

# Pre-stimulus beta power encodes explicit and implicit perceptual biases in distinct cortical areas

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## Abstract

Perception is biased by expectations and previous actions. Pre-stimulus brain oscillations are a potential candidate for implementing biases in the brain. In two EEG studies on somatosensory near-threshold detection, we investigated the pre-stimulus neural correlates of an (implicit) previous choice bias and an explicit bias. The explicit bias was introduced by informing participants about stimulus probability on a single-trial level (volatile context) or block-wise (stable context). Behavioural analysis confirmed adjustments in the decision criterion and confidence ratings according to the cued probabilities and previous choice-induced biases. Pre-stimulus beta power with distinct sources in sensory and higher-order cortical areas predicted explicit and implicit biases, respectively, on a single subject level and partially mediated the impact of previous choice and stimulus probability on the detection response. We suggest that pre-stimulus beta oscillations in different brain areas are neural correlates of explicit and implicit biases in somatosensory perception.

**Keywords:** expectations, choice history, somatosensory perception, oscillations, pre-stimulus, beta oscillations, EEG

## Introduction

Perception is biased by our knowledge of what is probable. This has been successfully formalised in the Bayesian brain theory,<sup>1</sup> which assumes an integration of prior beliefs and the sensory signal. It follows that the brain should rely more on prior beliefs when sensory signals are “uncertain”, i.e., weak. Accordingly, providing human observers with information about stimulus probability has been shown to bias perceptual reports of weak visual stimuli<sup>2</sup>. In such situations, human observers adjust their decision criterion while sensitivity to the sensory signal remains unaffected<sup>3</sup>. Additionally, providing individuals with prior information about the probability of a stimulus has been shown to impact confidence in a perceptual decision<sup>4</sup>. Besides external and explicit information about the probability of upcoming stimuli, the perceptual choice history also influences decision-making, with stronger choice history biases in ambiguous perceptual decisions<sup>5</sup>. In the remainder, we refer to the bias induced by choice history as implicit bias, as this bias originates from internal processes which are not explicitly controlled by the experimenter. Although studies have demonstrated the adaptability of choice history biases to participants' models of the environment<sup>6,7</sup>, whether and how they interact with biases induced by stimulus probability environments remains poorly understood.

In addition, while a substantial body of research has established that explicit expectations and choice history shape perception at the behavioural level, a notable gap remains in our understanding of the distinct and/or shared neural correlates of these processes<sup>2,8-10</sup>. Gustatory stimulation in rats in combination with computational modelling showed that general stimulus expectations modulated pre-stimulus metastable dynamics of neural activity<sup>11</sup>. Using MEG recordings in humans, Kok and colleagues<sup>12</sup> reported that neural representations of expected visual stimuli in pre-stimulus activity closely resembled the evoked activity following the onset of expected stimuli. The findings<sup>12</sup> support the idea that the brain generates stimulus templates in the sensory cortex to anticipate expected inputs. Importantly, pre-stimulus activity has also been shown to reflect biases in perceptual choice history<sup>13,14</sup>.

EEG and MEG studies have emphasised the impact of pre-stimulus oscillations, particularly in the alpha and beta frequency range on perceptual decision-making. Multiple studies have shown that pre-stimulus power in alpha and beta band oscillations in the somatosensory cortex is negatively correlated with detection rates for a subsequent weak tactile stimulus<sup>15–20</sup>. According to the baseline sensory excitability model (BSEM)<sup>21</sup>, pre-stimulus alpha power correlates positively with the participants' decision criterion in detection tasks. Indeed, recent studies in the visual<sup>22</sup> and the somatosensory domain,<sup>23</sup> confirmed a positive correlation between spontaneous modulations of pre-stimulus alpha power and the participants' criterion. So far, only two studies have examined the causal nature of this effect in humans. Both studies employed a visual detection task, inducing criterion changes either through reward strategy<sup>24</sup> or priming<sup>25</sup>. The study by Kloosterman et al.<sup>24</sup> incentivised either a liberal or conservative criterion and showed a correlation between visual pre-stimulus alpha power and the experimentally induced criterion change. A study by Zhou et al.<sup>25</sup>, however, did not find a correlation between visual pre-stimulus alpha power and criterion changes that were induced via priming.

The beta frequency band has generally been suggested to carry signals of top-down predictions<sup>26,27</sup>. Consistent with this notion, the control of goal-directed sensory processing has been linked to beta power or more precisely occurrence of beta bursts<sup>28</sup>. Beta power has also been proposed to be related to the maintenance of cognitive states<sup>29</sup>, with evidence pointing to beta power not only maintaining but also reactivating cognitive states that are required for the current task<sup>30</sup>, which again supports the idea of a pre-stimulus template of expectations as has been suggested by Kok and colleagues<sup>12</sup>.

Taken together, while previous work strongly supports the idea that pre-stimulus alpha and beta rhythms in sensory areas influence perceptual decision-making, it is not clear whether and how these influences are related to explicit and implicit biases. To address this gap, we conducted two EEG studies that differed in the temporal context of stimulus occurrence<sup>31</sup>. In the first study, participants were informed about the signal probability

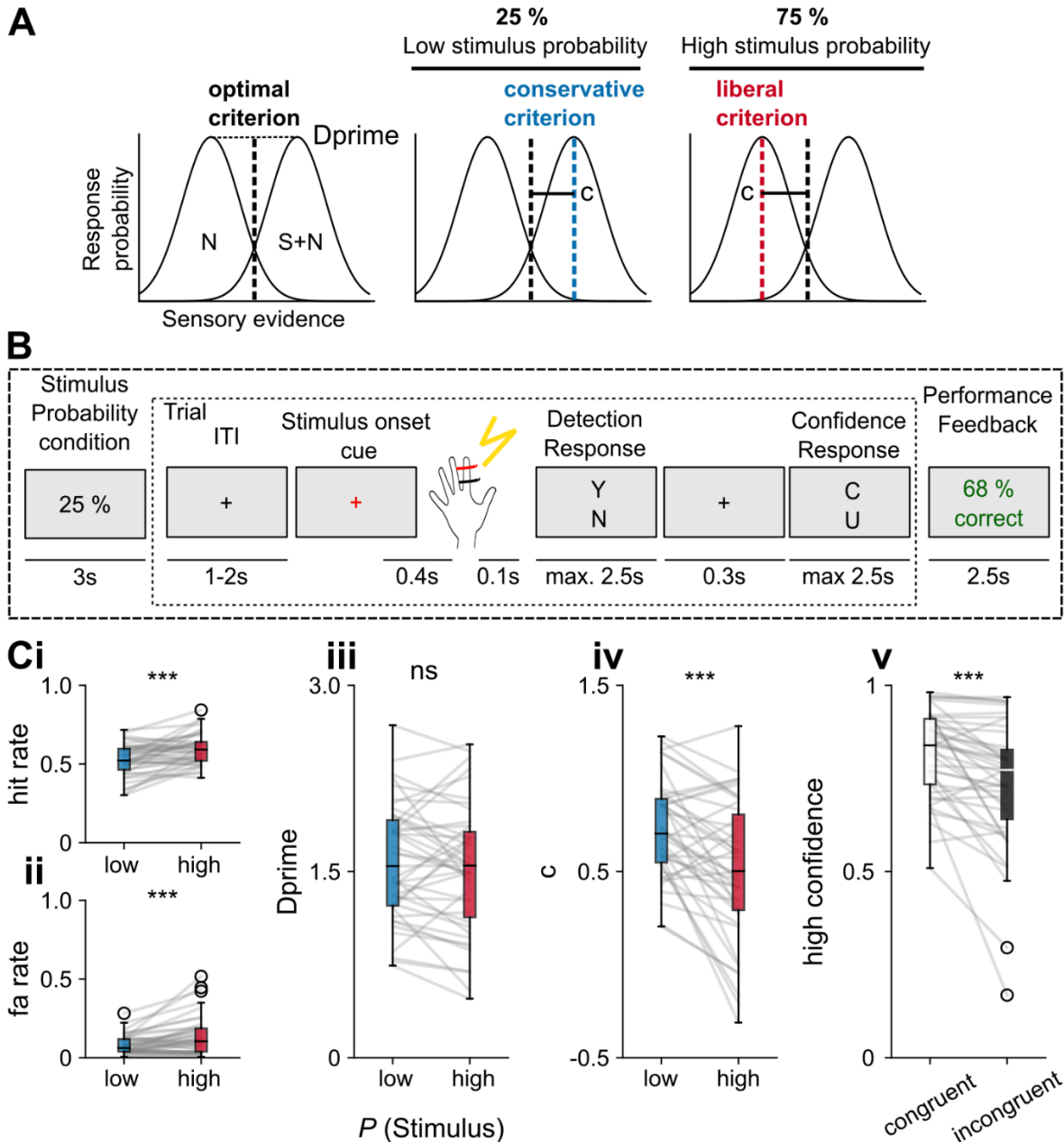
for a block of stimuli (“stable environment”), in the second study, the stimulus probability was randomly assigned for each trial (“volatile environment”). The two studies with different probability contexts allowed us to account for previous choice biases both in a more ecologically valid paradigm (block design) and in a paradigm in which we experimentally controlled for previous choice distributions (trial-by-trial design). We hypothesised that human observers would adjust their detection and confidence ratings based on the instructed stimulus probability and exhibit biases based on choice history in both studies. Based on previous findings these biases should be reflected in pre-stimulus alpha and beta frequency oscillations.

## Results

### Behavioural criterion shifts in correspondence to stimulus probability

We tested the effect of stimulus probability on somatosensory near-threshold detection in two separate studies. The first study ( $n=43$ ) informed participants about stimulus probability at the *beginning of each block* consisting of 12 trials (stable environment). The stimulus onset within a trial was cued by a colour change of the fixation cross. The second study ( $n=39$ ) provided information about stimulus probability at the *beginning of each trial* (volatile environment). In both studies, signal detection theoretic (SDT) analyses verified that participants adjusted their criterion to report a stimulus based on the instructed stimulus probability, i.e., the criterion was lower (more “liberal”) in the high probability condition (mean criterion change high vs. low stimulus probability:  $\Delta_{\text{crit. stable}} = -.21$ ,  $W = 172$ ,  $p < .0001$ , fig. 1Civ;  $\Delta_{\text{crit. volatile}} = -.21$ ,  $W = 91$ ,  $p < .0001$ , fig. 2Biv). Participants reported that they perceived a stimulus more often in both signal (mean hit rate (HR) change high minus low stimulus probability:  $\Delta_{\text{HR stable}} = .07$ ,  $W = 151$ ,  $p < .001$ ;  $\Delta_{\text{HR volatile}} = .08$ ,  $W = 69$ ,  $p < .0001$ ) and noise trials (trials without a stimulus) (mean false alarm rate (FAR) change high minus low stimulus probability:  $\Delta_{\text{FAR stable}} = .06$ ,  $W = 185$ ,  $p < .001$ ;  $\Delta_{\text{FAR volatile}} = .03$ ,  $W = 169$ ,  $p = .002$ ) under the high as compared to the low probability condition (fig. 1Ci & ii and fig. 2Bi & ii). Stimulus sensitivity (measured by the SDT parameter  $D_{\text{prime}}$ ) did not significantly differ between conditions (mean  $D_{\text{prime}}$

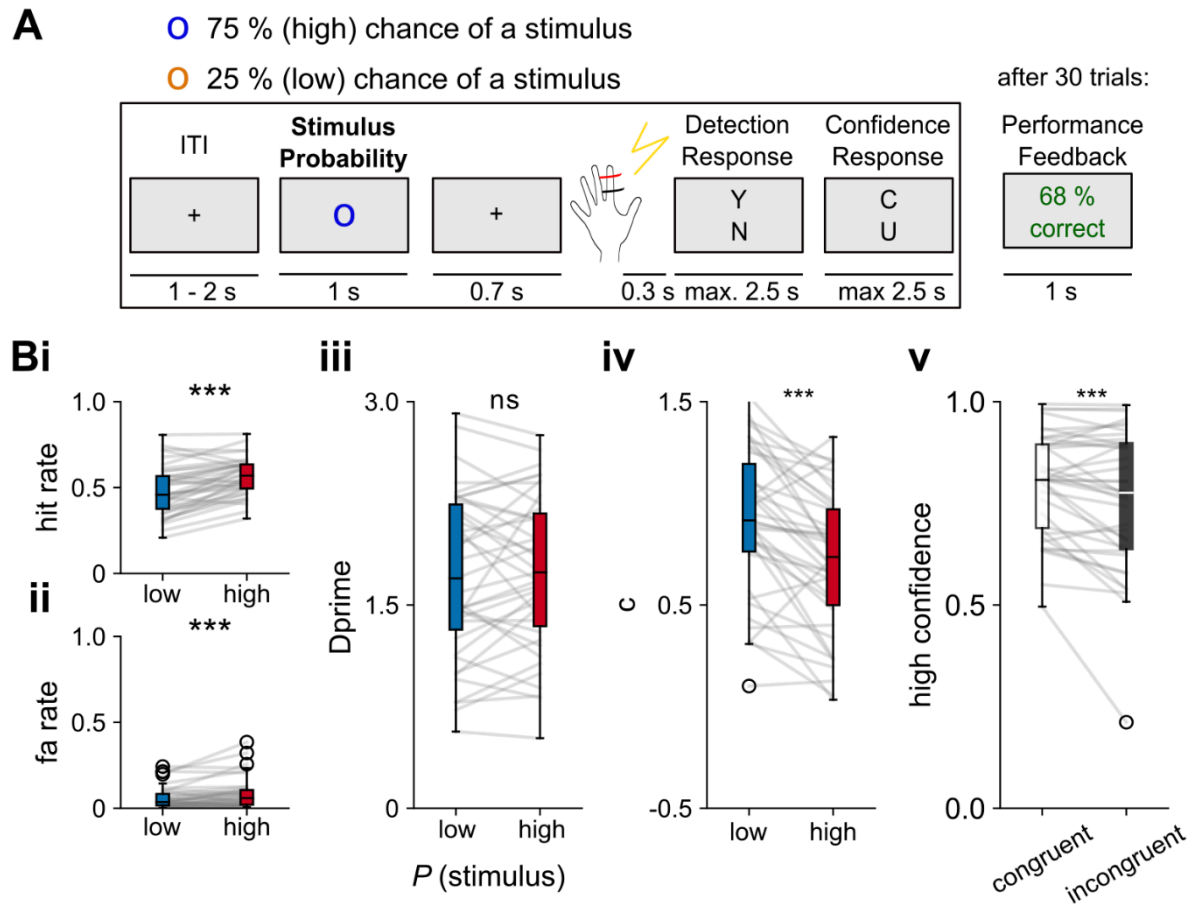
change high minus low stimulus probability:  $\Delta_{D_{\text{prime stable}}} = -.06$ ,  $W = 391$ ,  $p = .329$ ,  $\Delta_{D_{\text{prime volatile}}} = .02$ ,  $W = 361$ ,  $p = .686$ , fig. 1Ciii & fig. 2Biii).



**Fig. 1: Experimentally controlled stimulus expectations shift detection threshold in a stable probability environment. A: Signal detection theory model:** According to SDT, valid stimulus probabilities should lead to a change in the decision criterion  $c$  while sensitivity  $D_{\text{prime}}$  should not be affected. S: Signal, N: Noise. **B: Overview of trial**

**structure:** Participants were presented with a valid probability cue (low or high) at the beginning of each block. Each block consisted of 12 trials, with the proportion of near-threshold and “catch” (i.e., no stimulus) trials according to the probability cue. **C:** **SDT analysis:** Participants had a higher hit rate (i) as well as a higher false alarm rate (ii) in the high expectation condition with no significant difference in Dprime (iii).  $c$  was significantly higher in the low probability condition indicating a more conservative criterion (iv). The mean of high confidence ratings in **correct** trials was higher in trials in which the response matched the participants' expectations (v). See also **S1**. **Significance:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ . **Abbreviations:** ns = not significant.

Analysis of confidence responses further confirmed that participants utilised stimulus probability to inform their decision-making process. Specifically, confidence ratings in correct trials were compared based on the congruency between the probability cue and the response on each trial. We expected participants to be more confident in their decision of a yes-response in high stimulus probability trials and of a no-response in low stimulus probability trials (congruent trials). Indeed, participants reported significantly higher confidence in congruent trials compared to incongruent trials (mean confidence congruent minus incongruent correct trials:  $\Delta_{\text{conf. stable}} = .08$ ,  $W = 92$ ,  $p < .0001$ ,  $\Delta_{\text{conf. volatile}} = .04$ ,  $W = 188$ ,  $p = .005$ , fig. 1Cv & fig. 2Bv). Notably, the exclusion of three participants with very high false alarm rates exceeding 40 % in the high stimulus probability condition did not change the statistical outcomes in the stable context (fig. S1). While we informed participants in both paradigms about the underlying stimulus probability, we reasoned that the previous choice would be more informative in the stable probability environment. In the volatile environment the stimulus probability changes from trial to trial, and might thus influence the subjective estimated stimulus probability that an ideal observer calculates less than compared to the blocked design (see fig. S2.1). We fitted signal detection theoretic generalised linear mixed models (GLMMs) for both stimulus probability environments, to investigate the relationship between the explicit, stimulus probability-induced bias and the implicit, choice history bias.



**Fig. 2: Single-trial cues of stimulus probability shift the criterion (indexed by a change in  $c$ ) with no significant change in Dprime. A: Overview of trial structure:** Participants were presented with a probability cue (orange or blue circle) at the beginning of each trial. **B: SDT analysis:** Participants had a higher hit rate (i) as well as a higher false alarm rate (ii) in the high expectation condition with no significant difference in Dprime (iii). The criterion was significantly more conservative in the low probability condition (indexed by a higher value of  $c$ ). (iv) The mean of high confidence ratings in **correct** trials was higher in trials in which the response matched the participants' expectations (v). See also Supplementary figures **S2.1, S2.2, S2.3, S2.4**. **Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ . **Abbreviations:** ns = not significant.



## Response history bias interacts with stimulus probability in a stable environment

To investigate how previous choices influence current choices, we included the previous detection response as a regressor in our model, which improved the model fit in both probability environments ( $\Delta_{\text{AIC stable}} = -229$ ,  $\chi^2(5) = 229.83$ ,  $p < .001$ ;  $\Delta_{\text{AIC volatile}} = -80$ ,  $\chi^2(5) = 90.94$ ,  $p < .001$ ). Overall, participants demonstrated a tendency to repeat their previous choice ( $\beta_{\text{stable}} = .117$ ,  $\text{SE} = .050$ ,  $p = .021$ ,  $\beta_{\text{volatile}} = .177$ ,  $\text{SE} = .043$ ,  $p < .001$ ). Importantly, even after controlling for the effect of the previous response, stimulus probability still accounted for a significant amount of variance in the detection response ( $\beta_{\text{stable}} = .141$ ,  $\text{SE} = .054$ ,  $p = .010$ ,  $\beta_{\text{volatile}} = .180$ ,  $\text{SE} = .056$ ,  $p = .001$ ). Finally, we fitted a model that included the interaction between the previous choice and stimulus probability, which improved the model fit in the stable but not in the volatile context ( $\Delta_{\text{AIC stable}} = -13$ ,  $\chi^2(1) = 14.91$ ,  $p < .001$ ;  $\Delta_{\text{AIC volatile}} = +2$ ,  $\chi^2(1) = 0.08$ ,  $p = .777$ ). Specifically, the model fitted with the data from the stable environment showed a significant interaction between the stimulus probability and the previous choice regressor ( $\beta_{\text{stable}} = .163$ ,  $\text{SE} = .042$ ,  $p < .001$ ). Post-hoc tests showed a significant influence of the previous choice on the detection response both in the high and low stimulus probability conditions, but the effect was weaker in the low probability condition (conditioned on low stimulus probability and previous yes response:  $\beta_{\text{stable}} = .058$ ,  $\text{SE} = .025$ ,  $p = .021$ , high stimulus probability and previous yes response:  $\beta_{\text{stable}} = .140$ ,  $\text{SE} = .027$ ,  $p < .001$ , FDR corrected, see fig. S.2.2 for the visualisation of the model-free interaction effect of criterion (indexed by c) and previous choice, model summaries in suppl. table 1 & 2).

A key feature of the stable environment is the difference in the previous response distributions between the probability blocks. While in both environments the instructed probability matched the actual stimulus probability ("valid cues"), the randomization of probability cues within the volatile environment effectively balanced the distributions of previous "yes" and "no" responses (fig. S2.3 Biii).

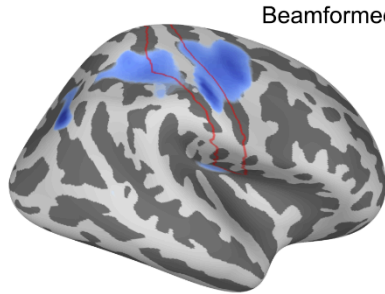
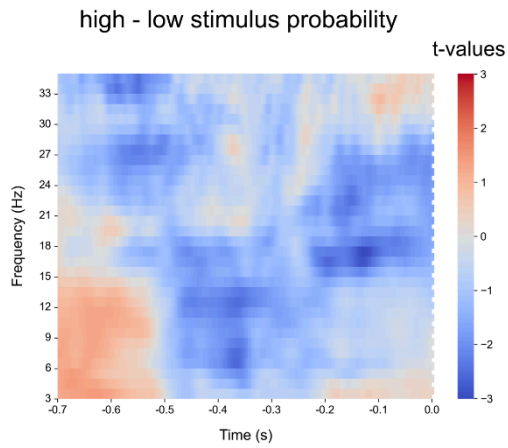
Next, we fitted the interaction model separately for signal and noise trials, to investigate whether the interaction effect was driven by the unequal amount of signal and noise trials within the probability conditions. Both the “signal trials only” model ( $\beta = .182$ ,  $SE = .063$ ,  $p = .004$ ), as well as the “noise trials only” model ( $\beta = .213$ ,  $SE = .097$ ,  $p = .027$ ) showed a significant interaction between the choice history induced bias and the stimulus probability induced bias. The model fitted with trials that previously contained a signal confirmed an interaction between stimulus probability and previous response ( $\beta = .149$ ,  $SE = .065$ ,  $p = .021$ ). Interestingly, the interaction effect was no longer statistically significant for trials that followed noise ( $\beta = .029$ ,  $SE = .090$ ,  $p = .742$ ). Previous research has shown that choice history biases are stronger after previous decisions of high confidence<sup>6,32</sup>, which is confirmed by our data. Participants are more likely to repeat their previous response if they indicated high confidence in the previous trial and alternate their response if they indicated low confidence in the previous trial (interaction  $\beta = .351$ ,  $SE = .045$ ,  $p < .001$ ).

## Lower pre-stimulus beta power in distinct areas associated with bias introduced by stimulus probability and previous choice

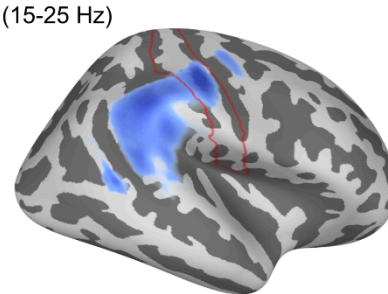
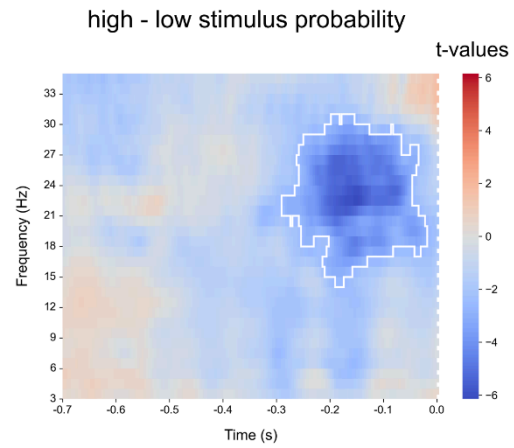
After having confirmed the behavioural effects of the explicit stimulus probability manipulation both on detection as well as confidence responses, we set out to determine the neural correlates of both explicit and implicit biases on somatosensory near-threshold detection. Our initial analysis in sensor space focused on low-frequency oscillations in the pre-stimulus window. To determine the somatosensory region of interest, we selected the EEG channel that showed the strongest early somatosensory stimulus-evoked response (i.e., here assessed by the P50 component at around 50 ms post-stimulus). In both studies, this was channel CP4, which is located over centro-parietal areas contralateral to the somatosensory stimulation site (suppl. fig. S3.1) Next, we computed time-frequency representations in the pre-stimulus window in the frequency range from 3 to 35 Hz for both environments for our channel of interest. A cluster-based permutation test showed no significant cluster for the contrast between high and low stimulus probability trials (fig. 3Ai) in the stable environment (minimum

cluster  $p$ -value: .175) but a significant cluster in the volatile environment, most likely driven by lower power in the beta range in the high stimulus probability condition (minimum cluster  $p$ -value:  $<.001$ , fig. 3Bi, see fig. S.3.2 for a shorter pre-stimulus window). Next, we performed source reconstruction of pre-stimulus beta power. After having validated our beamformer on post-stimulus data (fig. S3.3), we contrasted pre-stimulus beta power for high minus low stimulus probability (visualisation of  $t$ -values in each vertex obtained by a permutation  $t$ -test) and located the strongest modulation in the postcentral gyrus for both environments (fig. 3Ai & 3Bi). Next, we aimed to identify the effect of previous choices in the same pre-stimulus window. Threshold-free cluster-based permutation testing in the pre-stimulus window showed a significant cluster for the previous response contrast in the stable environment (minimum cluster  $p$ -value: .020, fig. 3Ai), but no significant cluster in the volatile environment (minimum cluster  $p$ -value: .443, fig. 3Bii). The strongest power modulation for the previous response contrast was in the secondary somatosensory cortex for the stable environment and in the posterior parietal cortex for the volatile environment.

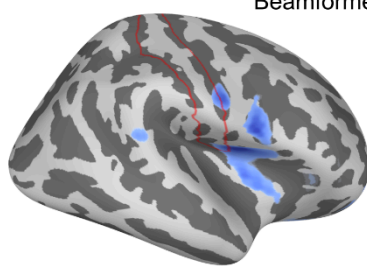
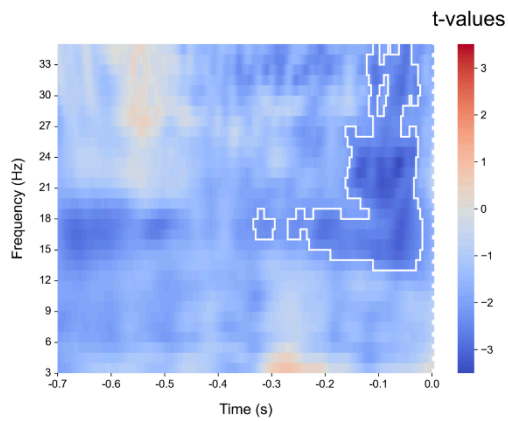
## Ai Stable environment



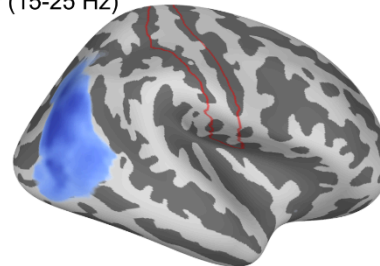
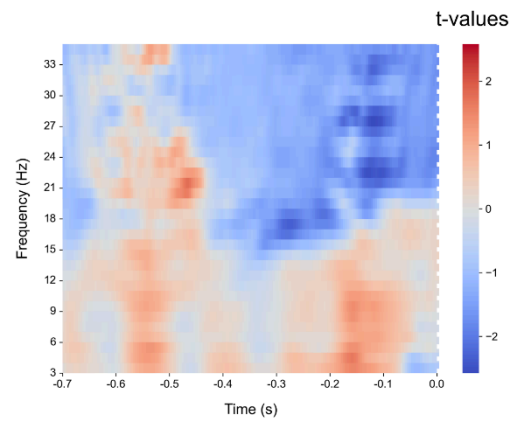
## Bi Volatile environment



## ii previous yes - no response



## ii previous yes - no response



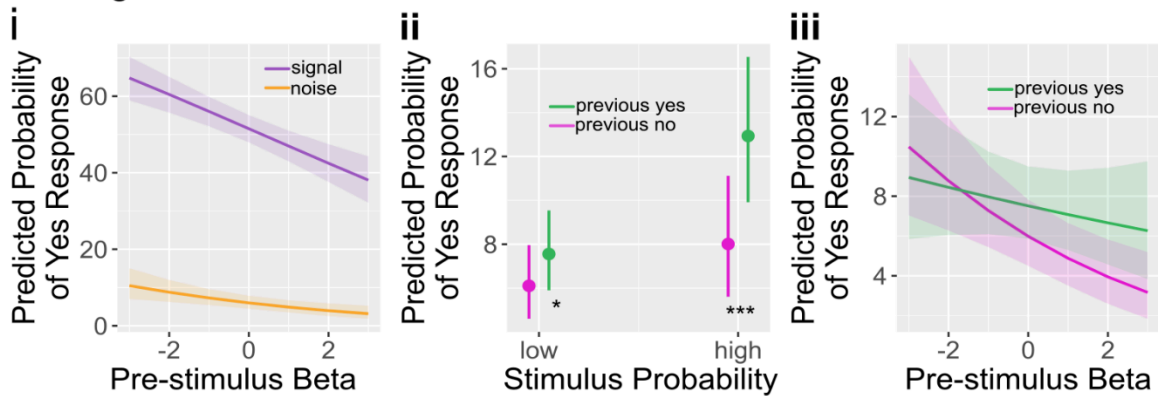
**Fig. 3: Lower pre-stimulus beta power in high probability trials and after a previous yes response in distinct cortical areas.** **Ai:** In the stable environment, a threshold-free cluster permutation test showed no significant cluster for the difference between high and low stimulus probability in the pre-stimulus window (minimum  $p$ -value: .175). A t-test on the source reconstructed pre-stimulus beta power contrast shows the strongest modulation (most negative t-values) in the postcentral gyrus. **Bi:** In the volatile environment, a threshold-free cluster permutation test detected a significant cluster. The effect was most pronounced around stimulus onset in the beta band with lower power in the high stimulus probability condition (minimum  $p$ -value: < .001). The source was localised in the postcentral gyrus. **Aii:** A significant cluster was found in the pre-stimulus window for the contrast between previous yes - previous no responses, which was most likely driven by a beta power desynchronization (minimum  $p$ -value: .020) and for which the strongest beta modulation originated from the secondary somatosensory cortex (SII). **Bii:** No significant cluster for the contrast of previous choices was found in the volatile environment (minimum  $p$ -value: .443). The strongest beta modulation originated from the posterior-parietal cortex. The area marked in red highlights the postcentral gyrus. The 10 % most negative t-values are highlighted in source space, with darker colours representing more negative values. See **S3.1, S.3.2, S3.3.**

### Pre-stimulus beta power predicts criterion change in both environments and interacts with the previous response in the stable environment

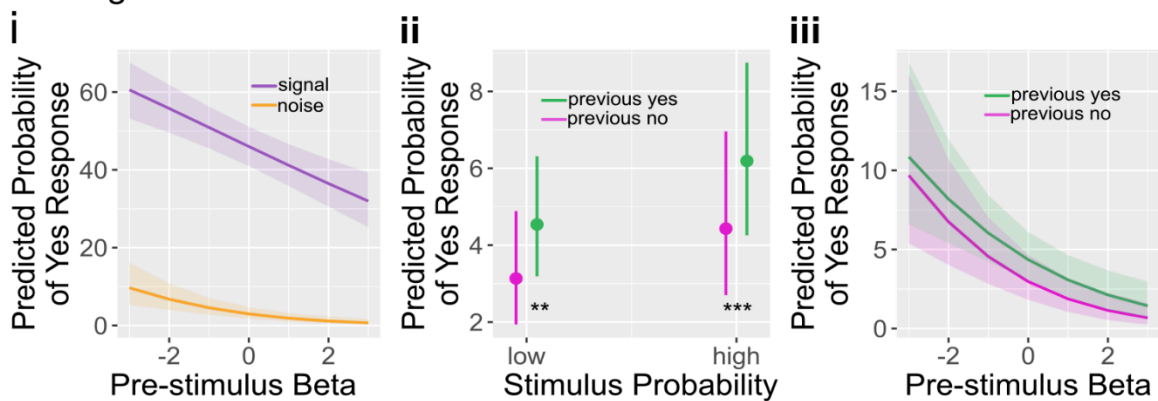
The analysis so far showed a modulation in beta power before–stimulation onset in distinct cortical areas. Next, we investigated how the pre-stimulus beta power modulations related to the behavioural outcomes of the stimulus probability manipulation. Therefore, we averaged pre-stimulus beta power over voxels in source space which were among the 10 % of voxels with the most negative t-values for the probability contrast. Note that in both environments the strongest beta modulation was in the postcentral gyrus. Behavioural modelling showed that the probability manipulation led to a change in participants' decision criteria in both studies, with an interaction

between the previous response and stimulus probability only in the stable environment. If pre-stimulus beta power is a neural correlate of the experimental manipulation of stimulus probabilities, i.e., reflecting the change in criterion, it should also predict the change in detection rates (for signal and noise trials) in both studies and mimic the interaction with the previous choice in the stable environment. For the single-trial analysis, we calculated the average pre-stimulus beta power averaged over the most discriminative voxels for the stimulus probability contrast. Brain-behaviour modelling confirmed that stimulus probability predicted pre-stimulus beta power on a single trial level in both environments ( $\beta_{\text{stable}} = -.025$ ,  $SE = .007$ ,  $p < .001$ ,  $\beta_{\text{volatile}} = -.053$ ,  $SE = .010$ ,  $p < .001$ ), with lower power in the high stimulus probability condition. Participants responded more often that they detected a stimulus both in signal and noise trials after lower pre-stimulus beta power, which suggests that pre-stimulus beta power is a neural correlate of the criterion change ( $\beta_{\text{stable}} = -0.100$ ,  $SE = .031$ ,  $p = .001$ ,  $\beta_{\text{volatile}} = -.175$ ,  $SE = .038$ ,  $p < .001$ , fig. 4Ai). In the stable environment, the best-fitting model included an interaction between the previous response and beta power ( $\Delta_{\text{AIC}} = -17.58$ ,  $X^2(2) = 21.578$ ,  $p < .001$ ). The interaction between beta power and previous choices was such that for low beta power, the effect of the previous choice on the detection response was reversed in comparison to the relationship for high beta power (fig. 4Aii). The best fitting model in the volatile environment did not include an interaction between previous choices and stimulus probability ( $\Delta_{\text{AIC}} = 2.65$ ,  $X^2(2) = 1.35$ ,  $p = .508$ ), participants responded more often that they detected a stimulus after low beta power and after previous yes responses (fig. 4 Bii, model summaries in suppl. table 3 & 4).

### A Marginal effects: Stable environment



### B Marginal effects: Volatile environment



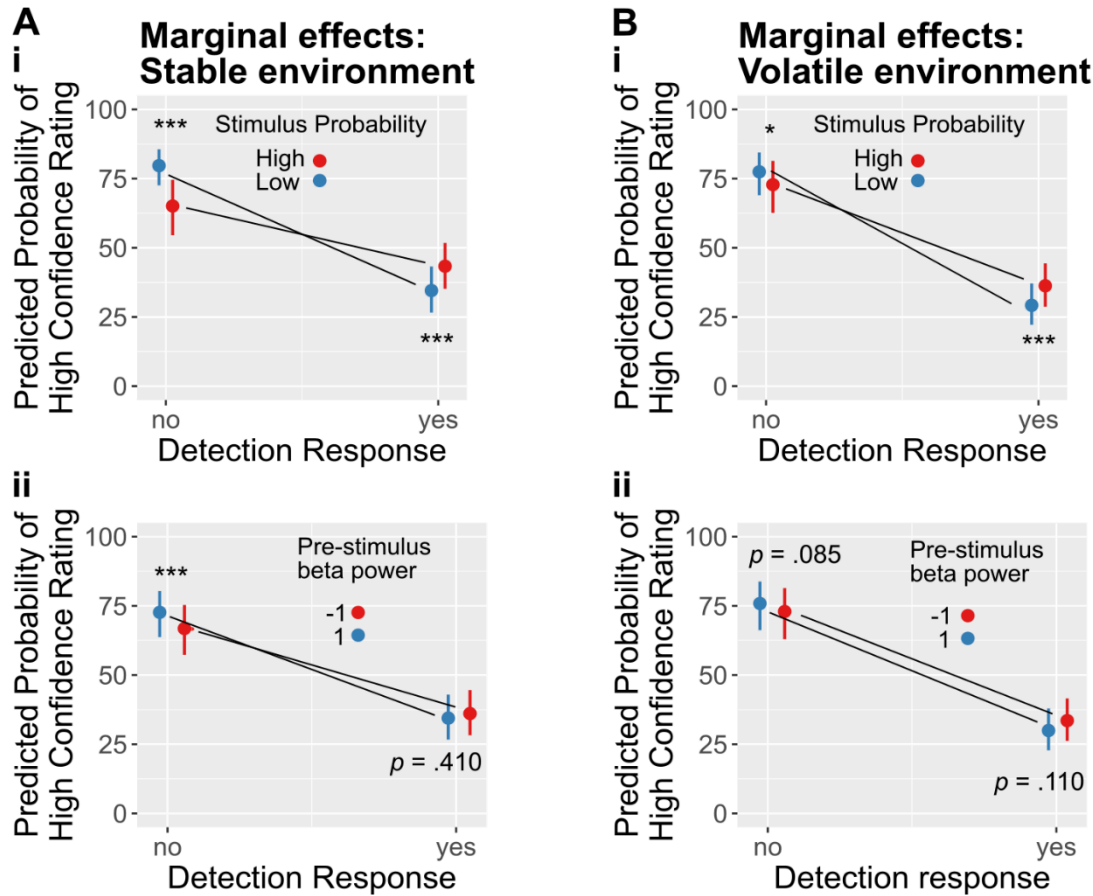
**Fig. 4: Pre-stimulus beta power predicts criterion change and interacts with stimulus probability in the stable environment. Ai:** the probability for a detection response decreases with higher pre-stimulus beta power for both signal and noise trials in the stable environment. **Bi:** the probability for a stimulus report decreases with higher pre-stimulus beta power for both signal and noise trials in the volatile environment. **Aii:** the effect of the previous response depends on the stimulus probability condition in the stable environment (significant interaction). **Bii:** participants respond more often that they detect a stimulus after previous yes responses in both probability conditions (no significant interaction) in the volatile environment. **Aiii:** in the stable environment, the previous response interacts with pre-stimulus beta power regarding its relationship with the probability of a yes response such that with previous "no response" the probability of a "yes response" decreases while there is no effect after a previous yes response. **Biii:** The probability for a yes response decreases with increasing beta power independent of

the previous response. **Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ , shaded areas and error bars show the 95 % confidence interval.

## Pre-stimulus beta power mirrors the congruency effect on confidence ratings

To reinforce the significance of pre-stimulus beta power as a neural correlate of stimulus expectations, we aimed to validate its ability to account for the congruency effect on confidence ratings observed in the behavioural model. Congruency was defined as the alignment between stimulus probability and the detection response. For example, a "yes" response in the high probability condition would be considered a probability-congruent response. Participants were more confident in correct trials, after a no response and following a previous high confidence rating. Crucially, pre-stimulus beta power mimics the response congruency effect on confidence: Participants were more confident in yes responses in the high probability condition as compared to the low probability condition ( $\beta_{\text{stable}} \text{ probability*response} = 0.673$ ,  $SE = .110$ ,  $p < .001$ ,  $\beta_{\text{volatile}} \text{ probability*response} = .342$ ,  $SE = .084$ ,  $p < .001$ , fig. 5Ai & Bi) and analogously in trials with low pre-stimulus beta power (a feature of the high probability condition) as compared to trials with high pre-stimulus beta power ( $\beta_{\text{stable}} \text{ beta*response} = -0.106$ ,  $SE = .035$ ,  $p = .002$ ,  $\beta_{\text{volatile}} \text{ beta*response} = -0.095$ ,  $SE = .040$ ,  $p = .019$ , fig. 5Aii & Bii). The inverse behaviour was seen for No-responses (for model summaries see suppl. table 5 & 6).





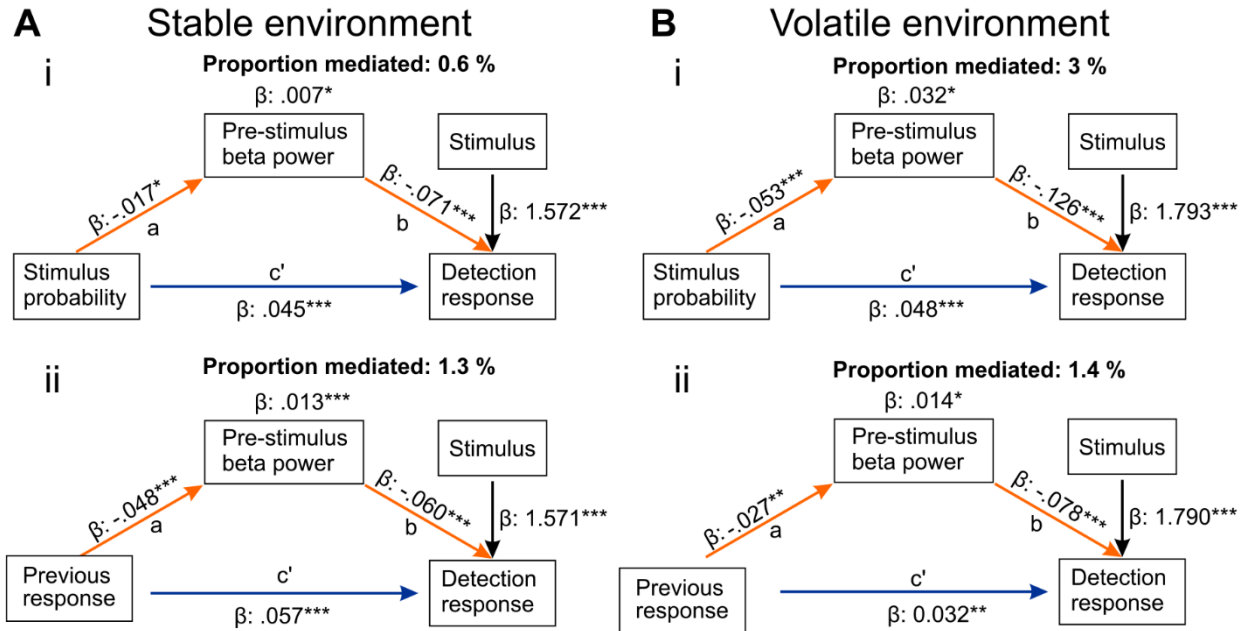
**Fig. 5: Pre-stimulus beta power predicts congruency effect on confidence ratings.**

**Ai:** the congruency effect on confidence between response and stimulus probability in the stable environment: participants are more confident in no responses in the low probability condition and more confident in yes responses in the high probability condition. **Bi:** the congruency effect on confidence between response and stimulus probability in the volatile environment: participants are more confident in no responses in the low probability condition and more confident in yes responses in the high probability condition. **Aii:** significant congruency effect on confidence between response and beta power in the stable environment: beta power does predict the confidence for both yes and no responses conditional on the probability condition. **Bii:** significant congruency effect on confidence between response and beta power in the volatile environment for yes responses: lower beta power increases confidence in yes

responses. The error bars show the 95 % confidence interval. **Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ .

## Distinct pre-stimulus beta power sources partially mediate the effect of stimulus probability and the previous response on somatosensory near-threshold perception

Finally, a neural correlate of both explicit and implicit biases should partially mediate the effect of stimulus probability and previous response on the detection response. Causal inference methods<sup>33,34</sup> allowed us to determine the indirect effect of either stimulus probability or previous choice on detection that is mediated by pre-stimulus beta source power (fig. 6A & B; c' path). We used linear mixed-effects models to estimate the “a path”, which represents the direct effect of either stimulus probability or previous choice on pre-stimulus power. The “b path” is represented via the effect of pre-stimulus beta power on the detection response. Pre-stimulus beta power in probability discriminative areas partially mediated the effect of stimulus probability on detection with a less pronounced effect in the stable environment (stable 0.6 % vs. 3 %, fig. 6Ai & Bi). The proportion mediated for previous choice via beta power was similar in both environments (stable env. 1.3 % vs. volatile env. 1.4 %, fig. 6Aii & Bii, model summaries in suppl. table 7 & 8). In summary, the mediation analysis supports the role of pre-stimulus beta power in implementing both explicit and implicit biases in distinct cortical areas.



**Fig. 6: Distinct pre-stimulus beta power sources mediate the effect of stimulus probability and previous choice on the detection response. A:** Partial mediation of probability (i) and previous response (ii) by distinct beta power sources on detection in the stable environment. **B:** Partial mediation of probability (i) and previous response (ii) by distinct beta power sources on detection in the volatile environment. **Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ .

## Discussion

Here, we investigated the neural mechanisms underlying biases in somatosensory perception in a stable and volatile stimulus probability environment. We manipulated the expectation of stimulus occurrence via visual cues either in blocks or on a single trial level in two separate studies. Participants adjusted both their perceptual decision criterion as well as their confidence ratings based on the cued stimulus probability. Next to the explicit biases, participants also exhibited strong previous choice biases. In EEG recordings we identified pre-stimulus beta power in distinct brain areas as neural correlates of explicit and implicit biases: Pre-stimulus beta power in the postcentral

gyrus predicted single subject criterion changes and partially mediated the effect of stimulus probability on the detection response. Pre-stimulus beta power also reflected a key feature of the stable environment: its interaction with the previous choice. In the volatile environment, the previous choice bias was reflected in pre-stimulus beta power in the posterior parietal areas, whereas in the stable environment, it was reflected in the secondary somatosensory cortex. Both mediated the effect of the previous response on the current response. Beta power changes also mimicked the impact of the explicit bias on confidence ratings in both environments. In summary, we suggest that pre-stimulus beta power in distinct cortical areas implements both explicit and implicit biases.

### **Implicit and explicit priors**

In the first experiment, participants were informed about stimulus probability in a block-wise manner, which arguably is a more ecologically valid design. However, since the probability cue was valid, the probability blocks contained an unequal amount of signal and noise trials and thus the response distributions (and hence previous choice frequencies) between the low and high probability conditions were unbalanced; for this reason, in the second experiment, the probability cue was provided on a trial-by-trial basis resulting in a balanced response (and previous choice) distribution. In both environments, the probability cues altered the criterion successfully as previously shown for the visual domain<sup>4,24,25</sup>. Also in both studies, the previous response significantly predicted the detection response on the current trial, in line with previous findings on the effects of response history<sup>35,36</sup>. Furthermore, in both environments, participants gave higher confidence ratings in trials where their expectation matched their response as shown in previous studies in the visual domain<sup>4,37,38</sup>. A difference between the two study designs is that in the stable environment, the last trial is more informative for the current subjective belief about stimulus probability within the same block (see S2.1). This difference was also reflected in our model-based analysis of the participants' behaviour: The best model for the stable environment included an interaction term between the previous response and stimulus probability, while the interaction term did not improve the model for the volatile environment. In summary, behavioural modelling confirmed

that both explicitly induced biases and implicit previous response biases determined somatosensory near-threshold detection in the two paradigms and that they interact in stable but not volatile probability environments.

### **Somatosensory pre-stimulus beta oscillations as a neural correlate of explicit biases**

After having confirmed the behavioural relevance of stimulus probability on somatosensory detection and confidence in both environments, we examined how this effect was implemented on a neural level before stimulation onset. Time-frequency representations for the contrast of high minus low stimulus probability in the pre-stimulus window showed a significant negative cluster, with a most profound effect in the beta band for the volatile environment. While there was no significant cluster in the stable environment, the t-values were also highest in the beta band. We speculate that the lack of statistical significance in the stable environment may be partly explained by the fact that the probability cue was presented only at the beginning of each block, which may have led to less pronounced pre-stimulus modulations compared to the probability cues before each stimulus in the volatile environment. Conversely, in the volatile environment, the probability cue before each trial appears to “dominate” the prestimulus characteristics over the effect of the previous trial. Nevertheless, and importantly, in both paradigms, the localised sources of the strongest beta power modulation for the probability manipulation were in similar locations within the postcentral gyrus.

Our finding of beta modulation reflecting explicit probability bias is consistent with the assumed role of beta for top-down modulation of perceptual decisions<sup>39</sup> and more generally as a neural correlate of top-down expectations<sup>40,41</sup>: For the somatosensory domain, the study by van Ede et al. (2010) suggested pre-stimulus beta power as a potential neural correlate of tactile expectations<sup>42</sup> with lower power before an expected somatosensory stimulus. Ede et al. regressed the impact of the trial history and were able to confirm the role of pre-stimulus beta power in implementing top-down expectations. This finding is consistent with the results from a study by Nickel et al.<sup>43</sup>

who showed a decrease in alpha and beta power in the pre-stimulus time window in trials with a high expectation for a painful stimulus in somatosensory channels. In the visual domain, a similar finding was recently obtained by Ruuskanen et al<sup>44</sup> (2024, preprint) showing a mediating effect of pre-stimulus beta power on participants' decision criterion. Weisz et al.<sup>45</sup> identified a pre-stimulus alpha/beta modulation in the contralateral secondary somatosensory cortex during a near-threshold somatosensory detection task. They interpreted these modulations as suggesting a change in the starting point for perceptual decisions, which is in line with our interpretation of a lower perceptual threshold in trials with low beta power.

Overall, our results show that beta power in the primary somatosensory cortex plays a key role in the implementation of explicit biases; this leaves open how the implicit (previous choice) bias, which we also clearly find in our behavioural analysis, is implemented, which we analysed next.

### **Posterior parietal pre-stimulus and SII beta oscillations as a neural correlate of implicit biases**

Time-frequency representations for the previous response contrast revealed a significant cluster in the beta band for the stable environment with lower power after previous yes responses. Source reconstruction of pre-stimulus beta power for the previous response contrast highlighted the posterior parietal cortex as the source of the strongest difference between previous responses in the volatile environment. Neural correlates of previous choice biases in non-human primates have been located in frontal and posterior parietal cortex (PPC)<sup>46,47</sup> and a recent study in humans suggested pre-stimulus gamma power in the parietal cortex as a neural marker of previous choice biases<sup>36</sup>. Consistently, also our findings emphasise the role of posterior parietal brain areas in addition to a mediating effect of beta oscillations.

Interestingly, in the stable environment, source localization for the previous response contrast highlighted another area, i.e., the secondary somatosensory cortex (SII). As outlined above, in the stable environment, the subjective relevance of the previous

response and thus the “cognitive process” underlying the previous choice bias must be different as there is an interaction with the expected probability which we also demonstrated computationally in our model. A study by Romo et al.<sup>48</sup> in non-human primates revealed that neurons in SII encoded both past and present sensory information during a frequency discrimination task. This aligns with findings from a rodent tactile working memory task<sup>49</sup>, which demonstrated that SII enables task information to persist across different behavioural states. Given the evidence from previous studies on the roles of both the PPC and SII, we tentatively conclude that both areas are involved in previous choice bias, with each region's role being more strongly emphasised in the corresponding paradigm. We suggest systematically disentangling their possible contributions in future studies.

### **Pre-stimulus beta power predicts explicit and implicit biases, mimics the congruency effect on confidence and mediates both stimulus probability and previous response bias in distinct brain areas**

To investigate the relationship between pre-stimulus power and behavioural outcomes, we added pre-stimulus source power averaged over the most discriminative voxel for either probability or previous responses in our perceptual models. The results confirm the role of prestimulus beta power in predicting responses both for signal and for noise trials in both experiments; pre-stimulus beta power also mimicked the interaction of the previous response with the stimulus probability in the stable environment, further confirming its role in implementing both biases. Finally, in a mediation analysis (fig. 6) we show that beta power (again on the source level) partially mediated the effect of stimulus probability and the previous response on the detection response in both environments, albeit to a lesser degree in the stable environment.

Taken together, our results from a total of 83 participants strongly confirm prior findings that link beta power to perceptual detection rates in both signal and noise trials<sup>22–24</sup>. A recent review indicates that beta oscillations, particularly beta bursts, occur across various cortical regions<sup>28</sup>. The authors suggest that beta oscillations act as spatiotemporal filters, thereby controlling information flow throughout the brain via brief

periods of functional inhibition. While we did not characterise beta bursting, our results are in line with this idea, as we show distinct beta sources for implicit and explicit biases in the pre-stimulus window that shape somatosensory perception.

The observed effect of higher confidence in response-congruent trials could be replicated by a model that included pre-stimulus beta power as a neural correlate of stimulus probability. Those results illustrate the intricate interplay between pre-stimulus power and confidence, as it is not the absolute level of beta power that determines confidence. Both high and low beta power before a stimulus can lead to a high confidence perceptual decision – it depends on the response and whether it matches the expected stimulus. Earlier studies have emphasised a negative association between pre-stimulus alpha power and confidence<sup>50,51</sup>. Extending this perspective, Baumgarten et al.<sup>15</sup> demonstrated in a somatosensory discrimination task that the correlation between pre-stimulus alpha power and confidence varies depending on accuracy. The results of our study suggest that the relationship between pre-stimulus beta power and confidence depends on the congruency between the response and the expectation, further supporting the idea that beta oscillations are crucial for implementing top-down biases.

### **Limitations and perspectives**

We conducted two separate studies with two different samples of participants, which allowed us to confirm the behavioural and neural results in an independent sample. A follow-up study with a longitudinal study design could examine the temporal stability of both externally induced biases and implicit previous-choice biases and their interaction in different probability environments. This would address the interesting question of how much of the results reported here are related to bias *traits*<sup>52</sup> or *states*. In addition, the computational models used are based on the assumption of a linear relationship between pre-stimulus power and the detection response<sup>33,53,54</sup>. Consequently, non-linear effects between power and behavioural outcomes might have been missed. Finally, the electrical stimulation used in our study – although widely used in research - is not a



naturalistic stimulus and therefore future studies could use more ecologically relevant tactile stimuli.

In summary, our results suggest that explicit and implicit perceptual biases are reflected in pre-stimulus beta power in distinct cortical areas.

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## **Author contributions**

C.F. and A.V. conceived the study. C.F., A.V., E.A. and M.G. designed the first study. C.F., A.V., T.S., E.P. and V.N designed the second study. C.F., M.G. and E.P. prepared the experimental setup. C.F. analysed behavioural and neural data for both studies with help from T.S. and V.N. C.F. wrote the first draft of the manuscript with input from A.V., S.H. and E.P. reviewed the analysis code. All authors reviewed, edited and approved the final manuscript.

## **Declaration of interests**

The authors declare no competing interests.

## Methods

### Participants

Forty-three healthy, young volunteers (22 females, age:  $26.7 \pm 4.4$  years, [mean  $\pm$  SD], range: 21 to 35 years) were recruited for the first study and forty for the second study (23 females, age:  $25.7 \pm 3.9$  years, range: 19 to 35 years) from the database of the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany. All participants reported to be right-handed. The study was approved by the Ethics Committee of the University of Leipzig's Medical Faculty (462/15-ek). All participants provided written informed consent and were reimbursed 9.00 Euro per hour for their participation in the first study and – due to a change of regulations – 12.00 Euro per hour in the second study.

### Experimental setup

This study aimed to investigate how stimulus probability influences tactile perception and confidence in humans. All data were acquired at the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig. Electrical finger nerve stimulation was performed with a constant-current stimulator (DS5 Isolated Bipolar Current Stimulator (RRID:SCR\_018001)) using single square-wave pulses with a duration of 200  $\mu$ s. A waveform generator NI USB-6343 (National Instruments) and custom MATLAB scripts using the Data Acquisition Toolbox (MATLAB (RRID:SCR\_001622)) were used to control the stimulation device. Steel wire ring electrodes were placed on the middle (anode) and the proximal (cathode) phalanx of the index finger on the left hand. The experimental procedure was controlled by custom MATLAB scripts using the Psychophysics Toolbox (RRID:SCR\_002881).

### Experimental paradigm

At the beginning of the experimental session, we recorded five minutes of resting state EEG with eyes open while participants were seated in a comfortable chair in the EEG cabin and fixated on a grey cross on the screen. Next, participants were familiarised

with the electrical finger nerve stimulation. An automatic threshold assessment was performed to determine the stimulus intensity corresponding to the somatosensory detection threshold. The threshold assessment entailed an up-and-down procedure (40 trials in the first run and 25 trials in subsequent runs) which served as a prior for the following Bayesian approach (psi method; 45 trials in the first run and 25 trials in subsequent runs) from the Palamedes Toolbox<sup>55</sup> (RRID:SCR\_006521) and finished with a test block (5 trials without stimulation and 10 trials with stimulation intensity at the threshold estimate by psi method). Based on the test block results for the psi method threshold estimate and weighting in the results of the up-and-down procedure, the experimenter selected a near-threshold intensity, approximately at a 60 % detection rate.

### **Stable environment**

In each trial, participants were instructed to indicate whether they perceived a weak somatosensory stimulus (Yes/No) and then to state their retrospective confidence in this decision using a binary rating (Confident/Unconfident). Participants were informed that they would receive cues about the probability of a stimulus on a given trial throughout the experiment. In study 1, a cue appeared at the beginning of each condition block for three seconds and was valid until the next probability cue appeared (12 trials, the number of trials in a block was not explicitly mentioned). The high stimulus probability condition (75 %) instructed participants that there was a 75 % chance of a stimulus on a given trial, whereas the low probability condition (25 %) informed participants that there was a 25 % chance of a stimulus on a given trial. Crucially, those cues were always valid, and participants were explicitly told about those contingencies. To ensure motivation throughout the experiment, we provided participants with feedback (percentage correct displayed for 2.5 seconds) at the end of each probability block. Each of the five blocks contained 144 trials with six repetitions for each probability condition. Thus, half of the trials included a near-threshold electrical pulse (mean intensity = 1.9 mA, range: 0.9 - 3.7 mA). The stimulus intensity was adjusted after each experimental block if the detection rate was no longer near-threshold. The other half of

the trials did not contain a stimulus (noise trials). The order of signal and catch trials and probability condition miniblocks were pseudo-randomized for each experimental block and participant using the Shuffle<sup>56</sup> function in Matlab. Participants responded with the right index finger on a two-button box. Before starting the main experiment, participants completed a training block of 48 trials.

### **Volatile environment**

In the second study, participants were instructed to indicate whether they perceived a weak somatosensory stimulus (Yes/No) and then to state their retrospective confidence in this decision using a binary rating (Confident/Unconfident) in each trial. Participants were informed that they would receive cues about the probability of a stimulus before each trial throughout the experiment. In the second study, either an orange or blue circle appeared at the beginning of each trial for one second and indicated either high or low stimulus probability (the colour assignment was randomised across participants). The high stimulus probability condition (75 %) instructed participants that there was a 75 % chance of a stimulus on a given trial, whereas the low probability condition (25 %) informed participants that there was a 25 % chance of a stimulus on a given trial. Crucially, these cues were valid, and participants were explicitly told about these contingencies. To motivate participants throughout the experiment, we provided participants with feedback (percentage correct displayed for 2.5 seconds) after 30 trials. Each of the five blocks contained 120 trials with an equal amount of high and low stimulus probability trials overall. Thus, half of the trials contained a near-threshold electrical pulse (mean intensity = 2.1 mA, range: 1.1 - 3.6 mA). The other half of the trials did not contain a stimulus (catch trials). The order of high and low probability trials and stimulus and noise trials was pseudo-randomized within blocks using the Shuffle<sup>56</sup> function in Matlab. Participants responded with the right index finger on a two-button box. Before starting the main experiment, participants completed a training block of 40 trials. Additionally, we asked participants about the colour-probability mapping after each experimental block to ensure the probability cues were correctly remembered.

## **Behavioural data preprocessing**

### **Stable environment (study 1)**

Across all participants, we collected 30.816 trials from 43 participants. 35 trials were rejected due to missing EEG triggers (EEG recording started too late). Next, we removed 39 no-response trials (no button pressed within 2.5 s) and 45 trials with a detection response time of less than 100ms. We excluded eleven blocks that had a hit rate greater than 90 % or less than 20 % and resulted from suboptimal threshold estimation. These criteria were determined based on values that deviated more than three times the standard deviation from the mean hit rate calculated across all blocks and participants (mean hit rate: 58 %, standard deviation: 10 %). Additionally, for one participant, one block was excluded based on a false alarm rate of more than 40 %. After behavioural preprocessing, 28.977 trials remained.

### **Volatile environment (study 2)**

We collected 24.000 trials from 40 participants. Data from one participant was rejected due to technical issues with the somatosensory stimulation device. From the remaining 39 participants, 12 trials were rejected due to missing EEG triggers (the battery died, EEG recording started too late). Next, we removed 133 no-response trials (no button pressed within 2.5 s) and 102 trials with a detection response time of less than 100 ms. We excluded ten blocks that had a hit rate greater than 90 % or less than 20 %. Additionally, two blocks were excluded based on a false alarm rate of more than 40 %. One block was excluded because the false alarm rate was higher than the hit rate. We used the same exclusion criteria as in the first study (mean hit rate: 53 %, standard deviation: 12 %). After behavioural data cleaning, 21.593 trials from 39 participants remained.

## **Signal Detection Theory Analysis**

We employed Signal Detection Theory (SDT)<sup>57</sup> to examine the sensitivity (Dprime) and response bias (criterion c) in this study. SDT allows us to distinguish between the ability to detect a signal (e.g., the presence of a stimulus) from a general tendency to report either stimulus presence or absence.

Sensitivity (Dprime):

Sensitivity, also known as Dprime, quantifies the ability to discriminate between signal and noise. It is calculated using the following formula:

$$d' = z(\text{hit rate}) - z(\text{false alarm rate})$$

where  $z(\text{hit rate})$  represents the z-score of the hit rate (proportion of correct responses when the signal is present), and  $z(\text{false alarm rate})$  represents the z-score of the false alarm rate (proportion of incorrect responses when the signal is absent).

Response Bias (criterion c)

Response bias, represented by criterion c, assesses the individual's tendency to respond "yes" or "no" irrespective of the presence (or absence) of the stimulus. It is calculated using the formula:

$$c = -0.5 * [z(\text{hit rate}) + z(\text{false alarm rate})]$$

In our analysis, we computed  $d'$  and  $c$  for each participant to examine their sensitivity to the stimuli and response bias. Higher values of  $d'$  indicate better sensitivity, while a positive value of  $c$  reflects a bias towards responding "no" (conservative criterion). The Hautus log-linear correction method<sup>58</sup> was employed to address zero false alarm rates.

### **Statistical Analysis: Behaviour**

Non-parametric Wilcoxon signed-rank tests were applied to compare the paired samples in this study. The Wilcoxon signed rank test is robust to deviations from

normality and assesses whether the median difference between paired observations is significantly different from zero.

## Estimation of Signal Detection Theory Parameters using Generalized Linear Mixed Effects Models

To investigate the influence of single trial variables on Signal Detection Theory (SDT) parameters<sup>59</sup>, we employed generalized linear mixed effects models (GLMMs) using the lme4 package<sup>60</sup> in R (version 4.2.2). We specified a GLMM with a Binomial distribution and probit link function to account for the binary nature of the outcome variable (signal present or absent response, high or low confidence). In the simplest model, the intercept represents the overall criterion ( $c$ ), and the regressor that codes whether the trial contained a stimulus corresponds to  $D'$ <sup>61</sup>. Random intercepts were included in all models, random slopes for the main effects and interaction effects only if the models did not show warnings about singularity<sup>62</sup>. To assess collinearity among the predictor variables in our analysis, we utilised the 'check\_collinearity' function from the 'performance' package and to ensure convergence of the models the check\_converge function<sup>63</sup> in R. Variance inflation factor (VIF) values were computed for all models and parameters, demonstrating low values ( $VIF < 3$ ) and indicating the absence of substantial multicollinearity for all SDT GLMMs. We used the emmeans (Estimated Marginal Means) R package<sup>64</sup> for FDR-corrected post-hoc tests on our fitted GLMMs. Model summaries were saved as tables in a html file with the sjPlot package<sup>65</sup>.

## EEG Recordings

EEG was recorded from 62 scalp positions distributed over both hemispheres according to the international 10–10 system, using a commercial EEG acquisition system (Standard 64ch actiCap Snap, BrainAmp; Brain Products, Brain Products (RRID:SCR\_009443)). The mid-frontal electrode (FCz) was used as the reference and a mid-frontal electrode was placed on the middle part of the forehead (between FP1 and FP2) as ground. One additional electrode was used to measure electroocular activity (placed below the right eye) and ECG activity (placed below the left clavicle),

respectively. Electrode impedance was kept at  $\leq 10$  k $\Omega$  for all channels. EEG was recorded with an online bandpass filter from 0.015 Hz to 1 kHz and digitised with a sampling rate of 2.5 kHz for study 1 (stable environment) and 1 kHz for study 2 (volatile environment).

## **EEG - preprocessing**

We used custom Python scripts and the MNE python package (MNE software (RRID:SCR\_005972)<sup>66</sup> to analyse the EEG data of both datasets. We applied a bandpass filter between 0.1 and 40 Hz to the raw EEG data with the following IIR filter parameters: Butterworth zero-phase (two-pass forward and reverse) non-causal filter, filter order 16 (effective, after forward-backwards, cutoffs at 0.10, 40.00 Hz: -6.02, -6.02 dB). Next, we linearly detrended and epoched the data between -1 second before stimulation onset and 1 second after stimulation onset. After downsampling the data to 250 Hz, we used the RANSAC package<sup>67</sup> to detect bad channels (channels interpolated study 1: mean = 1.0, max. = 4, study 2: mean = 0.7, max. = 5). Next, we ran ICA on the 1Hz high-pass filtered, epoched data using the extended infomax algorithm<sup>68</sup>. We correlated ICA components with EOG and ECG activity and rejected components that correlated strongly with eye movements and cardiac artefacts from the 0.1Hz filtered data (components rejected study 1: mean = 3.5, max. = 7, study 2: mean = 3.5, max. = 6). Finally, we re-referenced the data to the common average of all EEG channels.

## **Evoked potentials**

Electrode CP4 was selected as the channel of interest (COI) based on the post-stimulus contrast between signal and noise trials. To compare the experimental conditions, we initially averaged the epochs of the defined condition for each participant and ensured that the epoch counts were equalised across all conditions. Subsequently, we calculated the average evoked data across all participants. We used a baseline window of 100 ms before stimulation onset and subtracted the averaged activity from the post-stimulus activity for each epoch. To determine the channel of interest, we compared signal and noise trials in the post-stimulus window and focused on the



earliest somatosensory evoked potential, which was in our paradigm and with our data preprocessing a positive evoked potential around 50ms post-stimulation (which we refer to as P50 component in the following).

### **Time-frequency representation in the pre-stimulus window**

We used the multitaper method<sup>69</sup> to compute the time-frequency representation in the frequency range of 3 to 34 Hz with a resolution of 1 Hz and a time-bandwidth of 4 Hz. The number of cycles for each frequency was defined as a frequency divided by 4 cycles. The number of epochs was matched between conditions using the minimum time difference method implemented in MNE Python. For the contrast between high and low stimulus probability in the stable environment, we calculated averaged time-frequency representations separately for previous hits (previous yes response in previous signal trial), misses (previous no response in previous signal trial) and correct rejections (previous no response in previous noise trial) for the high and low stimulus probability conditions. Next, we subtracted the respective contrasts, e.g. high previous hits vs. low previous hits etc. Finally, we averaged the time-frequency representations of high vs. low stimulus probability corrected for previous trial history. The design in the volatile environment allowed us to average over high and low probability trials without controlling for previous trial characteristics, as the previous trial history was randomised (see suppl. fig. 2.3 Biii). To specifically examine the influence of past choices on power modulations, we restricted our analysis to trials occurring under high probability conditions and those following a signal in the stable environment. In the volatile environment, our analysis targeted trials with identical probability cues in both the preceding and current trial in the high probability condition.

### **Cluster-based permutation tests**

For statistical comparisons of the time and frequency domain, we used threshold-free cluster-based permutation testing implemented in MNE with a cluster and statistical threshold of  $p = 0.05$  and 10.000 permutations. The test statistic was a two-tailed one-sample t-test, as we tested whether the difference between conditions was

significantly different from zero. Adjacency was defined over time (neighbouring time points are considered as adjacent) and frequency (neighbouring frequencies are considered as adjacent). All conditions were compared using paired two-sided t-tests. We used a step size of 0.1 and an initial t-threshold of 0 for threshold-free cluster enhancement<sup>70</sup>. The MNE defaults for the cluster height (2) and cluster extent (0.5) were used.

### **Source localization of pre-stimulus beta band power contrast**

Source localization was performed using Dynamic Imaging of Coherent Sources (DICS)<sup>71</sup> beamforming implemented in MNE. The source space encompassed a total of 8196 individual sources (5mm spacing between sources). We used the MNE standard BEM (5120-5120-5120) model based on the freesurfer average brain and standard electrode positions. For each participant, source localization was computed for the beta band frequency range where we observed the strongest modulations in sensor space (15 - 25 Hz) in the pre-stimulus window, averaged over 600ms before stimulation onset (700ms to 100ms before stimulation onset). Cross-spectral density was computed for all epochs and separately for the high probability and low probability epochs and the previous yes and no previous no responses. To compute source power in the beta band, we estimated cross-spectral density for each epoch using Morlet wavelets with 4 cycles per frequency. Next, we averaged over all frequencies and computed a common spatial filter, before we applied the filter to the data of each condition. The filter was computed for the orientation that maximised power. Finally, we subtracted beta source power of low probability trials from beta source power of high probability trials before we averaged the contrast over participants. To visualise the contrast, we ran a permutation t-test (10 000 permutations) for all sources, and we highlight the source with the highest t-values on the fsaverage template brain. To make sure our beamformer source localization approach is valid, we located the beta power desynchronization for the post-stimulus contrast between signal and noise trials, which verified a source in postcentral gyrus (suppl. fig. 4.3).

Pre-stimulus beta source power per trial

To extract pre-stimulus beta power in source space, we created a mask based on the contrast for stimulus probability or previous response. We selected voxels based on the highest t-values for each contrast and extracted power for each trial averaged over those vertices. For the brain behaviour modelling, the source power was log-transformed, z-scored and detrended over all trials and for each experimental block. Trials with z-scored source power  $> 3$  were excluded from the analysis. Pre-stimulus beta power was entered as a continuous regressor in our models and only binned for visualisation purposes.

### **Moderated mediation analysis**

We conducted mediation analysis using the 'mediation' package<sup>72</sup> in R. The package provides a comprehensive set of functions for estimating and testing mediation effects in both simple and complex models. The mediation analysis focused on examining the mediating role of pre-stimulus power on the relationship between stimulus probability (independent variable) and the detection response (dependent variable). To conduct the mediation analysis, we set up a linear mixed effects model with the mediator as the dependent variable (pre-stimulus power) and the independent variable as the predictor (stimulus probability). Next, we fitted a GLMM with the detection response as the outcome variable (dependent variable) and both the mediator (beta power) and the independent variables as predictors. We included the stimulus on each trial, the previous response as well as the interaction between stimulus probability and the stimulus as additional predictor variables. Finally, we computed the indirect effect, the total effect and the direct effect. The 95 % confidence intervals of the regression weights were estimated using quasi-Bayesian approximation with 1000 Monte-Carlo draws.

### **Data and code availability**

The experimental and analysis code is publicly available on [Github](#). The raw behavioural and electrophysiological data will be shared on [EDMOND](#) after publication.

## Supplemental information legends

**Fig. S1: Figure 1 after excluding participants with a false alarm rate > 40 % (n=3) in the high expectation condition.** All statistical results remain after the exclusion. **Significance levels:** \*\*\*  $p < .001$ , \*\* $p < .01$ , \* $p < .05$ . **Abbreviations:** ns = not significant.

**Fig. S2.1: The previous choice has a greater influence on the subjective stimulus probability in the stable compared to the volatile environment.** The block design creates small environments of a stable stimulus probability. In the example (left box) the stimulus probability is high (0.75 % of all trials contain a stimulus in the block). An ideal human observer tries to track the previous choices and updates the current (subjective) stimulus probability accordingly. The previous choice has a lesser influence on the subjective stimulus probability in the trial-by-trial design (right box) as the participant must track the previous choices over the whole experimental block of 120 trials.

**Fig. S2.2: Model-free analysis of the interaction between criterion and previous response:** The criterion is always significantly higher (more conservative) in the low probability condition in both environments. The criterion is also always more conservative after previous no responses in both environments, except for the low probability condition in the stable environment. This is in line with the model-based results. **Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ . ns = not significant.

**Fig. S2.3: Response and confidence distributions differ significantly between stimulus probability conditions in both environments. Previous response distributions differ significantly in the stable but not in the volatile environment.** **Ai & Bi:** Participants respond more often that they detected a stimulus in the high probability condition in the stable environment and the volatile environment. **Aii & Bii:** confidence ratings are significantly higher for no responses in both environments. **Aiii & Biii:** there are significantly fewer previous yes responses in the low probability condition but there is no significant difference in the distribution of previous responses for the

volatile environment due to the randomization of probability cues in the second study.

**Significance levels:** \*\*\*  $p < .001$ , \*\*  $p < .01$ , \*  $p < .05$ . ns = not significant.

**Fig. S3: Somatosensory region of interest definition based on the contrast between signal and noise trials.** **A:** Topography for the contrast signal - noise around the earliest somatosensory evoked potential (P50), averaged between 40 and 56 ms in the stable environment. **B:** Somatosensory evoked potential averaged over participants for the contrast signal-noise trials in electrode CP4 in the volatile environment. **C:** Topography for the contrast signal - noise around the earliest somatosensory evoked potential (P50), averaged between 40 and 56 ms in the stable environment. **D:** Somatosensory evoked potential averaged over participants for the contrast signal-noise trials in electrode CP4 in the volatile environment. The signal was baseline corrected with a mean from -100ms to stimulus onset.

**Fig. S3.2: Cluster-based permutation test for a shorter pre-stimulus window.** Time-frequency contrasts for high – low stimulus probability (first row) and previous yes – no response (second row). The time window was restricted to 400ms.

**Fig. S.3.3: Control analysis for source reconstruction using DICS beamforming:** Beta power source reconstruction for signal–noise contrast in the post-stimulus window. Lighter blue values indicate more negative t-values. The area highlighted in red marks the postcentral gyrus.

**Table 1:** Generalized linear mixed effects model predicting the detection response on each trial in the stable environment.

**Table 2:** Generalized linear mixed effects model predicting the detection response on each trial in the volatile environment.

**Table 3:** Generalized linear mixed effects model predicting the detection response in each trial including beta power in the stable environment.

**Table 4:** Generalized linear mixed effects model predicting the detection response in each trial including beta power in the volatile environment.

**Table 5:** Generalized linear mixed effects model predicting the confidence response in each trial including either the probability cue or pre-stimulus beta power in the stable environment.

**Table 6:** Generalized linear mixed effects model predicting the confidence response in each trial including either the probability cue or pre-stimulus beta power in the volatile environment.

**Table 7:** Generalized linear mixed effects models for mediation analysis predicting the detection response by including pre-stimulus beta power for the probability contrast or pre-stimulus beta power for the previous response contrast in the volatile environment.

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