form of low- and high-level trans-saccadic predictions of visual content (18). Notably, active predictions of visual content differed between inferred and veridical visual information presented inside or outside the blind spot, respectively. We could not find differences between low-level error signals, but high-level error signals differed markedly. We concluded that the inferred content is processed *as if* it were veridical for the visual system, but knowledge of its reduced precision is nevertheless preserved at later processing stages. Thus, only an absence of a bias for the veridical peripheral stimulus could have been explained by this finding of early *as if* veridical processing. The participants in the EEG study were a subset of the subjects of experiment 1 and thus the same subjects who showed activity congruent with a differential processing of filled-in and veridical inputs. They nevertheless choose the unreliable, filled-in stimulus in this perceptual decision-making task. In other words, the implicit knowledge that a filled-in stimulus is less reliable seems to be unavailable for perceptual decision-making.

In conclusion, we find a new behavioral effect where subjects reliably prefer a partially inferred stimulus over a veridical one. Though both appear to be continuous, the filled-in one could hide an inset and is therefore less reliable. In this perceptual decision-making task, in contrast to predictions about future content over saccades, subjects do not make use of high-level assessments about the reliability of the filled-in stimulus. Even more so, they prefer the unreliable percept, possibly due to physiologically superior signal extraction, less noise accumulation or both.

METHODS

Many of the methods are taken from Ehinger et al. 2015. All data and analyses are available at https://osf.io/wphbd .

Subjects:

Overall, 136 subjects took part in the experiments. Of the subjects, 33% (n=45) were removed due to the screening experiments described below. An additional 4% (n=6) were removed due to low performance ([n=2, <75%] in at least two conditions with a visible unique inset) or because they responded to the stimuli with the inset stimulus instead of the continuous stimulus (n=4). The experimental data were not recorded in 7% (n=10) due to eye tracking calibration problems (n=3) and other issues during data collection (n=7). The remaining 75 subjects were recorded and analyzed in the following experiments.

For the first experiment, we analyzed the data of 24 subjects (average age 21.9 years, age range 18–28 years, 12 female, 20 right-handed, 16 right-eye dominant) with a subset of 15 taking part in the EEG study of Ehinger et al. In the second experiment, we analyzed the data of 27 subjects (average age 22.4 years, age range 19–33 years, 15 female, 25 right-handed, 19 right-eye dominant). In the third, 24 subjects (average age 21.9 years, range 19–27 years, 19 female, 23 right-handed, 16 right-eye dominant).

All subjects gave written informed consent, and the experiment was approved by the local ethics committee. We disclose that in the second experiment, we planned to record 18 subjects, but the results of the initial analysis with this first group were not conclusive about differences between the location inside and the location above the blind spot. Therefore, we decided to increase the number of subjects by 50% (n=9).

Screening:

As described above, many subjects failed a simple screening test. In this pre-experiment, we showed a single stimulus in the periphery either inside or outside the blind spot in the left or right visual field. In two blocks of 48 trials, subjects indicated which stimulus (no inset vs. inset) had been perceived. We thought of this simple experiment to evaluate our blind spot calibration method, as an inset stimulus inside the blind spot should have been reported as no inset. The first block was used as a training block. In the second block, we evaluated the performance in a conservative way. If the performance was below 95% (three errors or more), we aborted the session because the participant was deemed to be too unreliable to proceed further with our experiment. Later analysis suggested that the errors of those subjects were unrelated to the blind spot. There was no clear pattern among subjects in terms of eye-lateralization or location (i.e., inside vs. outside). In most cases the low performance was probably due to inattention. Overall, about 66% (n=75) of recruited subjects passed this test and were admitted to subsequent experiments.

Eye Tracking, Screen, Shutter Glasses

A remote, infrared eye-tracking device (Eyelink 1000, SR Research) with a 500 Hz sampling rate was used. The average calibration error was kept below 0.5° with a maximal calibration error of 1.0°. Trials with a fixation deviation of 2.6° from the fixation point were aborted. We used a 24-inch, 120 Hz monitor (XL2420t, BenQ) with a resolution of 1920x1080 pixels in combination with consumer-grade shutter glasses for monocular stimulus presentation (3D Vision, Nvidia, wired version). The shutter glasses were evaluated for appropriate crosstalk/ghosting using a custom-manufactured luminance sensor sampling at 20 kHz. The measured crosstalk at full luminance was 3.94%. The subject screen distance was 60cm in the first two experiments and 50cm in the third experiment.

Stimuli

Modified Gabor patches with a frequency of 0.89 cycles/° and a diameter of 9.6° were generated. Two kinds of patterns were used (Fig. 1A): one completely continuous and one with a small perpendicular inset of 2.4°. For comparison, the blind spot typically has a diameter of 4°–5°. The Gabor had constant contrast in a radius of 6.3° around the center. This ensured the same perception of the continuous stimulus outside the blind spot in comparison to a filled-in stimulus, where the inner part is inside the blind spot. To account for possible adaptation effects, horizontal and vertical stimuli were used in a balanced and randomized way across the trials. Stimuli were displayed using the Psychophysics Toolbox (31) and Eyelink Toolbox (32). The stimuli were displayed centered at the individually calibrated blind spot location. The stimulus at the location above the blind spot in experiment 2 was at the same distance as the blind spot but was rotated by 25° to the horizon around the fixation cross. For the inward and outward condition of experiment 3, stimuli were moved nasally or temporally by 8.6°, thus the stimuli had an overlap of only 1°. Less overlap is not possible without either cutting the border of the screen or overlapping with the fixation cross.

Task

After a fixation period of 500 ms, we presented two stimuli simultaneously in the left and right peripheries. Subjects were instructed to indicate via button press (left or right) which stimulus was continuous. Each stimulus was presented either in the temporal or nasal field of view. In some trials, the required response was unambiguous, when one of the stimuli showed an inset and the other did not (and at least the inset stimulus was presented outside the blind spot). In many trials (80% of all experiments and locations, 46% when the stimulus was shown above the blind spot in experiment 2), both stimuli were continuous and no unique correct answer existed. All trials were presented in a randomized order. If the subject had not given an answer after 10 seconds, the trial was discarded and the next trial started. All in all, subjects answered 720 trials over 6 blocks; in experiment 1 the trials were split up into two sessions. After each block the eye tracker and the blind spot were re-calibrated. After cleaning trials for fixation deviation and blinks, an average of 498 trials (90%-quantile: 402, 567) remained. For two subjects, only 360 trials could be recorded.

Blind Spots

In order to calibrate their blind spots, subjects were instructed to use the keyboard to move a circular monocular probe on the monitor and to adjust the size and location to fill the blind spot with the maximal size. They were explicitly instructed to calibrate it as small as necessary to preclude any residual flickering. The circular probe flickered from dark gray to light gray to be more salient than a probe with constant color (33). All stimuli were presented centered at the respective calibrated blind spot location. In total, each subject calibrated the blind spot six times. For the following comparisons of blind spot characteristics we evaluated one-sample tests with the percentile bootstrap method (10,000 resamples) of trimmed means (20%) with alpha = 0.05 (34). For paired two-sample data, we used the same procedure on the difference scores. We used bias-corrected, accelerated 95% bootstrapped confidence intervals of the trimmed mean (20%). In line with previous studies (18, 35), the left and right blind spots were located horizontally at -15.48° (SD=0.49° CI:[-15.68°,-15.30°]) and 15.8° (SD=0.56° CI:[15.59°,16.02°]) from the fixation cross. The mean calibrated diameter was 4.92° (SD=0.43° CI:[4.76°,5.08°]) for the left and 5.13° (SD=0.4° CI:[4.98°,5.29°]) for the right blind spot. Blind spots did significantly differ in size ($p<0.001$, CI:[-0.26°,-0.08°]) and in absolute horizontal position (in relation to the fixation cross; $p<0.001$, CI:[0.21°,0.43°]); on average, the right blind spot was 0.32° further outside of the fixation cross. No significant difference was found in the vertical direction ($p=0.86$), but this is likely due to the oval shape of the blind spot in this dimension and the usage of a circle to probe the blind spot. These effects seem small, did not affect the purpose of the experiments and will not be discussed further.

GLMM Analysis

We fitted a Bayesian logistic mixed-effects model predicting the probability of responding "right" with multiple factors that represent the temporal over nasal bias and several other covariates described below. Because we were interested in the bias between the nasal fields and the temporal fields of view, we combined both predictors for the left and right temporal (and nasal, respectively) locations and reported the combined value.

Data were analyzed using a hierarchical logistic mixed effects models fitted by the No-U-Turn Sampler (NUTS, STAN Development Team). The model specification was based on an implementation by Sorensen and Vasisth (36). In the results section we report estimates of linear models with the appropriate parameters fitted on data of each experiment independently. We also analyzed all data in one combined model: there were no substantial differences between the results from the combined model and the respective submodels (Appendix table 1). The models are defined as follows using the Wilkinson notation:

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

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

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

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

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

Two factors were between subjects: *handedness* and *dominant eye*. In total, we have four within-subject factors, resulting in eight parameters: There are two main factors representing whether the left, and respectively the right, stimulus was inside or outside the *temporal* field. Depending on the experiment, the main factor *location* had up to three levels: the stimuli were presented outwards (3rd experiment), inwards (3rd), above (2nd) or on (1st, 2nd, 3rd) the blind spot. In addition, we modeled the interactions between location and whether the left stimulus (and the right stimulus, respectively) was shown temporally. In order to assure independence of observation, an additional within-subject main factor *answer(t-1)* was introduced, which models the current answer based on the previous one. In frequentist linear modeling terms, all within-subject effects were modeled using random slopes clustered by subject and a random intercept for the subjects. We used treatment coding for all factors and interpreted the coefficients accordingly.

In the model we estimated the left and right temporal field effects separately. For the statistical analysis, we combined these estimates by inverting the left temporal effect and averaging with the right temporal effect. We did this for all samples of the mcmc-chain and then took the median value. We then transformed these values to the probability domain using the invlogit function, subtracting the values from 0.5 and multiplying by 100. All results were still in the linear range of the logit function. We calculated 95% credible intervals the same way and reported them as parameter estimates (CDI_{95} lower-upper) in the text. These transformed values represent the additive probability (in %) of choosing a left (right) stimulus that is shown in the left (right) temporal field of view compared to presenting the left (right) stimulus in the nasal field of view, keeping all other factors constant.

Reaction Times

Initially, we did not plan to analyze the reaction time data. These analyses are purely explorative. Our setup consisted of a consumer keyboard, thus delays and jitters are to be expected. But with an average of 498 trials per subject, we did not expect a bias between conditions from jitter in our analyses. Our reaction time data were analyzed with a simple Bayesian mixed linear model:

$$RT \sim 1 + Temporal_{Selected} * Location + (1 + Temporal_{Selected} * Location \mid subject)$$

Only trials without a visible inset stimulus were used. *Temporal selected* consists of all trials where a temporal stimulus was selected. Because of the bias described in the results, there is a slight imbalance in the number of trials between the two conditions: 234.9 CI:[228.5, 241.3] for the nasal selection and 263.1 CI:[257.5, 269.4] for the temporal selection.

Bayesian Fit:

We did not make use of prior information in the analysis of our data. We placed implicit, improper, uniform priors from negative to positive infinity on the mean and 0 to infinity for the standard deviations of our parameters, the default priors of STAN. An uninformative lkj-prior ($\nu = 2$) was used for the correlation matrix, slightly emphasizing the diagonal over the off-diagonal of the correlation matrix (36, 37).

We used six mcmc-chains using 2000 iterations each, with 50% used for the warm-up period. We visually confirmed convergence through autocorrelation functions and trace plots, then calculated the scale reduction factors (38), which indicated convergence as well (Rhat < 1.1).

Effects not reported in the result section

We report other effects based on a combined model over all experiments. We did not find evidence for a different global bias (main effect location) in any of the four stimulation positions tested here. Dominant eye has a 12.3% effect (CDI_{95}2.78%-21.04%) on global bias; thus subjects with a dominant right eye also preferred the right stimulus over the left one (irrespective of whether the stimulus was visible through the left or the right eye). We find a global bias (in the intercept of -27.6% CDI_{95} -40.08% - -9.66%, with treatment coding) toward choosing the left stimulus; this might reflect that in the first two experiments we instructed subjects to use the right hand, thus they used their index and middle fingers. In the third experiment we instructed subjects to use both index fingers, resulting in a decreased bias to the left, with a shift more to the right (and thus more to balanced answers) of 12.24% (CDI_{95} -1.98-24.16%]).

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

There was a strong influence of the previous answer on the current answer. We observe a global effect of 9.57% (CDI_{95}1.7%-17.03%), and the coding suggests that subjects are more likely to choose the right stimulus again when they have just chosen "right" in the previous trial. For this effect it is more important to look at random effect variance, which is quite high with a standard deviation of 29.9% (CDI_{95} 26.28%-33.7%), suggesting that there is large variation between subjects. Indeed, a closer look at the random slopes of the effect reveals three different strategies: Some subjects tend to stick the same answer, some subjects are balanced in their answers without any trend and some subjects tend to regularly alternate their answers in each trial.

Other models we considered showed no effect when both stimuli were in the temporal field, nor any three-way interaction. In order to simplify the final model, we removed these effects from future fits.

REFERENCES

1. Shadlen M, Britten K, Newsome W, Movshon J (1996) A computational analysis of the relationship between neuronal and behavioral responses to visual motion. *J Neurosci* 16(4):1486–1510.
2. Shadlen MN, Newsome WT (2001) Neural basis of a perceptual decision in the parietal cortex (area LIP) of the rhesus monkey. *J Neurophysiol* 86(4):1916–1936.
3. Wahn B, König P (2016) Attentional resource allocation in visuotactile processing depends on the task, but optimal visuotactile integration does not depend on attentional resources. *Front Integr Neurosci* 10:13.
4. Wahn B, König P (2015) Audition and vision share spatial attentional resources, yet attentional load does not disrupt audiovisual integration. *Front Psychol* 6:1084.
5. Wahn B, König P (2015) Vision and haptics share spatial attentional resources and visuotactile integration is not affected by high attentional load. *Multisens Res* 28(3-4):371–392.
6. Quigley C, Onat S, Harding S, Cooke M, König P (2008) Audio-visual integration during overt visual attention. *J Eye Mov Res* 1(2):4.
7. Schall S, Quigley C, Onat S, König P (2009) Visual stimulus locking of EEG is modulated by temporal congruency of auditory stimuli. *Exp Brain Res* 198(2-3):137–51.
8. Hollensteiner KJ, Pieper F, Engler G, König P, Engel AK (2015) Crossmodal integration improves sensory detection thresholds in the ferret. *PLoS One* 10(5):e0124952.
9. Ernst MO, Banks MS (2002) Humans integrate visual and haptic information in a statistically optimal fashion. *Nature* 415(6870):429–33.
10. Alais D, Burr D (2004) The ventriloquist effect results from near-optimal bimodal integration. *Curr Biol* 14(3):257–262.
11. Körding KP, Wolpert DM (2004) Bayesian integration in sensorimotor learning. *Nature* 427(6971):244–247.

12. Tickle H, Speekenbrink M, Tsetsos K, Michael E, Summerfield C (2016) Near-optimal integration of magnitude in the human parietal cortex. *J Cogn Neurosci* 28(4):589–603.

13. Gu Y, Angelaki DE, Deangelis GC (2008) Neural correlates of multisensory cue integration in macaque MSTd. *Nat Neurosci* 11(10):1201–10.

14. Fetsch CR, Pouget A, DeAngelis GC, Angelaki DE (2012) Neural correlates of reliability-based cue weighting during multisensory integration. *Nat Neurosci* 15(1):146–154.

15. Heekeren HR, Marrett S, Bandettini PA, Ungerleider LG (2004) A general mechanism for perceptual decision-making in the human brain. *Nature* 431(7010):859–862.

16. Bankó EM, Gál V, Körtvélyes J, Kovács G, Vidnyánszky Z (2011) Dissociating the effect of noise on sensory processing and overall decision difficulty. *J Neurosci* 31(7):2663–2674.

17. Tassinari H, Hudson TE, Landy MS (2006) Combining priors and noisy visual cues in a rapid pointing task. *J Neurosci* 26(40):10154–10163.

18. Ehinger B V., Konig P, Ossandon JP (2015) Predictions of visual content across eye novements and their modulation by inferred information. *J Neurosci* 35(19):7403–7413.

19. Tong F, Engel S (2001) Interocular rivalry revealed in the human cortical blind-spot representation. *Nature* 411(6834):195–9.

20. Fahle M, Schmid M (1988) Naso-temporal asymmetry of visual perception and of the visual cortex. *Vision Res* 28(2):293–300.

21. Curcio CA, Sloan KR, Kalina RE, Hendrickson AE (1990) Human photoreceptor topography. *J Comp Neurol* 292(4):497–523.

22. Rovamo J, Virsu V, Laurinen P, Hyvärinen L (1982) Resolution of gratings oriented along and across meridians in peripheral vision. *Invest Ophthalmol Vis Sci* 23(5):666–670.

23. Pöppel E, Held R, Frost D (1973) Residual visual function after brain wounds involving the central visual pathways in man. *Nature* 243(5405):295–296.

24. Paradiso MA, Carney T (1988) Orientation discrimination as a function of stimulus

eccentricity and size: nasal/temporal retinal asymmetry. *Vision Res* 28(8):867–874.

25. Crossland MD, Bex PJ (2009) Spatial alignment over retinal scotomas. *Invest Ophthalmol Vis Sci* 50(3):1464–1469.
26. Friston K, Kilner J, Harrison L (2006) A free energy principle for the brain. *J Physiol Paris* 100(1-3):70–87.
27. Friston K, Adams R a, Perrinet L, Breakspear M (2012) Perceptions as hypotheses: saccades as experiments. *Front Psychol* 3(May):151.
28. Summerfield C, de Lange FP (2014) Expectation in perceptual decision making: neural and computational mechanisms. *Nat Rev Neurosci* (October). doi:10.1038/nrn3838.
29. Kok P, Bains LJ, van Mourik T, Norris DG, de Lange FP (2016) Selective Activation of the Deep Layers of the Human Primary Visual Cortex by Top-Down Feedback. *Curr Biol* 26(3):371–376.
30. Komatsu H (2006) The neural mechanisms of perceptual filling-in. *Nat Rev Neurosci* 7(3):220–31.
31. Brainard DH (1997) The psychophysics toolbox. *Spat Vis* 10(4):433–436.
32. Cornelissen FW, Peters EM, Palmer J (2002) The eyelink toolbox: eye tracking with MATLAB and the psychophysics toolbox. *Behav Res Methods, Instruments, Comput* 34(4):613–617.
33. Awater H (2005) Cortical representation of space around the blind spot. *J Neurophysiol* 94(5):3314–3324.
34. Wilcox RR (2012) *Introduction to Robust Estimation and Hypothesis Testing* (Academic Press). 3rd Editio.
35. Wolf E, Morandi A (1962) Retinal sensitivity in the region of the blind spot. *JOSA* 52(11):806–812.
36. Sorensen T, Vasishth S (2015) Bayesian linear mixed models using stan: a tutorial for psychologists, linguists, and cognitive scientists. *bioRxiv*:30.

37. Carpenter B, et al. (2016) Stan: a probabilistic programming language. *J Stat Softw* In Press.

38. Gelman A, Hwang J, Vehtari A (2014) Understanding predictive information criteria for Bayesian models. *Stat Comput* 24(6):997–1016.

ACKNOWLEDGEMENTS

We thank Tim C. Kietzmann for his valuable suggestions on the design of the experiment and Frank Jäkel for his valuable discussions of the analysis. This work was supported by SPP 1665, the European Union through the H2020 FET Proactive project socSMCs (GA no 641321) and SFB 936, project B1.

SUPPLEMENTARY

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%]

Table 1: Overview of the results of all experiments individually and the combined estimates. Empty cells indicate that the condition was not measured in this study.