

Competitive Frontoparietal Interactions Mediate Implicit Inferences

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Frequent experience with regularities in our environment allows us to use predictive information to guide our decision process. However, contingencies in our environment are not always explicitly present and sometimes need to be inferred. Heretofore, it remained unknown how predictive information guides decision-making when explicit knowledge is absent and how the brain shapes such implicit inferences. In the present experiment, 17 human participants (9 females) performed a discrimination task in which a target stimulus was preceded by a predictive cue. Critically, participants had no explicit knowledge that some of the cues signaled an upcoming target, allowing us to investigate how implicit inferences emerge and guide decision-making. Despite unawareness of the cue–target contingencies, participants were able to use implicit information to improve performance. Concurrent EEG recordings demonstrate that implicit inferences rely upon interactions between internally and externally oriented networks, whereby prefrontal regions inhibit parietal cortex under internal implicit control.

Key words: consciousness; decision-making; EEG; inferences; neural networks dynamics; prefrontal cortex

Significance Statement

Regularities in our environment can guide our behavior providing information about upcoming events. Interestingly, such predictive information does not need to be explicitly represented to effectively guide our decision process. Here, we show how the brain engages in such real-world “data mining” and how implicit inferences emerge. We used a contingency cueing task and demonstrated that implicit inferences influenced responses to subsequent targets despite a lack of awareness of cue–target contingencies. Further, we show that these implicit inferences emerge through interactions between internally and externally oriented neural networks. The current results highlight the importance of prefrontal processes in transforming external events into predictive internalized models of the world.

Introduction

Frequent exposure to regularities in our environment allows us to exploit consistencies to anticipate upcoming events. For instance, when strolling in an unfamiliar supermarket in search of a favorite chocolate bar, one typically does not pay much attention when passing by the detergents, but when the cookies come in sight, attention starts to focus. Without being explicitly told where to look for the product, the attentional system is able to use prior information (i.e., experience with supermarket layouts) and cur-

rent sensory input to aid in the quest for chocolate. This example demonstrates that, in addition to externally observable information, internally oriented processes (e.g., memory, prospection) play a crucial role in efficiently guiding our behavior in everyday settings.

To understand decision-making in terms of network dynamics, it is essential to understand the mechanisms by which information is routed between brain regions. It has been proposed that alpha activity serves as a mechanism that gates the flow of information to relevant brain regions through inhibition (Fu et al., 2001; Klimesch et al., 2007; Mathewson et al., 2009, 2011; Jensen and Mazaheri, 2010; van Diepen et al., 2015; Vissers, 2018). Alpha effects are typically measured after explicitly instructing participants about cues predicting a subsequent stimulus or indicating the location of an upcoming target (Worden et al., 2000; Foxe and Snyder, 2011), thereby mainly probing networks associated with external information processing (i.e., the dorsal attention network). In many cases, however, we learn to use predictive information in our environment in an implicit manner (Chun, 2000;

Received Oct. 3, 2018; revised April 16, 2019; accepted April 18, 2019.

Author contributions: M.E.W. and T.R. designed research; M.E.W. performed research; M.E.W. and T.R. analyzed data; M.E.W. wrote the paper.

This work was supported by the National Science Foundation (Grant 1561518 to T.R.) and the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement (Meta_Mind-DLV-704361 to M.E.W.).

The authors declare no competing financial interests.

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<https://doi.org/10.1523/JNEUROSCI.2551-18.2019>

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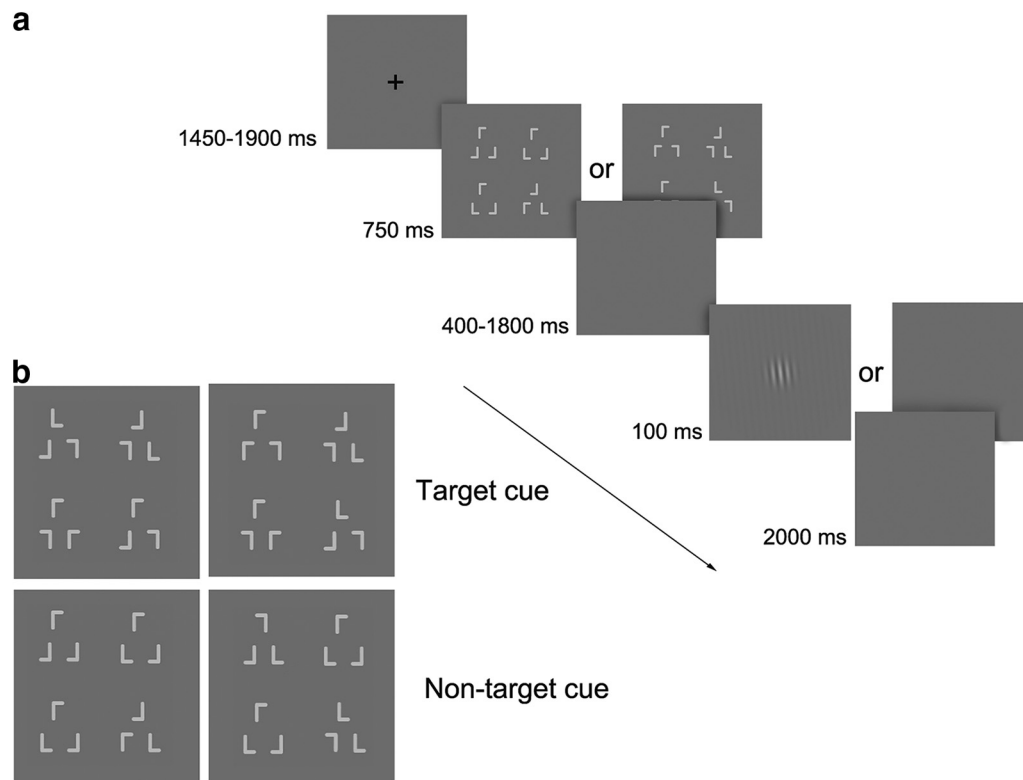


Figure 1. *a*, Participants had to respond as quickly as possible to a slightly right- or left-tilted vertical Gabor stimulus. Before target presentation, a cue signaled either an upcoming target (100% validity) or a blank (66% validity). Participants were unaware of the relationship between the cue stimulus and target presentation during the experiment. *b*, Cues were made up of configurations of L-like shapes. The top left and bottom right configurations determined the identity of the cue (target or nontarget cue). For illustration, four of the eight cues are shown.

Goldfarb et al., 2016), without the need of explicit knowledge about existing stimulus associations (Cleeremans et al., 1998; Cleeremans and Jiménez, 2002; Frensch and Rüniger, 2003; Wokke et al., 2017). In such settings, internally oriented networks play an important role in the formulating and testing of internally generated hypotheses (Christoff and Gabrieli, 2000) and in comparing past and current sensory inputs (Wilson et al., 2014). To date, it remains unclear how predictive information from our environment guides decision-making when explicit instructions are absent. Further, it is unknown how internally and externally oriented networks contribute to implicit inferences.

In the present study, we investigated how implicit contingencies guide decision-making. Participants performed an orientation discrimination task in which a target stimulus was preceded by a predictive cue. Critically, participants were not instructed and had no explicit knowledge that some of the cues signaled an upcoming target. Therefore, the information content of the cues was not “directly observable” (Wilson et al., 2014; Schuck et al., 2016) and required information from previous trials (i.e., frequent exposure to cue–target pairings). During the task, we recorded electroencephalographic (EEG) signals, allowing us to measure whether implicit cues were able to influence behavioral responses, modulate alpha activity, and affect target processing, despite the fact that subjects were not explicitly aware of the meaning of the cues.

Materials and Methods

Participants. Seventeen participants (9 females; mean age = 25.4 years; SD = 6.3) took part in this study for financial compensations. All participants had normal or corrected-to-normal vision and were naive to the purpose of the experiment. All procedures complied with international and institutional guidelines and were approved by the Institutional Re-

view Board of The City University of New York. Before the experiment, participants were instructed on the task, after which all participants provided their written informed consent.

Experimental design and statistical analysis. Stimuli were presented full screen (1024 × 768 pixels) on a 17 inch CRT monitor (Trinitron Multi-scan 220GS, Sony) with a refresh rate set at 100 Hz. The monitor was placed at a distance of ~57 cm in front of each participant. Each trial started with a centrally presented fixation cross that was presented for 1455, 1685, or 1915 ms, after which the cue was presented for 750 ms. The cue consisted of four configurations of four L-shaped figures (Fig. 1*b*) presented in each quadrant of the screen. After presentation of the cue, a blank screen was presented for 400, 800, 1200, or 1600 ms, after which a target or another blank screen was presented for 100 ms. Participants were instructed to keep their eyes open and to minimize blinks from cue onset until they gave their response to the target or the end of the trial (Fig. 1*a*). A target stimulus consisted of a slightly left- or right-tilted vertical Gabor patch (Fig. 1). We tilted the Gabor between 1° and 3° to ensure that performance was kept below ceiling and above chance (~80% correct during practice trials; see below). After target presentation, participants had to indicate as quickly as possible the orientation of the Gabor (left or right) by pressing a corresponding left or right response button. Next, participants provided their confidence about their decision, on a scale ranging from 1 to 4 by pressing one of four buttons. Participants were instructed to assign a low value to a decision that was accompanied by low confidence in being correct and a high value when they were very confident about being correct. Participants were encouraged to make use of the whole scale. However, we did not present a confidence scale or an explicit question on the screen during the experiment due to time considerations. In this way, participants gave their metacognitive judgment during the blank that followed the target, immediately after the first-order task response. During our pilot studies ($n = 60$, spread over five different sessions), we arrived at the conclusion that we should not exceed ~2 h of experimentation, and therefore decided to use the current experimental design. On trials when no target

was presented, the participants were instructed not to respond and wait for the onset of the next trial (2 s). We customized two (computer) mice to create four response buttons that registered responses through a Teensy LC Board at microsecond temporal resolution.

A target cue (Fig. 1*b*) always predicted an upcoming target (100% valid), whereas a nontarget cue was followed by a target on one-third of the trials or no target on two-thirds of the trials). We used four different target cues and four different nontarget cues. The top right and bottom left configuration of the cues determined the cue type (i.e., the top right and bottom left configuration remained the same within the cue type; Fig. 1). Participants performed two separate sessions at least \sim 1 week apart. Crucially, in the first session participants were not instructed about the types of cues signaling target stimuli or about the general purpose of the cue stimuli in the experiment. The cue parameters were based on data from the pilot studies and were set such that participants were able to learn the contingencies between cue and target without gaining explicit knowledge about the meaning of the cue stimuli (i.e., explicitly recognize them as being cues). In the second session, we explicitly instructed participants about the identity of the cues, explaining to the participants that the top right and bottom left configuration of each cue was predictive of trial type and which cue was most likely to be followed by a blank.

In both sessions, participants started with 120 trials of practice to get accustomed to the task. At the end of the first session, we determined whether participants gained explicit knowledge about the nature of the cue stimuli. In four steps, we probed participants' knowledge about the cues. First, we asked participants whether they noticed anything about the stimuli appearing in the experiment. Second, we asked whether they noticed if the stimulus with the L-shaped figures had any purpose in the experiment. Next, we asked whether they noticed whether specific configurations of L shapes signaled an upcoming target or whether configurations of specific L shapes were more related to the appearance of a blank. Finally, we showed participants the cues and tested whether they could tell the difference between the cues and their relation to target presentation. Of all 17 participants, only 1 noticed a relationship between the cues and the appearance of a target stimulus. For the other 16 participants, there was no explicit knowledge of the presence of cues on any of the above-described questions (Chun and Jiang, 2003; Geyer et al., 2012; Goujon et al., 2014). All analyses were based on these 16 participants.

In each session, we presented 720 trials equally divided over six blocks. Within each block, 48 (validly) cued target trials, 24 (invalidly) noncued target trials, and 48 (validly) cued blank trials (i.e., nontarget cue trials without a target) were presented in pseudorandom order. Participants took a 10 min break after completing three blocks. Each session lasted \sim 2 h.

Behavioral analyses. To assess whether response times, target discrimination accuracy, and metacognitive judgments differed depending on implicit cue type, we calculated reaction times (RTs) and task performance (d' ; see Macmillan and Creelman, 2004) on first-order task responses and metacognitive sensitivity (meta- d') and metacognitive efficiency (meta- $d'-d'$; Maniscalco and Lau, 2012; Fleming and Lau, 2014) based on confidence judgments. First-order task sensitivity (d') and metacognitive sensitivity (meta- d') are bias-free measures of task performance (left from right target orientation in this case) and the ability to distinguish right from wrong decisions, respectively (both in units of first-order d'). By subtracting d' from meta- d' (metacognitive efficiency), we were able to measure metacognitive sensitivity relative to changing levels of first-order task performance (Fleming and Lau, 2014). Because first-order task performance is known to influence metacognitive sensitivity (Fleming and Lau, 2014), it is necessary to assess metacognitive sensitivity relative to different levels of first-order task performance. We performed three separate 2 (first and second half of the experiment) \times 2 (target and nontarget cue) repeated-measures ANOVAs on reaction times, performance (d'), and second-order task performance (meta- d'). Unfortunately, confidence judgments of two participants were not registered due to a technical error in the implicit condition, basing the second-order performance analyses on 14 participants. All behavioral analyses were performed using Matlab (Matlab 12.1, MathWorks), type 2 SDT (signal detection theory) scripts (Maniscalco and Lau, 2012), and JASP (version 0.8.6).

EEG measurements and analyses. EEG was recorded and sampled at 1000 Hz using a 32-channel EASYCAP system. Two additional electrodes were placed on the outer eye canthi to record eye blinks. Electrode impedance was kept to <20 k Ω . Off-line, the data was high-pass (0.5 Hz) and low-pass (40 Hz) filtered and then referenced to the left and right mastoid. The data were epoched at -0.7 to $+1.7$ s around cue onset. These time windows avoided edge artifacts resulting from time–frequency decomposition (see below). We removed trials containing irregularities due to eye blinks or other artifacts by visually inspecting all trials. To increase spatial specificity and to filter out deep sources, we converted the data to spline Laplacian signals (Perrin et al., 1989; Cohen, 2015).

As we expected to measure implicit contingency effects in the second half of the first session, the last 70 target cue with target and last 70 nontarget cue without target trials were selected after artifact rejection for all analyses (after artifact rejection, these 70 trials roughly corresponded to the data gathered in the second half of the session). We selected the nontarget cue trials without a target to make sure the trials in each condition were taken from the same phase of the experiment (i.e., target cues followed by a target and nontarget cues without a target were just as frequent in each block). We decomposed the cue-locked, epoched EEG time series for these trials into their time–frequency representations by convolving them with a set of Morlet wavelets (frequencies ranging from 1 to 30 Hz in 1 Hz steps). Complex wavelets were created by multiplying perfect sine waves with a Gaussian. The range of the width of the Gaussian was set between 4 and 10 in 40 logarithmically scaled steps, to have a good trade-off between temporal and frequency resolution for each frequency. We applied the fast Fourier transform to the EEG data and the Morlet wavelets, after which these were multiplied in the frequency domain. Next, the inverse FFT was applied, allowing us to define an estimate of frequency-specific power at each time point and an estimate of the frequency-specific phase at each time from the resulting complex signal (van Driel et al., 2015). We normalized the data (dB Power $tf = 10 \times \text{Log}_{10}[\text{Power } tf / \text{Baseline Power } f]$) using an interval of -300 to 0 ms relative to cue onset as baseline. For our hypothesis, we specifically focused on signals in the alpha frequency band between cue offset and earliest target onset (i.e., a time window of $0-400$ ms after cue offset).

To further examine the way information might be gated via alpha oscillatory mechanisms, we assessed measures of inter-regional functional connectivity in the alpha range. Consistencies of the difference of time–frequency phase values between two channels in the alpha band across trials were computed [intersite phase clustering (ISPC); Siegel et al., 2012; Cohen, 2014]. We chose P4 as our “seed” electrode based on previous studies demonstrating the involvement of right parietal cortex in attention and alpha oscillations (Bareham et al., 2018). We used the same preprocessing steps as described above for the time–frequency analyses and a baseline period of -300 to 0 ms before cue onset for both cue types.

We performed a 3 (channel location) \times 2 (target and nontarget cues) \times 2 (implicit/explicit condition) repeated-measures ANOVA on mean alpha power changes and a 2 (channel location) \times 2 (target and nontarget cue) \times 2 (implicit/explicit condition) repeated-measures ANOVA on mean ISPC changes.

Finally, we were interested whether implicit information influenced neural signals related to target processing. Therefore, we epoched the EEG data from -100 to 600 ms around target onset, using the same preprocessing steps as described above. Unfortunately, for two participants there were too many artifacts ($>50\%$ of trials) in the epoch after target presentation, likely because of the long interval between cue onset and response in which we instructed participants not to blink, resulting in 14 participants for our target ERP analyses. We focused on the P3a and P3b components, which have been shown to be highly associated with stimulus environment updating processes (i.e., comparing present and previous stimuli in working memory) and differences in levels of access consciousness, respectively (Donchin, 1981; Polich and Kok, 1995; Sergeant et al., 2005; Muller-Gass et al., 2007; Naccache et al., 2016; Wokke et al., 2016). In light of findings demonstrating that the P3b indexes different levels of access consciousness, we tested ERP differences in both the implicit as well as the explicit condition. For the P3a component, we selected mid central electrode Cz values between 250 and 400 ms, while

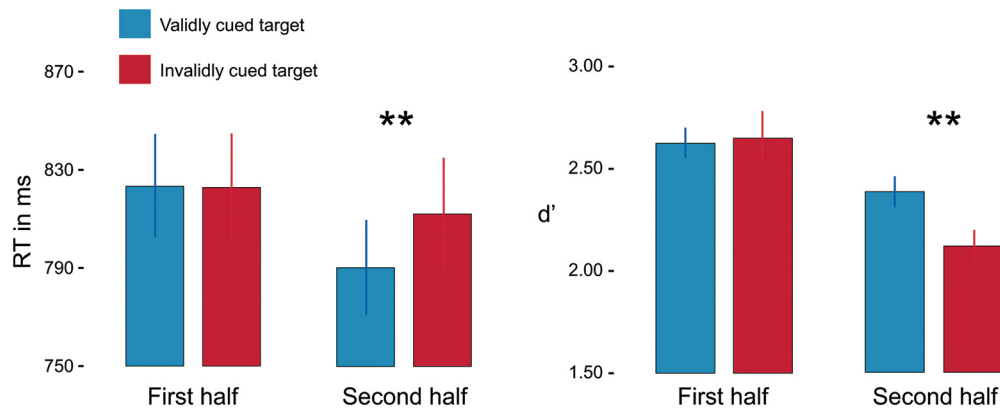


Figure 2. Participants responded faster (left) and performed better (right) when a target was preceded by a target cue than when preceded by a nontarget cue. Bars are the mean \pm within-subject SEM. * indicates a significant difference (see results).

we selected central parietal electrode Pz values between 350 and 500 ms after target onset for P3b comparison (Polich, 2007).

All signal-processing steps were completed using EEGlab (Delorme and Makeig, 2004) and X code (Cohen, 2014) in Matlab (Matlab 12.1, MathWorks), and statistical analyses were performed using Matlab (Matlab 12.1, MathWorks), JASP (version 0.8.6), and SPSS (version 20.0; IBM).

Results

Behavioral results

To determine whether participants were able to use implicit information to guide their behavior, we compared reaction time differences and differences in task performance (d') between implicitly (validly) cued and implicitly (invalidly) noncued targets (Fig. 1). We expected differences to occur specifically in the last half of the experiment when the cue–target context had been established (i.e., after extensive exposure to pairings of target cue with the presentation of a target stimulus). Therefore, we split the data into the first and second halves of the session (Fig. 2). Further, we assessed whether metacognitive performance (meta- d' and metacognitive efficiency) was affected by the implicit cues. For task performance there was a significant main effect of first/second half (block) of the experiment ($F_{(1,15)} = 8.75, p = 0.010$). For both RT and task performance, there was a significant interaction effect between block and cue type (RT: $F_{(1,15)} = 5.17, p = 0.038$; d' : $F_{(1,15)} = 14.43, p = 0.002$). These interactions reflect differences in RT and performance that change over the course of the experiment depending on the cue type that preceded a target. To investigate these interactions further, we compared cued targets versus noncued targets for each half of the experiment separately using paired t tests (two tailed). As expected, there were no differences in the first half of the experiment for both RT [$t_{(15)} = 0.058, p = 0.955, BF_{10}$ (Bayes factor for each model against the null model) = 0.256] and performance ($t_{(15)} = -0.23, p = 0.821, BF_{10} = 0.262$). In contrast, for the second half of the experiment, there were significant differences in RT and performance depending on cue type (RT: $t_{(15)} = -3.144, p = 0.007, BF_{10} = 7.639$; d' : $t_{(15)} = -3.058, p = 0.008, BF_{10} = 6.596$; Fig. 2). These results demonstrate that participants learned to use the cues to increase the efficiency of their performance despite not having any explicit knowledge about the presence of cues.

We repeated the same analyses for the second session, in which participants had explicit knowledge about the information conveyed by the cues. Importantly, we observed a significant main effect of cue for both RT ($F_{(1,15)} = 8.76, p = 0.010$) and performance ($F_{(1,15)} = 12.57, p = 0.003$). In addition, we also

observed a block \times cue interaction for RT ($F_{(1,15)} = 5.37, p = 0.035$). Reaction times were only significantly faster for cued targets in the second half of the session (RT first half: $t_{(15)} = -1.74, p = 0.103, BF_{10} = 0.872$; RT second half: $t_{(15)} = 3.57, p = 0.003, BF_{10} = 15.889$), while performance was better in both the first and second halves of the experiment for cued targets compared with noncued targets (d' first half: $t_{(15)} = 2.50, p = 0.025, BF_{10} = 2.628$; d' second half: $t_{(15)} = 2.77, p = 0.014, BF_{10} = 4.052$).

For metacognitive performance, we observed a main effect for block (first three blocks vs last three blocks) in the implicit condition for metacognitive efficiency ($F_{(1,13)} = 8.16, p = 0.014$). Participants were better in determining right from wrong decisions in the second half of the experiment compared with the first half ($t_{(13)} = 4.15, p = 0.001, BF_{10} = 34.97$). In the explicit condition, we observed a main effect of cue type for meta- d' ($F_{(1,15)} = 4.68, p = 0.047$). Participants had higher meta- d' when targets were validly cued ($t_{(15)} = 2.16, p = 0.047, BF_{10} = 1.58$).

EEG results

To determine whether alpha activity was influenced when (implicit/explicit) information guided behavior, we compared alpha power changes in a 400 ms time window after cue offset (before earliest target onset) between trials in which a target cue and a nontarget cue were presented. We expected to measure implicit contingency effects in the second half of the first session and therefore used the trials from this part of the experiment for this main analysis (see Materials and Methods). We observed a significant interaction ($F_{(2,30)} = 15.79, p < 0.001$) among cue type (target/nontarget), channel location (P4, C4, and Fp2; see Materials and Methods), and awareness condition (explicit/implicit). These results demonstrate that, depending on awareness and electrode location, there is a difference in alpha power between the two cues. Next, we performed a 2×2 repeated-measures ANOVA per cue awareness condition separately. We observed a significant interaction between cue type and channel location in both the implicit condition ($F_{(2,30)} = 5.86, p = 0.007$) and the explicit condition ($F_{(2,30)} = 11.60, p < 0.001$). In the implicit condition, there was lower alpha power over Fp2 ($t_{(15)} = 2.65, p = 0.018, d = 0.66, BF_{10} = 3.346$) for target cues compared with nontarget cues. In contrast, we observed a smaller alpha decrease in P4 for a target cue compared with a nontarget cue ($t_{(15)} = 2.65, p = 0.018, d = 0.66, BF_{10} = 3.334$; Fig. 3*b,c*). Interestingly, in the explicit condition we observed the opposite pattern. Alpha power was higher over Fp2 ($t_{(15)} = 2.61, p = 0.02, d = 0.65, BF_{10} = 3.147$) for target cues compared with nontarget cues, and alpha

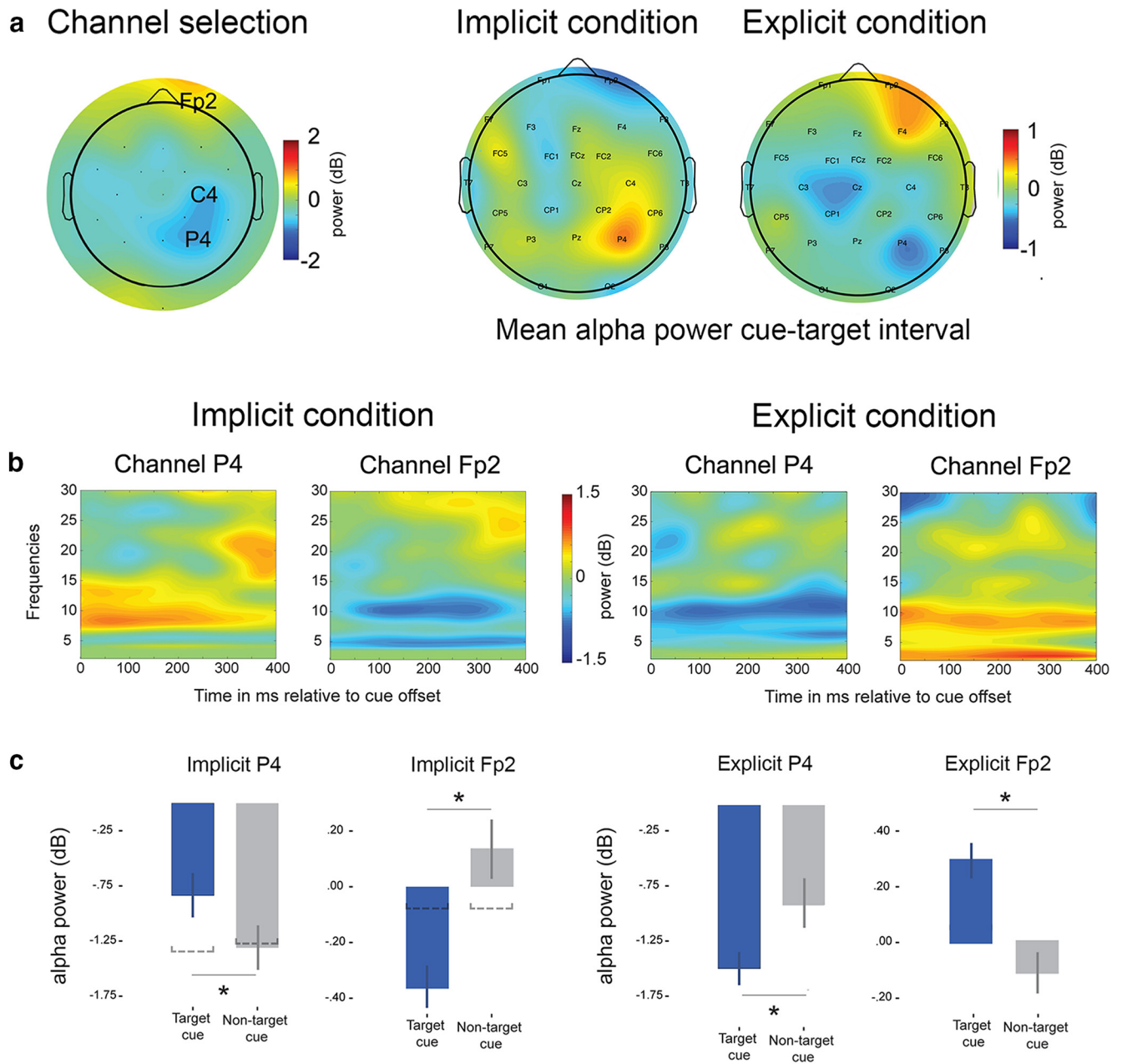


Figure 3. *a*, Electrodes with alpha activity differences between cue types in the first half of the explicit condition were used for further analyses (left). Topographic plot of alpha activity differences between cue types in the cue–target interval in the implicit condition and explicit condition (approximately the last half of the trials for each condition). *b*, Time–frequency plot of electrodes P4 and Fp2 of differences between cue types. *c*, We observed a smaller alpha power decrease in the right parietal region after target cue presentation compared with nontarget cue presentation. In contrast, alpha power decreased in right frontal regions exclusively in response to a target cue. The dashed lines represent the mean values observed in the first half of the experiment. In the explicit condition, we observed an opposite pattern: alpha power increased in the right frontal channel Fp2, while it decreased in P4 after target cue presentation. Bars represent the mean \pm within-subject SEM. * indicates a significant difference (see results).

decreased more in P4 after a target cue compared with a nontarget cue ($t_{(15)} = 3.08, p = 0.008, d = 0.77, BF_{10} = 6.897$; Fig. 3*b,c*). For C4, we observed no differences between cue types (all p values > 0.05).

To examine this effect further and test whether the observed cue type effects in P4 and Fp2 are related to implicit learning of cue–target contingencies and the buildup of task context, we investigated whether alpha power differences between cue types differed depending on which half of the implicit session trials the differences were taken from. We observed a significant interaction among session half (first or second), cue type, and channel ($F_{(1,15)} = 20.53, p < 0.001$). For both Fp2 and P4, we observed a cue-type and session-half interaction ($F_{s(1,15)} > 6.54, p$ values

< 0.023). No differences were observed in either P4 or Fp2 between the two cue types (t values < 0.339 , all p values > 0.744) in the first half of the implicit session (Fig. 3*c*, dashed lines are values from the first half of the implicit session).

To examine whether the observed power differences were accompanied by changes in interactions between frontal and parietal regions, we assessed measures of inter-regional functional connectivity (alpha phase synchrony) by calculating the ISPC between channels P4 and Fp2. We observed a significant main effect of cue ($F_{(1,15)} = 4.71, p = 0.047$) and a nonsignificant interaction between cue type and condition ($F_{(1,15)} = 3.22, p = 0.093$). In the implicit condition, we observed increased alpha-band synchronization between P4 and Fp2 ($t_{(15)} = 3.08, p =$

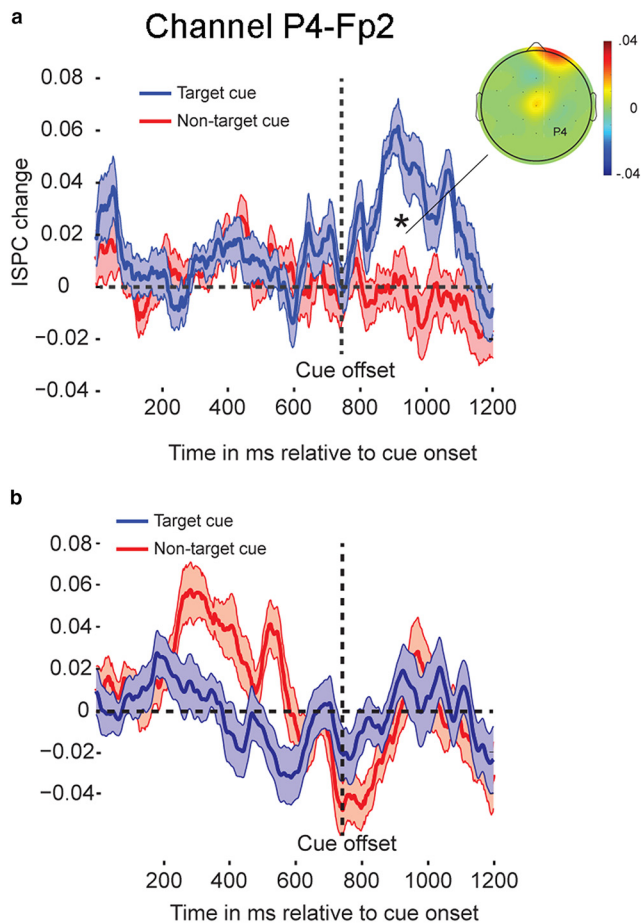


Figure 4. *a*, We observed significantly larger alpha phase synchrony between P4 and Fp2 for target cues in the cue–target interval. We plotted the period from cue onset to target onset for illustration purposes, while only comparing mean ISPC changes in the interval after cue offset (shaded areas are \pm within-subject SEM). *b*, In the explicit condition, we did not observe differences after cue offset. * indicates a significant difference (see results).

0.008, $BF_{10} = 6.892$) after a target cue was presented comparison with a nontarget cue (Fig. 4*a*; we plotted ISPC differences between P4 and all other electrodes for illustration purposes). We observed no significant difference in the explicit condition ($t_{(15)} = 0.606$, $p = 0.553$, $BF_{10} = 0.300$; Fig. 4*b*).

However, in the implicit condition we observed different amounts of alpha power for both cue types. Therefore, our ISPC results could be confounded as a result of different signal-to-noise ratios (Siegel et al., 2012; Bosman et al., 2012; Pesaran et al., 2018; for review, see Cohen, 2014; Bastos and Schoffelen, 2016). We therefore tested whether ISPC differences were still present after stratification of alpha power. Trials from both cue type conditions were randomly discarded until mean alpha power was similar for both cue conditions in channels Fp2 and P4 (where we observed alpha power differences between the cue types). These analyses confirm the results with all trials ($t_{(15)} = 2.83$, $p = 0.01$, $BF_{10} = 4.37$). In addition, we split the target–cue data in half based on median alpha power and tested whether ISPC differences existed between high and low alpha power trials. No difference between high and low alpha power trials were found ($t_{(15)} = 0.60$, $p = 0.56$, $BF_{10} = 0.30$).

To determine how neural measures relate to behavior, we correlated RT and d_a differences to cued and noncued targets with alpha power decreases after target cue offset for P4 and Fp2 and parietal–anterior frontal functional connectivity changes af-

ter target cue presentation. In the implicit condition, we observed a significant correlation between parietal–frontal ISPC change and the RT effect [$r = 0.769$, $n = 16$, $R^2 = 0.59$, FDR (false discovery rate) < 0.05 , $BF_{10} = 78.73$; Fig. 5]. We did not find any significant correlations that survived the multiple-comparisons correction between RTs and alpha power changes or between d' and ISPC change (all r values < 0.335 , FDR > 0.05). These findings demonstrate a strong link between enhanced alpha phase synchrony between P4 and Fp2 and the speeding of responses due to implicitly learning of cues predicting an upcoming target stimulus.

Finally, we investigated whether neural signals related to target processing differentiated depending on preceding cue type (target vs nontarget cue) in both the implicit and explicit conditions (see Materials and Methods). We examined whether we could find differences in P3a and P3b ERP components associated with “context updating” of the stimulus environment (Donchin, 1981; Polich and Kok, 1995) and linked to differences in access awareness (Naccache et al., 2016). We observed a significant cue (target/nontarget cue) \times ERP type (P3a/P3b) \times session (implicit/explicit) interaction ($F_{(1,13)} = 8.95$, $p = 0.010$). In the implicit condition, a significant cue (target/nontarget cue) \times ERP type (P3a/P3b) interaction ($F_{(1,13)} = 11.19$, $p = 0.005$) was found. In this condition, we observed an increased P3a when a target was preceded by a nontarget cue compared with when a target was preceded by a target cue ($t_{(13)} = 3.61$, $p = 0.003$, $BF_{10} = 14.627$; Fig. 6*a*). No significant P3b effect was observed between cue types in the implicit condition ($t_{(13)} = 1.95$, $p = 0.072$, $BF_{10} = 1.180$). In the explicit condition, we observed a nonsignificant cue (target/nontarget cue) \times ERP type (P3a/P3b) interaction ($F_{(1,13)} = 3.54$, $p = 0.082$). In contrast to the implicit condition, we found an increased P3b in the explicit condition when a target was preceded by a nontarget cue compared with when a target was preceded by a target cue ($t_{(13)} = 3.22$, $p = 0.007$, $BF_{10} = 7.902$; Fig. 6*d*). No significant P3a effect was observed between cue types in the explicit condition ($t_{(13)} = 0.084$, $p = 0.934$, $BF_{10} = 0.271$). These results seem to corroborate previous findings demonstrating the influence of contextual processes on the P3, where P3 activity is modulated when the model or context of a stimulus environment needs to be updated (Donchin, 1981; Donchin and Coles, 1988; Polich and Kok, 1995; Todorovic et al., 2011; Seppänen et al., 2012; Silverstein et al., 2015; Bang and Rahnev, 2017; Li et al., 2018).

Discussion

In everyday life, we are able to use predictive information in our environment to guide our behavior. However, sometimes information is not readily available and needs to be inferred (O’Doherty et al., 2001; Wilson et al., 2014). In such cases, it is necessary to compare past and current sensory inputs and use prior experience to select relevant information to anticipate upcoming events (Chun et al., 2011; Wilson and Niv, 2012).

In this experiment, implicit cues were used to investigate how unconscious contingencies may be able to control our decision process. Specifically, we focused on whether implicit cueing was able to affect behavioral responses in a discrimination task and modulate oscillatory neural activity in the alpha frequency range. Results demonstrate that participants were able to use implicit cues to improve performance and speed up responses (Chang et al., 2015; Pinto et al., 2015; Stein and Peelen, 2015; Meijs et al., 2018; Fig. 2). We observed a specific decrease of right frontal alpha power when a target stimulus was implicitly cued (Fig. 3*c*), whereas an alpha power decrease over right parietal cortex di-

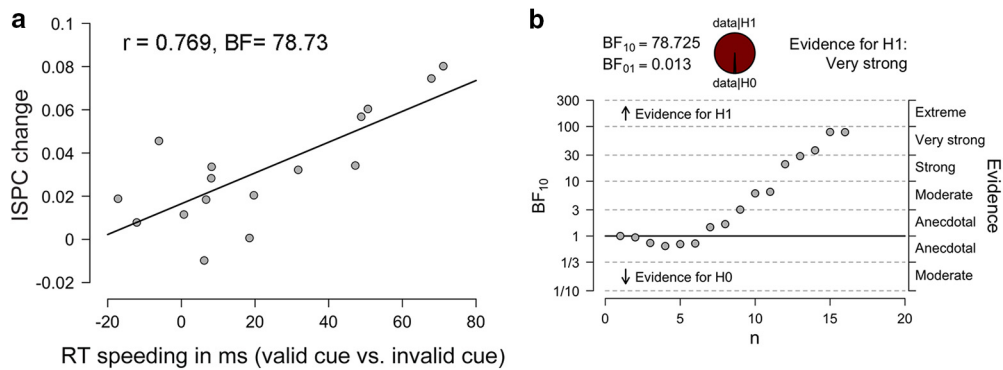


Figure 5. *a*, RT decreases are highly correlated with functional connectivity changes between P4 and Fp2. *b*, Sequential analysis of the Bayesian correlation pairs illustrates the strength of the effect and the number of participants included.

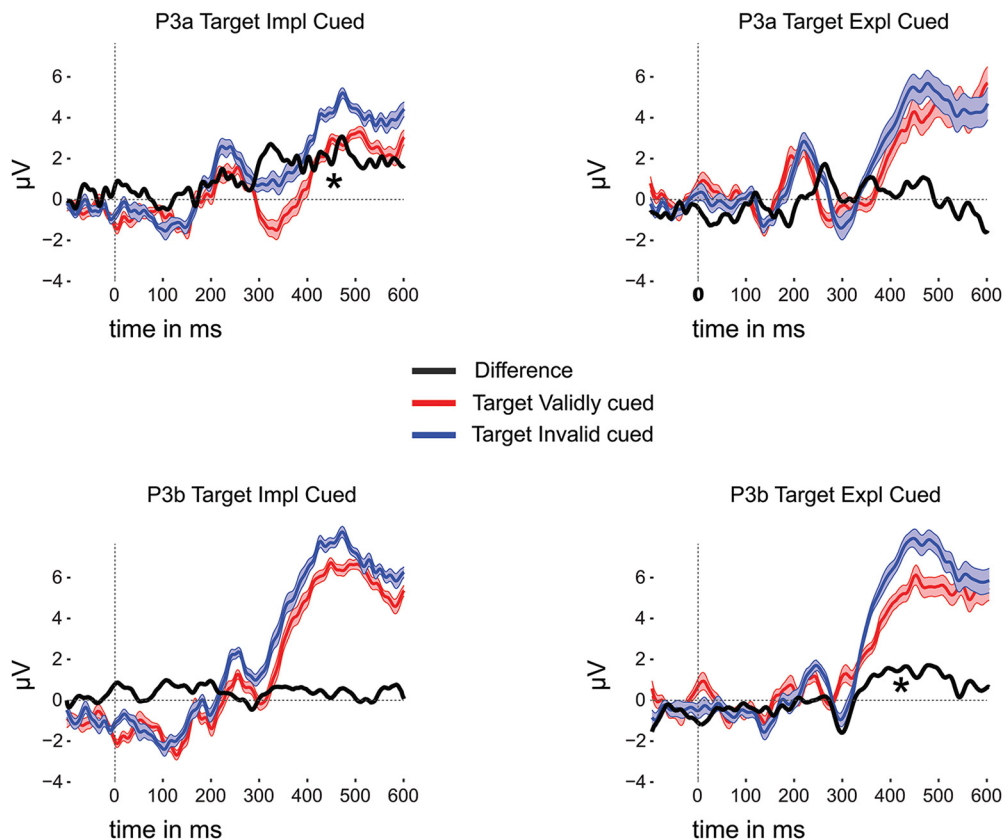


Figure 6. ERPs to targets on trials preceded by a target cue resulted in a smaller P3a in the implicit condition (top left and bottom left) and a smaller P3b in the explicit condition (top right and bottom right). Shaded areas are \pm within-subject SEM. * indicates a significant difference (see results).

minished after the presentation of an implicit target cue. These findings corroborate previous findings demonstrating that prefrontal cortex becomes recruited when information needs to be inferred (Christoff and Gabrieli, 2000; Wilson et al., 2014; Schuck et al., 2017). Furthermore, it has been shown that alpha power increases in parietal cortex when attention becomes internally oriented (Ray and Cole, 1985; Schupp et al., 1994; Cooper et al., 2003). Interestingly, we observed a specific increase in functional connectivity (alpha phase synchrony) between right parietal and right prefrontal channels when implicit information was used (Fig. 4). This change in functional connectivity in response to an implicit target cue correlated strongly with behavioral effects (Fig. 5). Finally, ERP differences (Fig. 6) between cued and non-cued targets showed that cued targets were implicitly anticipated

(Summerfield et al., 2008; Todorovic et al., 2011; Chennu et al., 2013). Figure 7 summarizes these results and provides a schematic of the mechanisms mediating implicit inferences.

Alpha oscillations and gating

Alpha activity has long been considered a marker for increased inhibition (Lopes da Silva, 1991). Recently, it has been put forward that alpha oscillations play a key role in the gating of the flow of information by suppressing the processing of information in task-irrelevant networks (Klimesch et al., 2007; Jensen and Mazaheri, 2010; Mathewson et al., 2014; Groen et al., 2016). It has been demonstrated that a shift of attention to either the left or right visual hemifield decreases alpha oscillations in the contralateral hemisphere, while increasing them in the ipsilateral

hemisphere (Worden et al., 2000; Sauseng et al., 2005; Thut et al., 2006). Furthermore, recent studies have shown that alpha power increases in the dorsal stream when a task relies on ventral stream processing (Jokisch and Jensen, 2007; Wokke et al., 2014). In the present study, we observed a smaller decrease of parietal alpha oscillation after presentation of a target cue when participants became sensitive to implicit cueing (Fig. 3). It has been previously shown that alpha power in parietal regions increases when attention becomes internally directed, suggesting the necessity of active inhibition of external sensory input for internally driven mental operations (Ray and Cole, 1985; Schupp et al., 1994; Cooper et al., 2003). Further, Sestieri et al. (2010) observed functional competition between internally (memory) and externally (perception) driven processes, where parietal cortex operated in a push–pull manner depending on the task engaging either internally (search in memory) or externally (search in the environment) oriented networks. Here, enhanced internally driven processes could dampen typical parietal alpha power decreases due to functional competition (Fox et al., 2005). This push–pull hypothesis seems to be supported by the recruitment of prefrontal regions, strongly associated with the evaluation of internally generated information (Christoff and Gabrieli, 2000; Schuck et al., 2017; Dixon et al., 2018). Further, a seemingly opposite pattern was observed in the explicit condition, when attention could be externally oriented (Figs. 3, 7).

Lesions to orbitofrontal cortex have been shown to induce a state in which subjects become solemnly dependent on information from the outside world that is directly observable (utilization behavior; Lhermitte, 1983; Brazzelli and Spinnler, 1998; Besnard et al., 2010), while internal models and information about context are no longer accessible (similar effects have also been observed in reversal learning tasks; Dias et al., 1996; Wilson et al., 2014). These findings have been associated with a disrupted balance in network functioning, where orbitofrontal damage results in a disinhibited state of parietal cortex (Lhermitte et al., 1986). Interestingly, the current results show increased functional connectivity between parietal and prefrontal channels, exclusively in the implicit condition (Figs. 3, 4). Measures of functional connectivity provide us with information about the formation and functional integration of networks, working either in concert or in a push–pull fashion (Fox et al., 2005; Srinivasan et al., 2007; Wokke et al., 2015). In the last decades, competing network dynamics have been demonstrated by opposed activity levels in intrinsic “outward oriented” networks and the “internally oriented” default-mode network on a variety of tasks (Raichle et al., 2001; Fox et al., 2005; Weissman et al., 2006; Kelly et al., 2008; Hampson et al., 2010; Wokke et al., 2015; Zabelina and Andrews-Hanna, 2016). As depicted in Figure 7, our results indicate a similar dynamic of internally and outward oriented network activity when participants learn to use implicit information. Further, the strength of the functional connectivity change between parietal and prefrontal regions strongly correlated with the behavioral RT effect. However, we did not find a significant correlation between the behavioral effect and alpha power in either parietal or prefrontal regions. These findings indicate that specif-

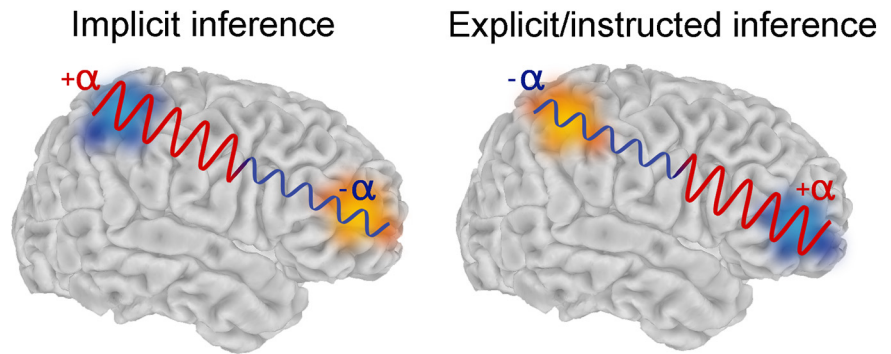


Figure 7. Left, Implicit inferences engage internally oriented networks, enhancing processing via anterior prefrontal regions. Competitive network dynamics result in decreased externally oriented network activity, where alpha activity serves as a mechanism to gate the flow of information within specific networks. Right, Explicit instructed inference results in an opposite pattern, whereby externally oriented networks are engaged.

ically the orchestration of activity in internally and externally oriented networks could be fundamental for situations when information needs to be inferred.

Prefrontal cortex and inferential decision-making

Activity in the orbitofrontal cortex (Brodmann areas 10, 11, and 47) has been consistently associated with support of adaptive decision-making by uncovering predictive values associated with stimuli in our environment (Walton et al., 2010; Boorman et al., 2016). The connectivity between orbitofrontal cortex and sensory, frontal, striatal, and hippocampal regions makes this region highly suited for the generation and testing of hypotheses (Frey and Petrides, 2002; Bar et al., 2006) and for providing predictions about specific outcomes associated with stimuli (Rudebeck and Murray, 2014; Goldfarb et al., 2016). Recently, the above-described observations have been captured in a “state-space” model in which the orbitofrontal cortex plays a crucial role. This state-space theory of orbitofrontal cortex (Gershman and Niv, 2010; Wilson et al., 2014; Schuck et al., 2016, 2017) focuses on the context in which decisions are being made and what the decision-making agent considers “the state of the world” at the moment of the decision (Schuck et al., 2017). Such states can be connected to external information (e.g., explicit cues) or they can contain internally generated information, which cannot be directly obtained from the immediate environment and has to be inferred (e.g., implicit cues or task context). Specifically, the orbitofrontal cortex seems critical for the representation of states that include such partially observable information (Brown et al., 2010; Wilson et al., 2014). The present findings are contributing to a growing amount of evidence demonstrating the critical role that prefrontal cortex plays in using information in the environment that is not directly observable.

Another influential proposal about the workings of the (orbito)frontal cortex involves the signaling of emotions and its influence on decision-making, the so-called “somatic marker hypothesis” (Damasio et al., 1991; Lang, 1994; Stalnaker et al., 2015; Poppa and Bechara, 2018). Central to the somatic marker hypothesis is that decision-making can be influenced through signaling of bioregulatory processes that are expressed in the body. In the current experiment, increased arousal elicited by target cues could be used as a cue itself. Unfortunately, the present study lacks spatial specificity, making it difficult to assess the role of key structures thought to be critical in the processing of such somatic markers (e.g., the amygdala, orbitofrontal, somatosensory, and insular cortex). Future work combining fMRI and

physiological measures (e.g., skin conductance, ECG) could provide useful insight into the role of somatic markers in the buildup of implicit inferences.

P3a/P3b: prediction and access consciousness

To further examine the consequences of implicit cueing, we investigated how cued and noncued target stimuli influenced P3a/P3b activity. A rich literature describes the role of the P3 in context updating (Donchin, 1981), in which a current stimulus is compared with a preceding stimulus in working memory (Donchin, 1981; Donchin and Coles, 1988; Polich and Kok, 1995; Silverstein et al., 2015). We therefore compared P3a and P3b responses to cued and noncued targets. These P3 components have been frequently studied using “oddball” designs, linking the P3 to updating of stimulus context (Donchin, 1981; Summerfield et al., 2008; Todorovic et al., 2011; Chennu et al., 2013). Interestingly, we observed an enhanced P3a when a target stimulus was preceded by a nontarget cue in the implicit condition, whereas we found an increased P3b in the explicit condition.

It has been suggested that the P3a component relies more on automatic (unconscious) processes (Muller-Gass et al., 2007), whereas the P3b component is linked to access consciousness (Faugeras et al., 2012; Naccache et al., 2016; but see Silverstein et al., 2015). These findings are in line with a recent study investigating the relationship between top-down expectations and access consciousness (Meijs et al., 2018). In that study, the authors observed that access awareness of a predictive stimulus is necessary to actively use top-down predictions for subsequent target processing (in an attentional blink design where T1 predicted T2). The present results and the findings of the study by Meijs et al. (2018) indicate that a predictive stimulus needs to be perceptually processed all the way up to the level of access awareness to be effective, but that the meaning of the stimulus (i.e., that the stimulus is in fact predictive) can still remain inaccessible for introspection without discarding its functionality. Further, Meijs et al. (2018) demonstrated that prediction errors could be triggered outside of conscious awareness. In the current study, we observed related effects by observing a P3a difference between cued and noncued targets in the implicit condition, while we found a P3b difference in the explicit condition that was not present in the implicit condition. These findings suggest that unconscious/implicit context updating effects proceed more automatically than in the conscious/explicit form (Faugeras et al., 2012; Naccache et al., 2016).

Previous work suggests that unconscious/automatic elicited responses are relatively short lived, while conscious detection results in more long-term behavioral adaptations (Cohen et al., 2009; van Gaal and Lamme, 2012), although it remains debated what the consequences of such differences exactly are. It would be interesting to investigate how long lived the observed effects of implicit learning are (e.g., by testing participants on multiple occasions in the implicit condition to examine the longevity of the effect of implicit learning). In the present study, we also did not focus on how or when implicit control of attention became accessible for introspection. It would be very fascinating to investigate how the use of implicit information progresses toward explicit knowledge and to observe whether such a transition would proceed in a gradual or in an all-or-none manner (Sergent and Dehaene, 2004; Windey and Cleeremans, 2015; King et al., 2016). It could be that hypotheses about implicit information gradually become strong enough, reaching increasingly higher signal-to-noise levels, resulting in stable (neural) representations (Schurger et al., 2010) and updating of internal predictive models of the

environment (O’Reilly et al., 2013). Such internalization of stimulus–outcome events (Cleeremans, 2011; Buzsáki et al., 2014; Wokke et al., 2017) could pave the way for implicit information to become accessible for introspection.

Limitations

In the present study, we investigated how implicit contingencies guide decision-making. The current results implicate competitive network dynamics during implicit inference. We also analyzed electrophysiological changes in response to explicit cues. However, with the current scalp EEG measures, precise neural localization of the differences between the implicit and explicit condition is not possible. Although we increased spatial specificity by converting the data to spline Laplacian signals (Cohen, 2015), our EEG results still suffer from limited spatial resolution. Recently, fMRI measures and appropriate experimental designs have proven to be able to reveal activity related to predictive stimuli (van Loon et al., 2016; de Lange et al., 2018). It would be interesting to use fMRI in future studies to localize regions involved during explicit and implicit inferences.

Another limitation of the present work is that we are not able to make claims about a causal relation between the observed behavioral and electrophysiological effects. Although the above-discussed lesion studies (Lhermitte et al., 1986; Damasio et al., 1991; Wilson et al., 2014) provide supporting evidence about the role of prefrontal cortex in implicit inference, future work could combine the present design with brain stimulation (e.g., transcranial magnetic stimulation) to assess the causal effects of disrupting (or injecting alpha rhythms into) prefrontal and/or parietal cortex.

Although the present sample size is in line with previous studies demonstrating alpha effects (van Dijk et al., 2008; Mathewson et al., 2009; Marshall et al., 2015; Becker et al., 2018), and the alpha effect sizes (Cohen’s $d = 0.66$) in the implicit condition are reasonable (medium-large), future studies could be valuable in determining whether the observed effects gain further strength through the aggregation of data (using Bayesian statistics).

There may also be concerns about the metacognitive measures used in the current design. Participants were instructed to provide an estimate about the quality of their decision immediately after the first-order response. However, we did not present a confidence scale or explicit question about their confidence on the screen during the experiment. The current setup could result in “sticky fingers,” where second-order responses are mapped onto the same button or hand as first-order choices. The use of different hands for these different responses would more definitively rule out contributions from these types of response biases. Finally, in the current study, hit rates were relatively high for some participants, creating potentially unstable estimates of second-order performance (Bor et al., 2017; Ruby et al., 2018). A staircase procedure before the experiment could address this issue in future studies.

Conclusion

In daily life, our decisions are frequently guided by regularities in our environment. However, such contingencies are not always explicitly present and sometimes need to be inferred. Using contingency cueing, we show that implicit inferences influenced responses to subsequent targets despite a lack of awareness of cue–target contingencies. These implicit inferences emerge through changes in internally and externally oriented neural networks. The current results demonstrate that prefrontal cortex plays an important role in the transformation of externally driven

stimulus–outcome events into predictive internalized models of the world.

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