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Conscious and unconscious expectancy effects: a behavioral, scalp and intracranial electroencephalography study

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Highlights

- Both supraliminal and subliminal cues can affect response times and modulate brain activity.
- Supraliminal CNV originates from temporal and mesio-frontal (Supplementary Motor Areas) neural sources.
- Subliminal CNV originates from temporal lobe sources.

Abstract

Objective: The scope of unconscious cognition stretched its limits dramatically during the last 40 years, yet most unconscious processes and representations that have been described so far are fleeting and very short-lived, whereas conscious representations can be actively maintained in working memory for a virtually unlimited period. In the present work we aimed at exploring conscious and unconscious lasting (>1 second) expectancy effects.

Methods: In a series of four experiments we engaged participants in the foreperiod paradigm while using both unmasked and masked cues that were informative about the presence/absence of an upcoming target. We recorded behavioral responses, high-density scalp EEG (Exp.2a), and intra-cranial EEG (Exp. 2b).

Results: While conscious expectancy was associated with a large behavioral effect (~150ms), unconscious expectancy effect was significant but much smaller (4ms). Both conscious and unconscious expectancy Contingent Negative Variations (CNVs) originated from temporal cortices, but only the late component of conscious CNV originated from an additional source located in the vicinity of mesio-frontal areas and supplementary motor areas. Finally, only conscious expectancy was accessible to introspection.

Conclusions: Both unmasked and masked cues had an impact on response times and on brain activity.

Significance: These results support a two-stage model of the underlying mechanisms of expectancy.

1-Introduction

During the last decades, a large range of unconscious cognitive processes, inaccessible to conscious report, have been discovered and characterized in conscious subjects using various paradigms such as visual masking, attentional blink or inattention blindness (Dehaene et al., 2001, 1998; Kouider and Dehaene, 2007; Mack and Rock, 1998; McCormick, 1997; Naccache, 2006; Sergent et al., 2005; van Gaal et al., 2008). Thereby, the combination of behavioral and brain activity measurements revealed the existence of unconscious perceptual, semantic, executive, motor and even emotional cognitive representations, correlated with the activity of various cortical areas and networks. The scope of unconscious cognition rapidly stretched its limits so dramatically, that the classical search for clear differences between conscious (reportable) and unconscious (unreportable) cognitive processes turned unexpectedly to a highly challenging issue. Which are the mental operations, - if any -, that require conscious mentation? Within this scientific context, one potential candidate that is still in the running deals with time. Indeed, most unconscious active representations and cognitive processes that have been described so far are fleeting and very short-lived (usually within a few tens or hundreds of milliseconds), whereas conscious representations can be actively maintained in working memory for a virtually unlimited period.

Time-related cognitive processes that can be viewed as the launching of an internal timer mechanism are of special interest. Among these processes, the expectancy of upcoming relevant stimuli is especially noteworthy because it can be measured both using reaction times (RTs) and EEG signals. Indeed, a rich literature demonstrated that expectancy is associated with the **Contingent Negative Variation (CNV)** ERP component (Macar and Vidal, 2004; Pfeuty et al., 2005; Walter et al., 1964). Typically, in the foreperiod paradigm a warning stimulus (S1) is followed by an imperative stimulus (S2). Once the contingency between S1

and S2 is learned after a few trials, the presentation of S1 triggers an expectancy towards S2, visible as a slow negative potential gradually increasing until the presentation of S2. This CNV then terminates abruptly right after the appearance of S2 (Walter et al., 1964). Importantly, the CNV temporally bridges S1 and S2 presentation over several seconds. Very few works investigated the relations prevailing between consciousness and expectancy (Capa et al., 2013; Faugeras et al., 2012; Hamon et al., 1994; Sergent et al., 2017; Yasuda et al., 2011).

A recent study reported that CNVs elicited consciously could be modulated by masked monetary reward cues (Capa et al., 2013) presented at the beginning of long runs of trials. Unconscious monetary cues seemed to induce changes in motivation, resulting in modifications of the CNV amplitudes. These results were interpreted as a long-lasting influence of monetary cues on motivation thus resulting in increased CNVs. Thus, unconscious monetary cues probably influenced the CNV indirectly. To our knowledge, no study has ever directly tried to probe the triggering of a CNV by subliminal stimuli or to directly influence an ongoing CNV with masked cues.

The CNV seems to be affected by levels of arousal. Indeed, subjects who had an undisturbed night of sleep show stronger CNVs than participants who were disturbed during their sleep (Yamamoto et al., 1984). These results suggest that arousal might be a key requirement to elicit a CNV. Hamon and colleagues (1994) tested the possibility of initiating anticipatory attention during sleep. They observed CNVs in awake subjects, and during rapid eye movement sleep (REM sleep), but noticed that the CNV was absent in deep sleep. Yasuda et al. (2011) also found an absence of CNV in deep sleep and a decrease of CNV amplitude with

sleep onset latency. All this evidence points toward the fact that consciousness might be necessary for endogenous anticipatory temporal attention.

The presence of CNV was also probed in patients with disorders of consciousness (DOC). In a study on two comatose patients, Dolce & Sannita (1973) found that after presenting paired auditory stimuli to these patients more than a hundred times, they observed a negative shift in the EEG between S1 and S2 resembling a CNV. The present work actually stems from a set of studies by our group in which we incidentally discovered the presence of a CNV in an auditory paradigm that was associated with a previously reported neural signature of conscious access. Indeed we recently tested DOC patients with the ‘local-global’ paradigm to probe brain responses to violations of auditory regularities (Faugeras et al. (2012)). We observed that patients showing a CNV were more prone to detect violations of both local (intra-trial) and global (inter-trial) regularities. Moreover, a CNV could be observed both in some patients in minimally conscious state (MCS), and in some patients in vegetative state (VS). Similarly, we also observed a CNV in three out of four clinically VS patients in a more recent work (Sergent et al. (2017)). Hence, some form of temporal expectancy might also occur in the absence of consciousness. Note however that the top-down modulation of CNV seemed to require a minimal level of consciousness. These questions also motivate the present work in a translational perspective. Indeed, defining the diagnostic and prognostic values of CNV signatures in DOC patients could be valuable in these very uncertain clinical conditions. However, one should be aware of the potential multiple differences between such an unconscious cognitive process that occurs in a subject who is in a conscious state, and an unconscious cognitive process of expectancy that occurs in a subject who is in a non-conscious state. In order to begin to address this difficult issue, we aimed here at exploring

expectancy in conscious participants as a function of their access to the information eliciting the expectancy process.

In the present work, we characterized conscious and unconscious expectancy effects in a foreperiod paradigm, and tested the hypothesis that short-lived unconscious representations elicited by subliminal cues could still trigger long-lasting CNV-associated processes and affect behavior. To this aim, we designed a series of masked and unmasked cueing experiments in which we explored the possibility of unconsciously initiating a sustained expectancy effect. Through four complementary experiments using behavioral measures, high-density EEG and intra-cranial recordings, we compared conscious and unconscious expectancy effects, and demonstrated that: i) consciously perceived cues elicit large behavioral expectancy effects (effect size >150 ms) that are accessible to introspection; ii) conscious expectancy is correlated with typical CNVs, the generators of which are located in temporal lobes (early component) and in the supplementary motor areas and related areas (late component); iii) subliminal cues that are not consciously reported can elicit small (effect-size ~ 5 ms) behavioral effects for values of cue-stimulus onset asynchrony (SOA) superior to one second; iv) these unconscious expectancy effects do not seem to be accessible to introspection, v) and they are associated with a Cz-centered CNV, the generators of which seem to be confined to the temporal lobe.

2-Materials & Methods

Experimental design

The four experiments included in this study aimed at measuring distinct correlates of expectancy effects (behavioral, electrophysiological effect), and were therefore different in

terms of trials types and trials composition, while sharing an identical general design (see Supplementary Material file for a detailed description of all experimental designs).

Commonalities between experimental designs of the four experiments:

Each trial started with the presentation of a fixation cross for 1s followed by the serial alternation of a blank (17 ms), a mask (33 ms), a blank (17 ms) and a neutral cue (50 ms; see Figure 1a). This sequence alternated for a variable time ranging from 500ms to 1433ms, and was then followed by the presentation of a cue (diamond or square, balanced across subjects) that predicted the upcoming presentation of a target within the current trial. These cues were either masked or unmasked. Specifically, a sequence of alternating masks and neutral cues preceded and followed the presentation of the masked cues, while unmasked cues were flanked by a 117ms blank, allowing their conscious perception (see above). One type of cue predicted the upcoming appearance of a target ('Cue-Tgt' cue), whereas the other type of cue predicted the absence of a target within the current trial ('Cue-NoTgt' cue). Comparing 'Cue-Tgt' and 'Cue-NoTgt' trials is our contrast of interest.

Each experiment was preceded by a training session exclusively made of unmasked cued trials with a cue predictability of 100% in order to maximize learning of the association between each cue and its corresponding target predictability. Only the number of trials varied between experiments (48 trials in Experiments 1 and 3, 100 trials in Experiment 2a, and 50 trials in Experiment 2b).

The visibility of the masked cue was tested in each experiment after the end of the main experiment by collecting subjective reports, and by engaging participants in a final forced-choice discrimination task on masked cue trials. Participants were presented with masked cues (50% 'Cue-Tgt', 50% 'Cue-NoTgt') similarly to the main experiment, and at the end of the trial were forced to categorize the cue using two keyboard response buttons.

Stimuli were presented on a DELL P170S 1280x1024 32bits 60Hz using Matlab R2012b (The Mathworks, Inc.) psychtoolbox 3 (Brainard, 1997).

Participants and instructions

All volunteers gave their written informed consent, experiments were approved by the Ethical Committee (APHP, CPP-IDF VI, Pitié-Salpêtrière Hospital), and were conducted according to the principles expressed in the Declaration of Helsinki.

Experiment 1

Thirty right-handed participants with normal or corrected to normal vision were included. Two participants were excluded due to better than chance perception of masked cues in the discrimination task (correct-response rate: 75% and 63% (chance-level = 50%); individual d' : 1.37 and 0.67 with χ^2 p-values ≤ 0.01). Twenty-eight participants were thus included in the statistical analysis (age= 25.4±3.81 ranging from 20 to 35 y.o.; median age= 25; 18 females).

Experiment 2a

Sixteen participants were included (age= 24.2±1.68 ranging from 22 to 27 y.o.; median age 24; 10 females) and performed the number comparison task (see Supplementary Material for details).

Experiment 2b

Fourteen epileptic patients were included (age mean =31.57±8.41 median=32 yo; 5 males). Neuropsychological assessment revealed normal or mildly impaired general cognitive functioning. These patients suffered from drug-refractory focal epilepsy and were implanted stereotactically with depth electrodes as part of a presurgical evaluation. Implantation sites

were selected on purely clinical criteria, with no reference to the present protocol. Instructions were identical to the ones used in Experiment 2a.

Experiment 3

Twenty-eight participants were included in this expectation introspection experiment. Two subjects were excluded for not understanding or not respecting the instructions concerning the use of the introspection scale: these two subjects were the only ones who did not report subjective expectation for Cue-Tgt unmasked cue trials that were consciously perceived and instructed to launch a voluntary expectancy process. Therefore, a total of 26 subjects were included in the statistical analysis (age= 25.2 \pm 4.4 ranging from 18 to 38 y.o. ; median age 24 ; 13 females).

Electrophysiological recordings

High-density scalp EEG (Experiment 2a)

EEG signal was collected at 250Hz with a 256 electrodes geodesic sensor net (EGI, Oregon, USA) referenced using a common average reference, and signal preprocessing was done using EGI waveform tool. To allow measuring of slow cortical potentials like the CNV, we deliberately used a 0.1Hz highpass, as well as 20Hz lowpass filters. Trials were segmented -200 +1600 ms relative to the appearance of the cue, voltages exceeding 150 μ V as well as blinks exceeding 100 μ V and eye movements exceeding 80 μ V were excluded. Additionally, electrodes with more than 30% rejection rate were excluded, bad electrodes were interpolated, and trials with more than 10 bad electrodes were excluded as well. A 200ms baseline correction was applied prior to cue onset.

Cortical sources of the grand average effects were reconstructed using the Brainstorm software (Tadel et al., 2011). The reconstruction was based on the MNI anatomical template

“Colin 27”. The overlapping spheres method was used for computing the forward model. The weighted minimal norm method was used for source reconstruction. For cortical sources visualization in the figures, source activity cutoff was set at 40pA with a minimum size of 10 contiguous vertices.

Intra-cranial recordings (Experiment 2b)

Electrode Implantation and Localization

Patients were implanted intracerebrally with depth electrodes, each bearing 4–12 recording sites (Ad-TechMedical Instruments). Electrodes were localized automatically in MNI space using each patient's CT and pre/post implantation MRI scans. The localization was performed using the Epiloc toolbox developed by the STIM (Stereotaxy: Techniques, Images, Models) engineering platform in the ICM (<https://icm-institute.org/en/cenir-stim-stereotaxy-core-facility-techniques-images-models-2/>), (Bardinet et al., 2009; D’Albis et al., 2015; Perez-Garcia et al., 2015). To precisely localize electrodes showing a significant effect, two experimenters (CR, TSM) labeled manually and independently the electrodes (inter-rater reliability $R=0.99$) based on anatomical landmarks in the patients’ native space, according to the parcellation of the Desikan atlas (Desikan et al., 2006).

iEEG recording and processing

Intracranial data were acquired with an audio–video–EEG monitoring system, 12 patients with Neuralynx and 2 with Micromed with a sampling rate of 4000Hz and 1024Hz, respectively, and were then resampled to a common sampling rate of 1000Hz. Epochs were extracted from –200 to 1550 ms relative to the onset of the cue. To avoid artifacts, recording sites exceeding the threshold of $\pm 300 \mu\text{V}$ in more than 5% of the epochs were excluded. All signals were re-referenced to their nearest neighbor on the same electrode (bipolar montage).

In the following, we will refer to these bipolar montages as “electrodes”. All data were visually inspected to discard any trial with epileptic or interictal activity. ERPs were obtained by averaging epochs for each condition. Data were filtered similarly to the scalp ERPs in Experiment 2a, with a 0.1Hz high-pass and a 20Hz fourth-order Butterworth low-pass filter in forward and reverse directions in order to avoid phase-shift. A 200ms baseline correction was applied.

Data analysis and statistics

Behavior

Analyses were performed on RTs superior to 100ms and inferior either to 1000ms in Experiments 1 and 3 that used a simple reaction time task, or to 1500ms for Experiment 2a and 2b that used a number comparison task. Additionally, RTs exceeding 3 standard deviations of the individual mean were excluded. ANOVAs and post-hoc Student t-tests were used. In all experiments, the visibility of masked cues was tested by computing individual d' objective discriminability, and by comparing the distribution of individual d' values against zero with Student t-tests.

Scalp and iEEG (Experiments 2a and 2b)

We used two complementary methods to assess ERP effects of expectancy: a region of interest (ROI) analysis as well as a whole-sensors analysis (see Supplementary Material for details). In these two complementary analyses we used cluster permutation statistics (temporal clusters for the ROI approach and spatio-temporal clusters for the whole-sensors approach) enabling to assess the significance of observed effects and to correct for multiple comparisons (Maris and Oostenveld, 2007). Data were analyzed using Fieldtrip toolbox and Matlab 2015b (The Mathworks, Inc.).

3-Results

3-1 Experiment 1: Behavioral effects of expectancy elicited by conscious and unconscious cues

In Experiment 1, participants performed a classical temporal expectancy paradigm: a geometrical cue (square or diamond or vice-versa) predicted the presence ('Cue-Tgt') or absence ('Cue-NoTgt') of an upcoming target letter ('W') in the current trial. Cues could be masked or unmasked and were randomized within the same blocks (see Figure 1a and Materials & Methods and SM for details). The 'Cue-Tgt' cue was fully predictive of target presentation (100% of trials) both in the masked and the unmasked conditions, while the 'Cue-NoTgt' cue was 88.5% predictive of the absence of a target in the unmasked trials, and non-predictive in masked trials (50% of trials were not followed by a target). This difference was made deliberately to increase the number of trials including a target preceded by a 'Cue-NoTgt' cue in masked trials, and therefore to increase the power to detect a masked cueing effect in RTs.

We analyzed RTs from trials containing a target, using a repeated measures analysis of variance (ANOVA) with two factors: Cue-type (2) X Cue-Visibility (2). A main effect of cue-type was found ($F(1,27)=62.42, p<10^{-7}$) with faster RTs for 'Cue-Tgt' than for 'Cue-NoTgt' cues (mean RT=493ms and 571ms respectively, post-hoc $p<10^{-6}$), as well a strong main effect of cue visibility ($F(1,27)=22.4, p<10^{-4}$) with faster RTs in unmasked cue trials than in masked cue trials (mean RT=516ms and 548ms respectively, post-hoc p value=0.01). These two factors interacted ($F(1,27)=52.2, p<10^{-7}$; see Figure 1b), reflecting a stronger expectancy effect for unmasked cues than for masked ones. Crucially, post-hoc tests revealed that both masked and unmasked expectancy effects were significant. Expectancy effect in unmasked cue trials reached a difference of 150ms in RTs ($p<10^{-7}$). A Bayesian test confirmed the

extreme evidence level supporting a genuine unmasked cueing effect ($BF_{+0}=4.6 \times 10^6$). Expectancy effect in masked cue trials was much smaller (effect size = 4.0 ms) but significant ($p=0.03$). A Bayesian test confirmed the moderate evidence level supporting a genuine masked cueing effect ($BF_{+0}=7.5$).

We checked the stability of unmasked and masked cueing effects along the experiment by testing the corresponding ANOVA interactions of the following two factors: Cue-Tgt/Cue-NoTgt X First Half/Second Half of experiment, and found no significant effect ($F(1,27)=0.83$, $p>0.37$).

Concerning cue visibility, none of the subjects reported a subjective impression of perceiving predictive cues in the serially alternating display in masked cue trials. Objective performance validated these subjective reports, by showing a mean d' value of -0.07, not significantly different from a null d' ($p>0.05$). No correlation was observed between individual d' values and the expectancy effect in masked cue trials ($p=0.28$).

This first behavioral experiment showed both a classic expectancy effect for consciously visible cues, as well as a small but significant expectancy effect driven by unconsciously perceived symbolic cues. Crucially, this subliminal expectancy effect spanned in time over more than a second (1166ms), far beyond the usual shorter stimulus-onset asynchronies (SOAs) previously used to probe masked priming effects (Dehaene et al., 2001; Greenwald et al., 1996; Rolls and Tovee, 1994).

3-2 Experiment 2: Neural correlates of conscious and unconscious expectancy effects

In Experiment 2, we aimed at discovering the neural correlates of these conscious and unconscious expectancy effects by using two time-resolved electrophysiological techniques: scalp EEG recorded in healthy participants (Experiment 2a), and iEEG recorded in epileptic patients undergoing a pre-surgical mapping (Experiment 2b). We kept the same global

structure as in Experiment 1, but used a number comparison task instead of a basic detection task. The other notable difference was related to cue predictability. Given that our major objective was to compare neural activity elicited by ‘Cue-Tgt’ and ‘Cue-NoTgt’ cues during the 1166ms time-window spanning from cue onset to target onset, we used fully predictive cues (100% correct cues). We also added a control condition corresponding to the absence of any predictive cue, in order to compare RTs and neural activity to a control condition (see Figure 2a).

3-2-1 Experiment 2a: Scalp EEG correlates of expectancy elicited by conscious and unconscious cues

3-2-1-1 Behavior:

Mean RTs on correct trials presented a typical numerical distance effect (Dehaene, 1992) (see Figure 2b): subjects were significantly faster at comparing targets far from five (1,2,8 and 9) than targets close to five (3,4,6 and 7) (effect size = 33.3ms, paired sample t-test, $p < 10^{-5}$). Subjects responded very accurately (mean percentage of correct responses = 97.6% \pm 0.5) and showed a typical numerical distance effect on error rates (see Figure 2b): they were significantly more accurate when comparing targets far from 5 (1,2,8 and 9) than targets close to 5 (3,4,6 and 7) (effect size = 3.6%, paired samples t-test, $p < 10^{-3}$). The parallel between RTs and error rates discards a speed-accuracy tradeoff.

Concerning the effect of the cues, subjects were significantly quicker at responding to targets when they were preceded by an unmasked ‘Cue-Tgt’, compared to when there were no cues (control condition), resulting in a conscious priming effect size of 88.7ms (t-test p value $< 10^{-6}$). Bayesian test confirmed the extreme evidence level supporting a genuine unmasked cueing effect ($BF_{+0} = 3.9 \times 10^5$). A trend to commit more errors for ‘Cue-Tgt’ than for control trials in

the unmasked condition (effect size=-1.2% ; t-test p-value=0.06) may reflect a form of impulsivity triggered by consciously perceived Cue-Tgt signals.

In the masked conditions, a trend was observed in the predicted direction: subjects tended to answer faster to targets preceded by a masked 'Cue-Tgt' than to answer cue-free trials (effect size = 5.7ms; t-test p-value p=0.1). Bayesian test confirmed the anecdotal evidence level of this masked cueing effect ($BF_{+0}=2.8$). Note that given that we used 100% predictive cues in this experiment in order to maximize ERP effects, behavioral cueing effects are not univocal: they may reflect a specific 'Cue-Tgt' effect, or be related to a warning signal irrespective of its symbolic content. No significant masked cueing effect was observed on the error rates (p=0.8).

None of the subjects reported conscious perception of masked cues in the subjective reports collected after the main experiment. Moreover, objective performance confirmed these subjective reports, by showing a mean d' value of 0.02 (p=0.8), and by the absence of significant correlation between individual d' and behavioral cueing effect (neutral - masked Cue-Tgt; $r=0.06$, $p=0.82$). Finally, an interpolation analysis revealed a trend for a masked cueing effect for a null d' (effect size=5.7ms; $p=0.14$) (Greenwald et al., 1996; Naccache and Dehaene, 2001).

However, even if the small but significant masked behavioral effect that we measured (4ms) did not correlate with the d' calculated in a dedicated session after the main experiment, one may still question the conscious type of this masked effect. Indeed, we did not control for cue awareness on a trial-by-trial basis. Rather, we preferred to let participants get used to the cue-target rhythmicity without interrupting them by an additional metacognitive task during the main task. One could therefore suppose that a minority of seen masked trials could have driven this small effect. In order to test this possibility, we computed RTs histograms of both masked and unmasked trials (see Figure S2, two upper graphs). Visual inspection of these

curves did not reveal any obvious bimodal distribution of masked trials. While the distribution of unmasked ‘Cue-Tgt’ RTs were largely left-shifted as compared to the one of unmasked ‘Cue-NoTgt’ RTs, the two masked cues distributions were very similar, and none of them did show a bimodal distribution. The tiny (4ms) left-shift of masked ‘Cue-Tgt’ trials as compared to masked ‘Cue-NoTgt’ trials affected the whole distributions. We computed the Hartigans’ test of unimodality (Hartigan and Hartigan, 1985) that confirmed the absence of evidence for a non-unimodal distribution in each of the four conditions (Masked/UnmaskedXCue_Tgt/Cue_NoTgt ; four p-values >0.8). These analyses do not fully discard the above mentioned hypothesis but do not support it. For the second experiment in which we discovered both a masked and an unmasked significant, we computed the very same analysis on the Cz ROI (see Figure S2, two lower graphs). Both masked and unmasked trials showed a global left-shift of CNV amplitude (more negative values) for ‘CueTgt’ than for ‘CueNoTgt’ trials. As for RTs, Hartigans’ tests confirmed the unimodal distributions of these voltage values for each of the four conditions (all p-values >0.6). Taken together, all these behavioral and EEG results support the interpretation of a genuine CNV and behavioral effect for masked cues that were not consciously perceived.

3-2-1-2 Scalp ERPs:

For unmasked trials, we observed a clear CNV, maximal in the midline electrodes (Cz,Pz), in response to Cue-Tgt cues. The critical statistical contrast between Cue-Tgt and Cue-NoTgt cues trials confirmed the significance of this CNV modulation by cue type (see Figure 2c). This Cz-Pz midline effect was maximum over the vertex (Cz ROI $p < 10^{-5}$ with a maximal effect-size of $-1.59\mu\text{V}$ at 1166ms after cue-onset (target onset), and Pz ROI $p = 0.01$ with a maximal effect-size of $-0.59\mu\text{V}$ at 888ms after cue-onset) and reached significance around 800ms after cue onset. Crucially, a smaller significant CNV effect was also observed for

masked cues. This effect was confined to the vertex region (Cz), and reached its peak of significance around 850ms after cue onset ($p=0.025$). This effect elicited by unconsciously perceived masked cues did not correlate with individual d' values obtained in the cue discrimination task. Importantly, a significant CNV was interpolated for a theoretical null d' (p -value=0.015). We noted that while masked and unmasked CNVs latencies were in the same range (840 and 812 ms), their offsets differed with an earlier offset for masked CNV (908ms) whereas unmasked CNV was still significant at target onset (1166ms).

A complementary analysis probing expectancy effects over the whole CNV time-window across all sensors confirmed the presence of a significant cluster for unmasked trials ($p=0.03$ see Figure S1a), while no such cluster could be found for masked trials in spite of CNV topography (see Figure S1b).

We then turned to source reconstruction analysis to estimate possible cortical sources of unmasked and masked scalp CNV components. **The purpose of running a source localization analysis of scalp ERPs effects here was simply to provide an indicative estimation of these neural sources, in order to bridge this experiment with iEEG data of Experiment 2b that provides robust and direct measurements of some CNV neural sources. To do so, - and as described in the M&M section -, we estimated brain sources from the grand-average differences of masked and unmasked CNV conditions. Note that we did not record precise positions of scalp electrodes with individual MRI and electrodes fiducials.** This descriptive analysis revealed that unmasked CNV had two major sources. First, we identified a sustained contribution of temporal cortices during the whole CNV period (see Figure 3). Then, a second cortical source appeared in addition to temporal cortices, around 800ms, in the mesio-frontal regions surrounding the supplementary motor area (SMA). This second source lasted until the resolution of the CNV. Interestingly, masked CNV showed a similar contribution of temporal

cortices but completely lacked the SMA source. Finally, a source located within mesio-orbitro frontal cortex was observed exclusively for the masked CNV.

Capitalizing on these scalp EEG discoveries combining a clear expectancy ERP effect for unmasked trials, with a weaker but significant and spatially more focal expectancy effect for masked trials, we moved to intra-cranial recordings that offer a unique combination of space and time resolution as well as higher signal detectability. **Note also that iEEG is not affected by the problem of eye movements artefacts that may still affect source reconstruction of scalp ERPs effects in spite of the precautions we took to discard artefacted trials (see M&M).**

3-2-2 Experiment 2b: iEEG correlates of expectancy elicited by conscious and unconscious cues

Implanted epileptic patients performed the same task as in the scalp EEG experiment. We performed both single-subject and group analyses of the behavior data of these 14 patients, while iEEG analysis was performed at the single-subject level exclusively.

3-2-2-1 Behavior

At the group-level, we replicated the classic numerical distance effect: mean RTs on correct trials were shorter for targets far from five (1 2 8 9) than for targets close to five (3 4 6 7) (effect size=25.8ms; t-test p value =0.002). Patients performed the task very accurately with a mean accuracy of 96.7% and also displayed a typical numerical distance effect on accuracy rates: they were more accurate when responding to targets far from five than to targets close to five (effect size=2.41%, t-test p value = 0.003).

Patients responded faster on trials with a 'Cue-Tgt' compared to neutral cue trials, resulting in a significant conscious priming effect (effect size = 50.3ms, t-test p value =0.005). There were

no such effects for masked ‘Cue-Tgt’ trials ($p=0.84$). Similarly to experiment 2a, no significant cueing effect was observed on error rates, neither for unmasked trials nor for masked ones (both $p>0.25$). Additionally, none of the 14 patients reported conscious experience of masked cues. On the forced-choice discrimination task, the mean d' did not differ from chance-level ($d'=0.05$, t-test against zero, $p=0.44$). Individual behavioral data are summarized in Table 1.

3-2-2-2 iEEG

We then explored unmasked and masked CNV effects by analyzing iEEG signals recorded from a total of 674 recording sites (mean of 48 per patient), with the following lobar distribution: 250 in frontal lobes, 334 in temporal lobes (either lateral or medial), and 90 in other structures (mostly in occipital and parietal lobes).

Given that masked cues elicited scarce behavioral (see Experiment 1) and early scalp EEG (see Experiment 2a) effects, we first looked for evidence of masked cue processing within early visual cortex, by comparing ERPs elicited by the relevant ‘Cue-NoTgt’ or ‘Cue-Tgt’ trials on the one hand, and by neutral cue trials on the other hand, in an early time-window following cue onset [0-200ms]. We detected significant early masked cue effects in 10 out of 62 (16.13%) occipital electrodes (4/19 in one patient; and 6/43 in a second patient; see Figure 4b).

Incidentally, visual inspection of occipital sites revealed clear iEEG oscillations at the exact rhythmic frequency (8.55Hz) of our visual paradigm (‘cue-blank-mask-blank’ repeated alternating sequence; see Figure 2a). In order to probe the spatial distribution of sites showing such a visual entrainment or steady-state response (SSR; we use indistinctly here these two expressions), we focused on control trials (in which the rhythmic pattern was repeated until target onset without interruption from a masked or unmasked instructive cue). We computed

for each recording site the mean spectral power centered on this 8.55 frequency (8-9Hz), and normalized this value to the total power within the 1-20Hz frequency band. We then calculated a Z-score for each site, in comparison to the distribution observed in the 673 remaining sites ($p \leq 0.01$ corrected for multiple comparisons with Bonferroni correction). As expected, this visual entrainment (or SSR) was mostly observed in the occipital cortex (27/62 sites = 43.5% versus 98/612 sites = 16% for all other regions: χ^2 p-value = 5.10^{-5}). Note however that this visual entrainment (or SSR) was also present in the ventral visual pathway, in parietal regions as well as in mesio-frontal structures, including the Anterior cingulate cortex (ACC) (see Figure 5a). The same analysis conducted on scalp EEG data yielded very similar patterns of results (see Figure 5b).

We then analyzed the cueing effect (Cue-Tgt versus Cue-NoTgt), respectively for the masked and unmasked conditions during the CNV window (400ms-1217ms after cue onset; see Figure 4a). In the unmasked condition, a CNV effect was observed both in the frontal lobe (30 significant electrodes on the permutation-based statistics, out of which 23 survived FDR correction, see Table 2) mostly in the SMA, the ACC, and the frontal gyrus; as well as in the temporal cortices (7 significant electrodes on the permutation-based statistics, 2 out of which survived FDR correction). These effects were sustained over the whole CNV time-window. In comparison, the masked CNV effect was mostly confined to temporal electrodes (permutation-based statistics identified 6 electrodes in the temporal lobe, and only 3 in the frontal lobe and 2 in other cortical structures). Individual results are shown in Table 3. This difference in spatial pattern between temporal/frontal regions and masked/unmasked conditions was statistically significant (Exact Fisher test comparing frontal and temporal electrodes in masked and unmasked conditions: $p=0.009$). Note also that masked effects decayed over time (see Figure 4a) whereas the SMA activation was sustained in the unmasked condition.

We then looked for inter-hemispheric asymmetry by computing Fischer's exact tests of the contingency tables related to the number of electrodes showing an expectancy effect in the left and right hemispheres respectively, across all patients (see Table 3). Interestingly, we observed a larger proportion electrodes showing a conscious expectancy effect in the left hemisphere than in the right hemisphere (20 out of 286 left hemisphere electrodes, versus 12 out of 388 right hemisphere electrodes ; p -value = 0.03). This effect difference was still significant when restricting the analysis to frontal lobe electrodes ($p=0.004$), while no effect was found in temporal lobe electrodes. Note however that much fewer electrodes showed an expectancy effect in temporal lobes as compared to frontal lobes (30 versus 7). No left/right asymmetry was observed for unconscious expectancy effects, but note again that few electrodes showed an effect.

3-3 Experiment 3: Introspection of expectancy of elicited by conscious and unconscious cues

Finally, having discovered behavioral, scalp EEG and iEEG evidence of expectancy effect elicited by masked cues, inaccessible to conscious report, we aimed at checking whether this effect was really unconscious, or if it could be accessible to conscious introspection despite the absence of conscious perception of the masked cues. Indeed, the possibility to consciously access a process elicited by a cue that in itself is inaccessible to conscious report has been postulated by several theoretical works (Dehaene and Naccache, 2001; Naccache, 2009). In other terms, in this last experiment (Experiment 3), we aimed at probing if subjects could consciously introspect the level of expectancy elicited by visible and invisible cues.

We used the same stimuli as in Experiment 1 and defined the following four conditions: 1) unmasked 'Cue-Tgt'; 2) masked 'Cue-Tgt'; 3) unmasked 'Cue-NoTgt'; 4) masked 'Cue-NoTgt'. For each of these four conditions a minority of trials (16.7%) were randomly interrupted at the precise timing when the target (or absence of a target) should have

appeared. An introspective question was presented and responses were given on a continuous scale ranging from ‘no expectancy’ to ‘maximal expectancy’. Finally, subjects performed a typical forced-choice discrimination task (see Figure 6a) to compute objective discriminability of masked cues.

None of the 26 subjects reported conscious perception of masked cues in the subjective reports collected after the main experiment. Moreover, objective performance validated these subjective reports by showing a mean d' of 0.036, not significantly different from a null d' ($p=0.68$).

In order to help subjects to introspect their target expectancy, we increased the predictability of unmasked cues (100% valid), whereas masked cues were partially predictive (75%) in order to be able to compute an objective measure (RT) of target expectancy in addition to the introspection judgment. One subject was excluded from the analysis of the priming effect because his RTs were abnormally long (mean RT=2.7s). We did not observe a significant priming effect for masked cues (effect size=0.86ms; $sd= 23.97$; t-test $p=0.86$), most probably due to a lack of power originating from the limited number of masked trials (24 ‘Cue-NoTgt’ with a target trials as compared to 128 trials in Experiment 1).

Note that the aim of Experiment 3 was not primarily to observe behavioral and neural correlates of the masked cueing effect already described in Experiments 1, 2a and 2b, but rather to check if expectancy effects elicited by masked cues could be accessible to conscious introspection.

A repeated measure ANOVA crossing cue type (2) and masking (2) showed a main effect of cue-type with larger introspection of expectancy on ‘Cue-Tgt’ trials than on ‘Cue-NoTgt’ trials ($F(1,25)=72.25$, $p<10^{-8}$), and the absence of a significant effect of visibility ($F(1,25)=0.66$; $p=0.42$). Crucially we found a strong interaction between cue type and visibility ($F(1,25)=54.58$; $p<10^{-7}$; see Figure 6b). Post-hoc tests showed that cue-type had a

strong impact in unmasked trials: introspection of expectancy was increased by 41% after an unmasked ‘Cue-Tgt’ cue as compared to an unmasked ‘Cue-NoTgt’ cue ($F(1,25)=66.08$, $p<10^{-7}$). In sharp contrast, the same test conducted on masked cue trials did not show any difference of introspection (expectancy rate difference = 1.09% ; $F(1,25)=0.85$; $p=0.37$). Given the importance of this negative result, we ran a Bayesian statistical analysis using an ‘ultra-wide’ prior regarding the directionality of expected effect. This analysis yielded a Bayesian factor supporting the null-hypothesis with moderate evidence ($BF_{0+}=3.712$).

4-Discussion

4-1 Synthesis of the main results

In a series of cueing experiments (see Table 4 for a synthesis), we probed sustained (>1 second) expectancy effects initiated by masked and unmasked cues using behavioral, high-density scalp EEG and iEEG recordings. Behaviorally, unmasked cues modulated expectancy as reflected by a strong conscious cueing effect on RTs. A small but significant cueing effect was observed in response to masked cues inaccessible to conscious report. To our knowledge, this finding is the first report of such a long (>1 second) unconscious cueing effect. High-density scalp EEG recordings revealed a large CNV effect induced and modulated by conscious cues, with a maximal amplitude in Cz but also extending to Pz: ‘Cue-Tgt’ strongly increased the CNV amplitude as compared to ‘Cue-NoTgt’ and neutral cues. Moreover, this effect increased in time up to the upcoming of the target. Crucially, a similar CNV effect was also elicited by masked cues, with a more focal topography restricted to Cz area. Intracranial EEG recordings completed this exploration by revealing the respective neural origin of unmasked and masked expectancy effects. While both unmasked and masked conditions were associated with temporal lobe generators of the CNV, including hippocampal structures, only masked trials were associated with an additional frontal generator including SMA and ACC

areas. Of interest, source reconstruction of scalp unmasked and masked CNVs were very coherent with the intracranial results. Notably, we did not identify iEEG effects in the orbitofrontal cortex for masked stimuli as estimated by source reconstruction of scalp high-density effects. This discrepancy may result from insufficient coverage of these regions in the set of implanted patients, or alternatively it may point to the limits of source reconstruction. The absence of individual MRI anatomy and of a precise localization of each scalp EEG contact supports this second hypothesis. Concerning temporal cortices, the estimated sources were mostly located outside of hippocampal structures. We also note that a reanalysis of the current iEEG datasets focusing on high-frequency broadband activities (70-150Hz) could be complementary to confirm and expand our results. Similarly, reanalyzing our scalp ERP data while focusing on beta-band activities, that were low-pass filtered here, and that contribute to timing processes is a promising perspective opened by our present findings (Köseme et al., 2014; Wiener and Kanai, 2016).

Finally, given the complex interplay existing between conscious and unconscious cognitive processes, we investigated whether the expectancy effect caused by unconsciously perceived cues was really unconscious, or if it might be accessible to introspection. Our results showed that while consciously visible unmasked cues elicited a conscious expectancy effect accessible to introspection, the unconscious expectancy effect caused by masked cues was not reportable.

We will now discuss our results in relation to conscious and unconscious expectancy effects, respectively.

4-2 Conscious expectancy

First, it is important to note that in the paradigm we used, cues predicted both target probability as well as target onset. Therefore, expectancy effects could stem from a mixture of

temporal attention and of response preparation processes that we did not dissociate in our experiments. This resulted from a methodological choice of studying a fixed temporal window between cue onset and target onset, in order to align all trials and conditions for neurophysiological measures. In spite of this limitation, our main electrophysiological results confirmed the presence of a strong CNV effect, that has been reliably identified as the main correlate of expectancy, which is interpreted as a temporal attention process (Macar and Vidal, 2009; Nobre et al., 2007; Walter et al., 1964). In the same vein, Faugeras et al. (2016) manipulated orthogonally temporal attention and motor preparation, and observed that while manipulation of the former was correlated with a modulation of the CNV, manipulation of the latter correlated with modulations of the cue-related P3 component. Therefore, it seems legitimate to interpret and discuss our findings both in terms of temporal attention and of response preparation effects.

Our results showed that expectancy effects were mainly located within frontal and temporal regions. Concerning the frontal lobe, our iEEG findings validated the SMA and ACC as being the generators of the CNV classically associated with temporal attention (Coull and Nobre, 2008, 1998; Faugeras and Naccache, 2016; Macar et al., 1999; Nagai et al., 2004). Interestingly, these regions have been shown to exhibit a phasic increase in activity at the time when the target is expected, suggesting it might be implicated in memorizing fixed time intervals (Pfeuty et al., 2003). The SMA has also been investigated as a potential neural substrate of the temporal accumulator (Casini and Vidal, 2011; Coull, 2009; Macar et al., 1999). On the response preparation side, the SMA is involved in the control of voluntary movements. Indeed, stimulating this region provokes a feeling of an urge to move. It has been proposed that the SMA is involved in the triggering of voluntary movements (Ball et al., 1999; but see Desmurget and Sirigu, 2009 for the implication of parietal networks in conscious agentivity of action), and its implication in temporal attention has also been

hypothesized within the framework of the motor theory of time representation (Coull and Nobre, 2008). Hence, our results are consistent with both an amplification of the temporal processing network, and with preparatory processes (Vallesi et al., 2009). In the present study, we discovered a left SMA predominance for the conscious expectancy effect. This finding seems congruent with previous works that reported a left lateralized network for the orientation of temporal attention, including left parietal sulcus, left cerebellum and left lateral inferior premotor cortex (Coull and Nobre, 2008, 1998). This left SMA predominance should be confirmed by additional studies, including MEG and fMRI recordings in non-epileptic healthy volunteers. An alternative interpretation of the SMA activity we report could be linked to motor preparation during the cue-target interval: could this SMA generator correspond to a *bereitschaft* potential (or readiness potential) rather than to a CNV (Kornhuber and Deecke, 1965). Notably, the cue onset did not convey any information about the upcoming left/right hand response to the target stimulus. Moreover, a rich literature reported motor response activation by masked stimuli, such as readiness potential, lateralized readiness potential (LRP) (Boulenger et al., 2008; Dehaene et al., 1998; Eimer and Schlaghecken, 1998; Neumann and Klotz, 1994). Therefore, one could have predicted that also masked cues should have elicited a subliminal motor preparation process. Taken together, these elements suggest that the SMA effect, exclusively present for unmasked stimuli, reflects a voluntary and conscious expectancy effect rather than a target-related non lateralized motor preparation effect. Additionally, in the context of the motor theory of time representation, these two hypotheses are not mutually exclusive. In order to disentangle between these two classes of interpretation, our approach should be reproduced while using non-motor expectancy tasks.

The second region correlated with the conscious cueing expectancy effect was the temporal lobe. Some electrodes showing such an effect were located within the hippocampal regions. This finding could be interpreted in the light of the mandatory implication of the hippocampus in bridging two stimuli separated by a temporal gap such as in the trace conditioning paradigm (Clark and Squire, 1998; Bekinschtein et al., 2009). Additionally, the hippocampus has also been shown to play a role in the explicit learning of the causal relation linking two stimuli (Bechara et al., 1995). Moreover, Faugeras et al. (2016) used source reconstruction on high-density scalp EEG to postulate the implication of temporal regions in the generation of the CNV elicited by consciously perceived cues. Note also that recent intracranial recordings in rodents have discovered the existence of time cells, similar to place cells, in the hippocampus and in the entorhinal cortex that seem to discharge for specific time intervals and might be implicated in trace conditioning learning, during the learning of paired stimuli that are separated by a time interval (Eichenbaum, 2014; MacDonald et al., 2011; Tsao et al., 2018)

In contrast with our expectations, we found only a single electrode showing a significant effect in parietal cortex, a region that is classically included in the temporal attention network (Coull and Nobre, 1998). This lack of effect in parietal cortex probably resulted from the low coverage of this lobe in our population of iEEG patients. Indeed, scalp EEG topography of the conscious expectancy effect extended over parietal regions.

Overall, the strong implication of the ACC and the SMA is consistent with an anticipatory effect and with the involvement of temporal attention and preparation processes. However, the absence of parietal effects usually found in the attentional network is surprising. Testing our paradigm with patients implanted specifically in the left parietal region could better inform us on the implication of the attentional network in our effect.

4-3 Unconscious expectancy

Behaviorally, we observed a small (4.0ms) but significant masked cueing effect in the first experiment that included both the ‘Cue-Tgt’ followed by a target condition, and the ‘Cue-NoTgt’ followed by a target condition. This masked cueing effect occurred for a SOA exceeding a second, and the cues were not perceived consciously. Indeed, both subjective and objective (d') measures, as well as the absence of correlation between objective visibility and cueing effects confirmed the absence of conscious perception of the cues.

In the EEG and iEEG experiments, we did not include the ‘Cue-NoTgt’ followed by a target condition in order to maximize the impact of the ‘Cue-NoTgt’, and therefore increase the EEG/iEEG differences between ‘Cue-Tgt’ and ‘Cue-NoTgt’ trials. Accordingly, we found a trend of a masked cueing effect in the EEG group when contrasting ‘Cue-Tgt’ trials with neutral cue trials, and no effect in the iEEG group. The last experiment was conceived to probe the modulation of subjective expectancy by unmasked and masked cues, and only included a limited number of trials (24) with a ‘Cue-NoTgt’ followed by a target. This probably decreased the power to detect a masked cueing effect.

We used a heavy visual masking procedure which efficiency was validated by the null d' values, and the absence of a correlation between the small but significant masked behavioral effect (4ms) and the d' calculated in a dedicated session after the main experiment. However, we did not control for cue awareness on a trial-by-trial basis. Rather, we preferred to let participants get used to the cue-target rhythmicity without interrupting them by an additional metacognitive task during the main task. Therefore, a potential confound might be that a minority of seen masked trials could have driven this small effect. In order to test this possibility, we computed RTs histograms of both masked and unmasked trials (see Figure S2, two upper graphs). Visual inspection of these curves did not reveal any obvious bimodal distribution of masked trials. While the distribution of unmasked ‘Cue-Tgt’ RTs were largely

left-shifted as compared to the one of unmasked ‘Cue-NoTgt’ RTs, the two masked cues distributions were very similar, and none of them showed a bimodal distribution. The tiny (4ms) left-shift of masked ‘Cue-Tgt’ trials as compared to masked ‘Cue-NoTgt’ trials affected the whole distribution. These analyses do not fully discard the above mentioned hypothesis but do not support it. For the second experiment in which we discovered both a masked and an unmasked significant effects, we computed the very same analysis on the Cz ROI (see Figure S2, two lower graphs). Both masked and unmasked trials showed a global left-shift of CNV amplitude (more negative values) for ‘CueTgt’ than for ‘CueNoTgt’ trials. Taken together, all these behavioral and EEG results support the interpretation of a genuine CNV and behavioral effect for masked cues that were not consciously perceived.

The last experiment suggested that this unconsciously elicited expectancy effect could not be accessible to conscious introspection.

One potential reason for the small size of the masked cueing effect may be related to the weak engagement of endogenous temporal attention during the presentation of masked cues. Indeed, we chose to present the cues with a variable temporal interval separating them from the fixation point, in order to avoid any possible temporal prediction triggered by the fixation point itself. However, this might have impaired the treatment of the masked cues. Indeed, Naccache et al. (2002) showed that when masked cues are not presented at a fixed time in a flow of stimuli, attention cannot be oriented towards the moment of appearance of the cue and this results in poorer processing of the masked cue and reduced priming effects. This effect has been replicated in other behavioral and ERP studies (Kiefer and Brendel, 2006). In our paradigm, since masked cues appear at random intervals, it is possible that they are not fully attended and thus their influence is limited.

From a neurophysiological point of view, we were able to track the processing of masked cues in cortical networks from their entrance into the occipital regions up to their impact on

the CNV brain signal. We observed an early perceptual effect of masked cues in the occipital cortex, as well as a CNV effect. Scalp topography of masked CNV effect revealed a more focal effect (confined to Cz region) as compared to the conscious CNV that spread to parietal areas. Similarly, iEEG recordings revealed the existence of temporal lobe generators of the unconscious CNV, whereas the conscious CNV resulted from a combination of both temporal and frontal generators. In agreement with our finding of an unconscious modulation of hippocampal activity during the cue-target interval, hippocampal activations have been reported during unconscious relational encoding using masked words (Duss et al., 2014).

These spatial differences are in line with the global workspace (GW) model of conscious access. According to this theory, unconscious representations are confined to specific regions, whereas conscious representations are characterized by wide-spread neural effects and recurrent loops within a brain-scale network including fronto-parietal areas (Dehaene et al., 2006; Dehaene and Naccache, 2001). Interestingly, previous works showed that visual and auditory perception of various stimuli (e.g.: words, numbers, sounds) followed a two-stage model: an initial unconscious stage of processing, followed by a late conscious stage of processing within GW structures (Bekinschtein et al., 2009; Gaillard et al., 2009; Rohaut et al., 2015; Sergent and Dehaene, 2004; Sergent and Naccache, 2012). Similarly, our current results could be integrated into a two-stage model of expectancy: first, an unconscious and non-intentional expectancy effect could be generated within temporal structures (including hippocampal regions), whereas a second, later and sustained conscious and intentional expectancy effect would be processed in the frontal lobe, in particular within SMA and ACC regions. This hypothesis is compatible with the proposal of Desmurget and Sirigu (2009) that an intentional action would follow a non-conscious stage.

We conclude by noting that while this work was partly inspired by our previous findings about CNV in non-communicating DOC patients (Faugeras et al., 2012; Sergent et al., 2017),

the present results do not translate immediately into a new clinical test. However, they cast some light on the physiology of conscious and unconscious expectancy processes. For instance, the presence of a lasting Fz-Cz centered CNV component for SOA exceeding one second whose cortical sources are located within the frontal lobe (including SMA and ACC regions) could potentially be informative of a cognitive expectation related to consciously accessed stimuli.

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Conflict of interest

The authors declare that they have no conflict of interest.

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Figure Legends

Figure 1: Behavioral masked & unmasked expectancy effects

(a) Experimental paradigm: sequences of visual events are shown for the six types of trials. Each trial began with a fixation cross presented for 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a 'Cue-Tgt' or 'Cue-NoTgt', followed by a blank or a target (W) according to the six possible types of trials.

(b) Box-plots of individual mean unmasked (left) and masked (right) reaction times (ms) cueing effects ('Cue-NoTgt'-'Cue-Tgt'). Subjects showed a strong priming effect for unmasked cues ($p < 0.001$ ***), as well as a significant but smaller priming effect for masked cues ($p < 0.05$ *).

Figure 2: Scalp EEG masked and unmasked expectancy effects

(a) Experimental paradigm: sequences of visual events are shown for the five types of trials. Each trial began with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a 'Cue-Tgt' or 'Cue-NoTgt', followed by a blank or a target (W) according to the five possible types of trials.

(b) Numerical distance effect is shown on RTs and accuracy. Error bars represent standard error.

(c) ERP effects are shown for the four ROIs (Fz,Cz,Pz,Oz). Averaged ERP waveforms are displayed for 'Cue-Tgt' (red), 'Cue-NoTgt' (green) and neutral cue (blue) in the unmasked and masked conditions. First and second vertical dashed lines indicate the appearance of cue and target respectively. Bold line marks the significance of 'Cue-Tgt' versus 'Cue-NoTgt' conditions ($p < 0.05$ using a permutation-based temporal cluster statistics, see M&M), on a minimum of 10 successive samples (40ms)). Scalp topographies were computed on the time-window of significance for the Cz ROI prior to target onset, respectively for unmasked (812-1116ms) and masked conditions (840-908ms).

Figure 3: Sources of masked and unmasked scalp-recorded Contingent Negative Variation (CNVs)

Using the weighted minimal norm method proposed by Brainstorm toolbox (Matlab®), we computed the cortical sources of masked (left panel) and unmasked (right panel) scalp-recorded CNVs during the cue-target time window. If both conditions showed a sustained contribution of temporal lobe sources, only unmasked cues elicited a later effect originating from mesio-frontal structures including the supplementary motor area (SMA) (see top and low panels).

Figure 4: Intra-cranial EEG masked and unmasked expectancy effects

(a) Timing of unmasked and masked cueing effects are shown: each black dot represents an electrode. Significant effects ('Cue-Tgt' vs 'Cue-NoTgt' conditions) are colored (red for $p_{\text{corr}} < 0.05$ and yellow for $0.05 < p_{\text{corr}} < 0.1$). Top (unmasked) and bottom (masked) left images summarize significant effects across the Contingent Negative Variation (CNV) time-window (400-1217ms). The time course of this effect is presented in six successive time-windows from 0ms to 1200ms after cue onset (bins of 200ms).

(b) The central panel replicates the left images of figure 4a. For six representative electrodes, the time-course of averaged iEEG signal is shown for the three conditions (red – 'Cue-Tgt', green – 'Cue-NoTgt', and blue – neutral cue), both for unmasked and masked conditions separately. The two dashed lines mark the appearance of the cue and target respectively. Five of these electrodes (tagged with red axes), show significant cueing effects indexed by a horizontal black line ('Cue-Tgt' vs 'Cue-NoTgt' with $p_{\text{corr}} < 0.05$). The occipital electrode (right panel with a black axis) presents early cue-related ERPs. Rhythm of visual stimulation (cue-blank-mask-blank sequence) is represented by small vertical segments on the X-axis (8.55Hz). Horizontal red and green lines indicate significant differences ($p < 0.05$) between masked 'Cue-Tgt' (green) and masked 'Cue-NoTgt' (red) trials as compared to neutral cue trials.

Figure 5: Intracranial EEG and scalp EEG visual entrainment or steady-state response

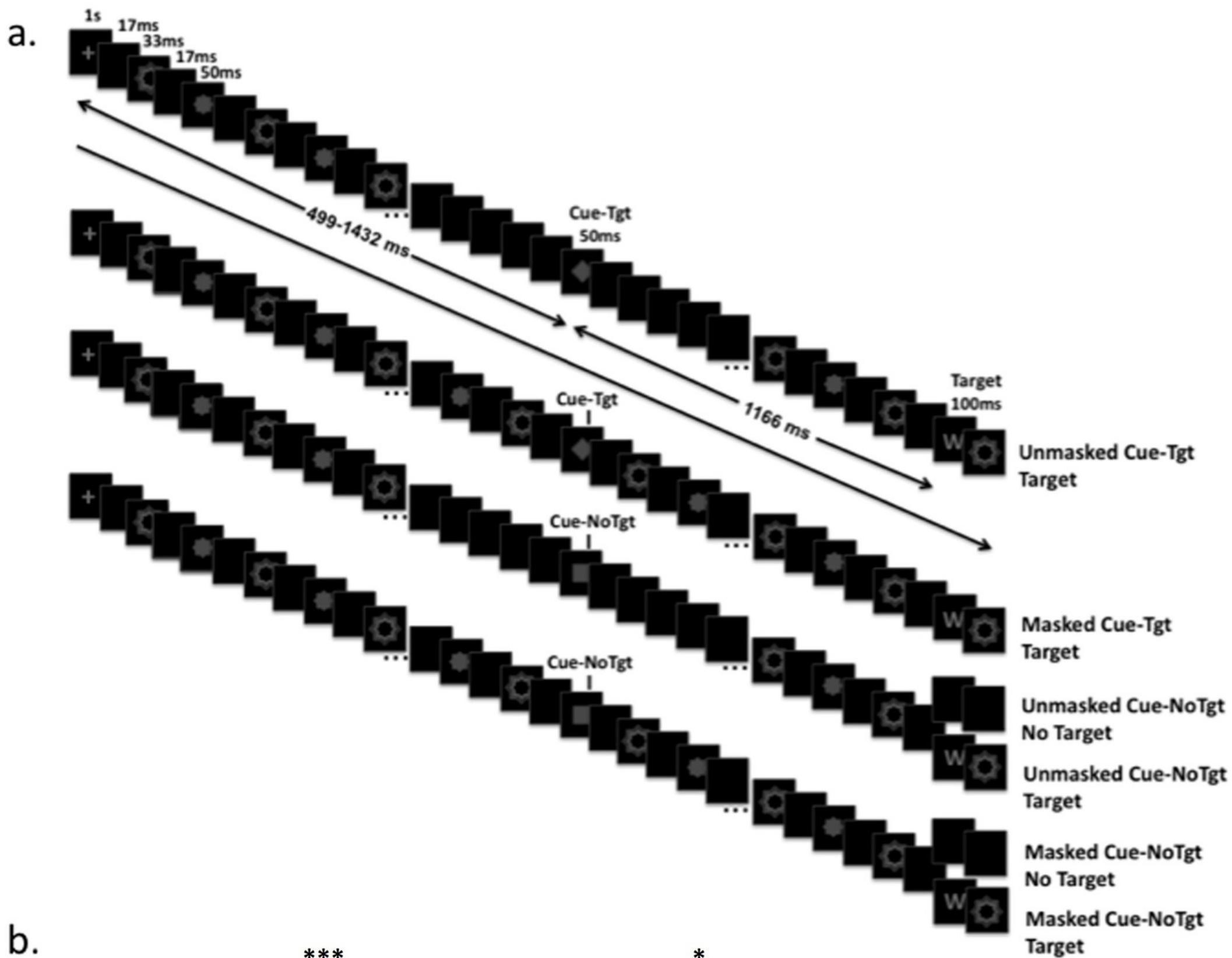
Visual entrainment effects (or SSR) were observed in iEEG data (a): the top-left view shows the relative spectral power of all contacts for the 8.55Hz frequency (visual stimuli frequency), and the bottom-left view shows electrodes resisting the Bonferroni correction at $p \leq 0.01$ (red electrodes). Right corresponding panels shows averaged ERPs elicited in the neutral cue condition in four representative electrodes with and without significant visual entrainment (or SSR). A similar analysis is presented in the right panel (b) on scalp EEG recordings: the top topography shows the relative spectral power for the 8.55Hz frequency, while the bottom topography displays the positive Z scores. Left panels presented three representative averaged ERPs curves elicited in the neutral cue condition with and without visual entrainment (or SSR).

Figure 6: Introspection of masked & unmasked subjective expectancy

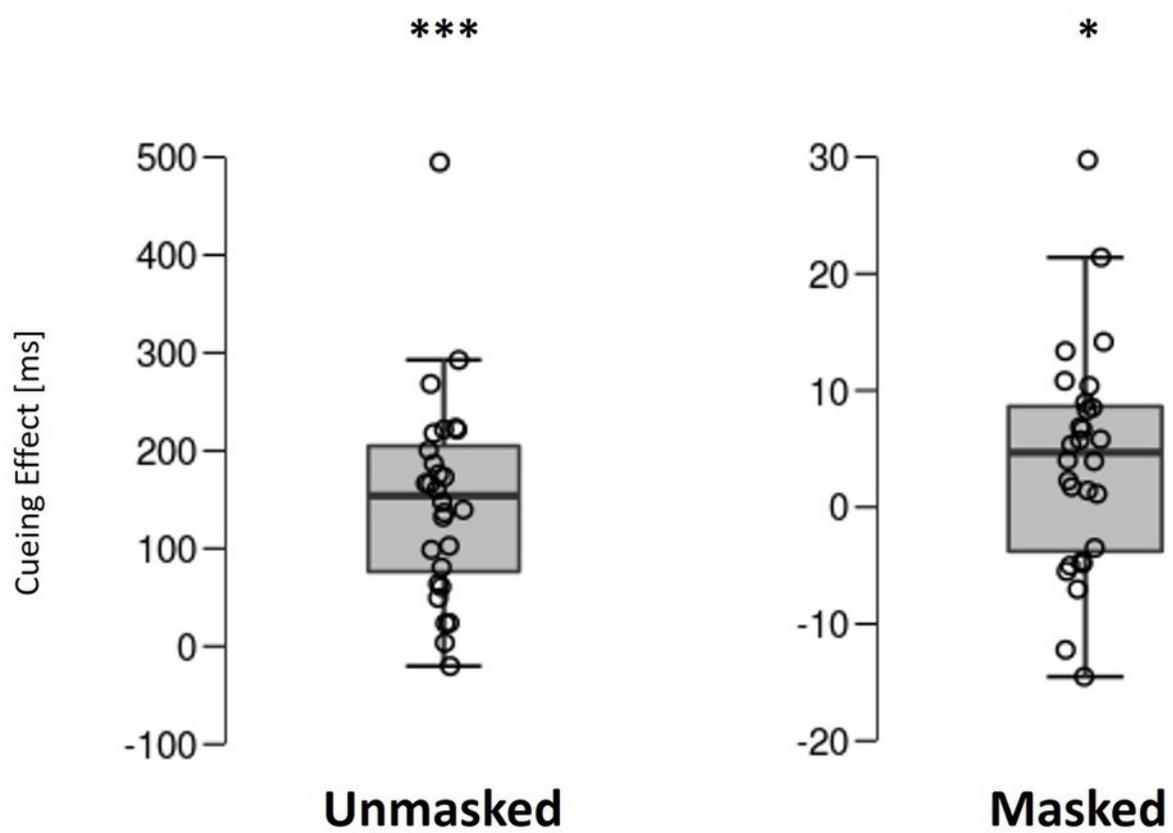
(a) Sequences of visual events are shown for the six types of trials. Each trial began with a fixation cross presented 1s followed by the repetition of the following pattern: blank (17ms), mask (33ms), blank (17ms) and neutral cue (50ms), interrupted by the presentation of a 'Cue-Tgt' or 'Cue-NoTgt' followed by a blank or a target (W) according to the six possible types of

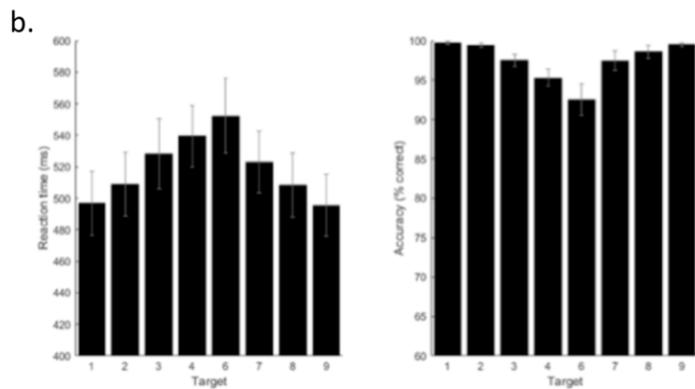
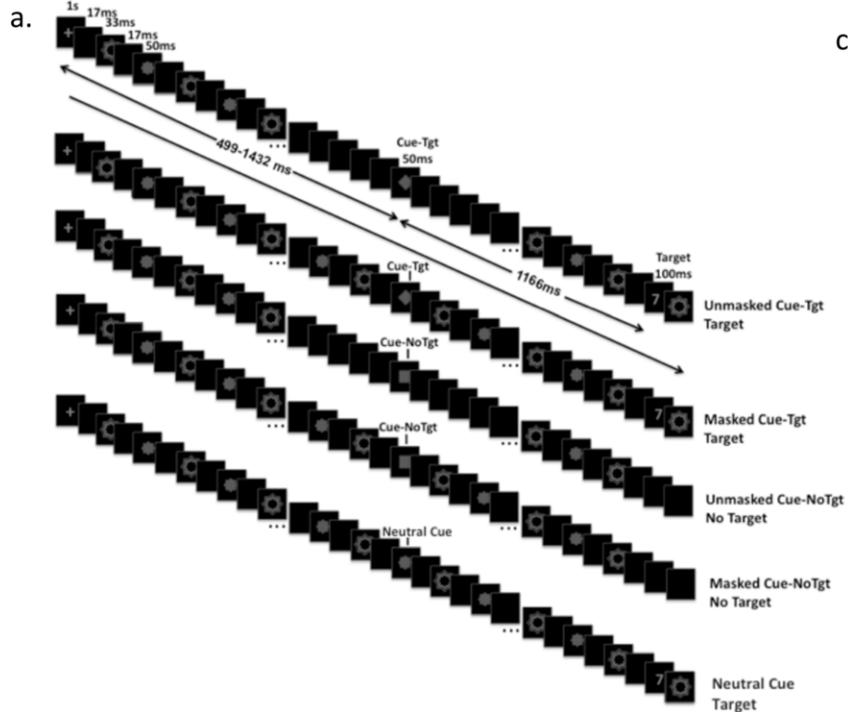
trials. One trial out of six was interrupted at the supposed moment of appearance of the target or blank and subjects were asked to rate their expectancy using a scale like the one presented at the bottom of this figure.

(b) Mean expectancy score is shown as a function of masking and of cue type (green and red for 'Cue-NoTgt' and 'Cue-Tgt' respectively). Subjects presented a strong expectancy effect for unmasked cues ($p < 0.001$ ***), but did not show any significant expectancy effect for masked cues (ns).

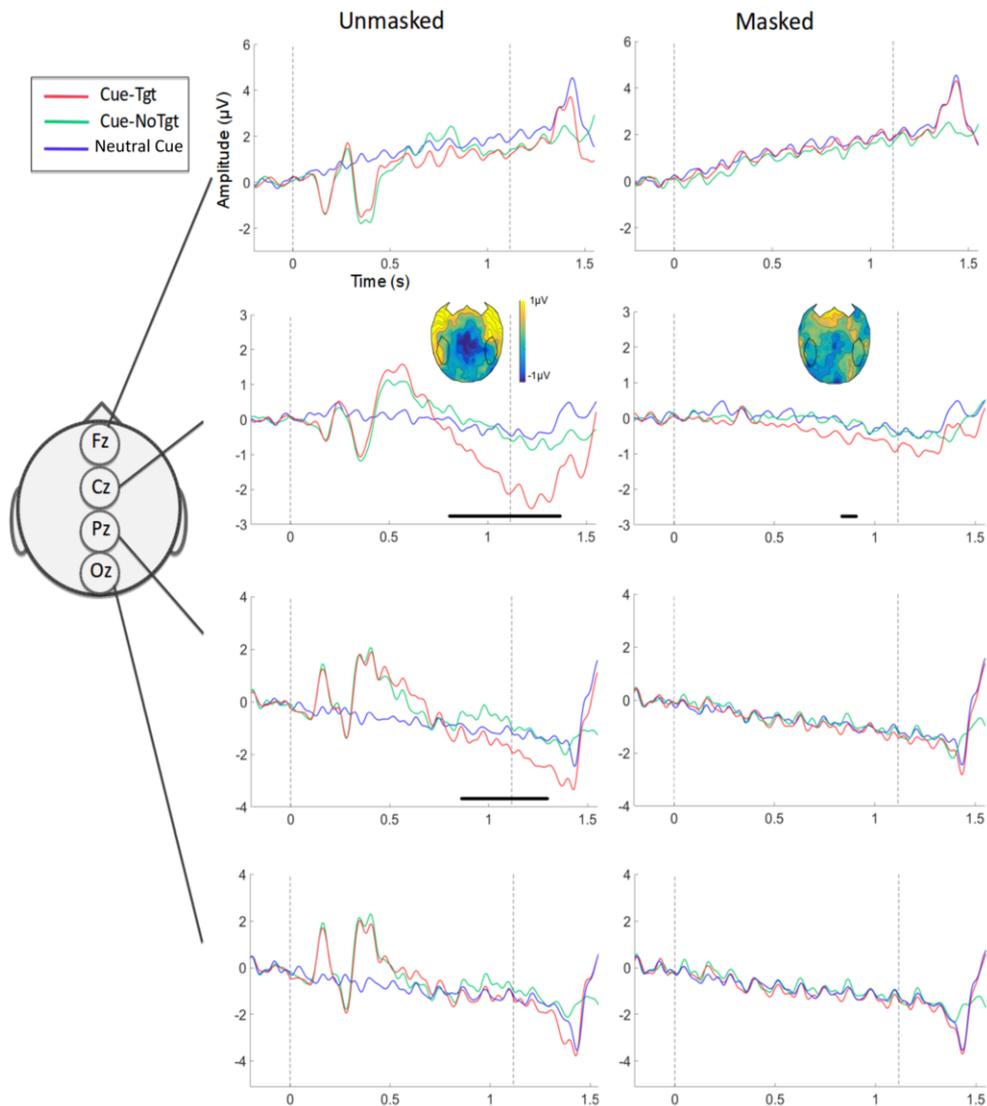


b.

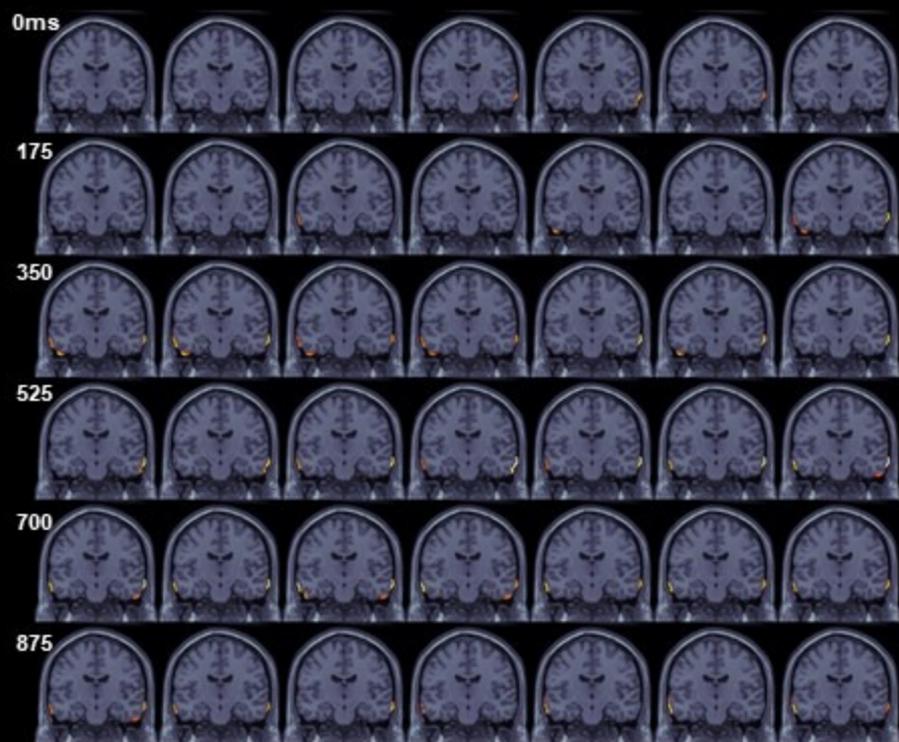




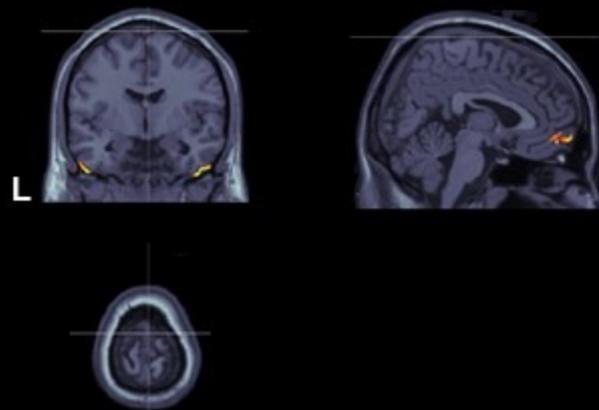
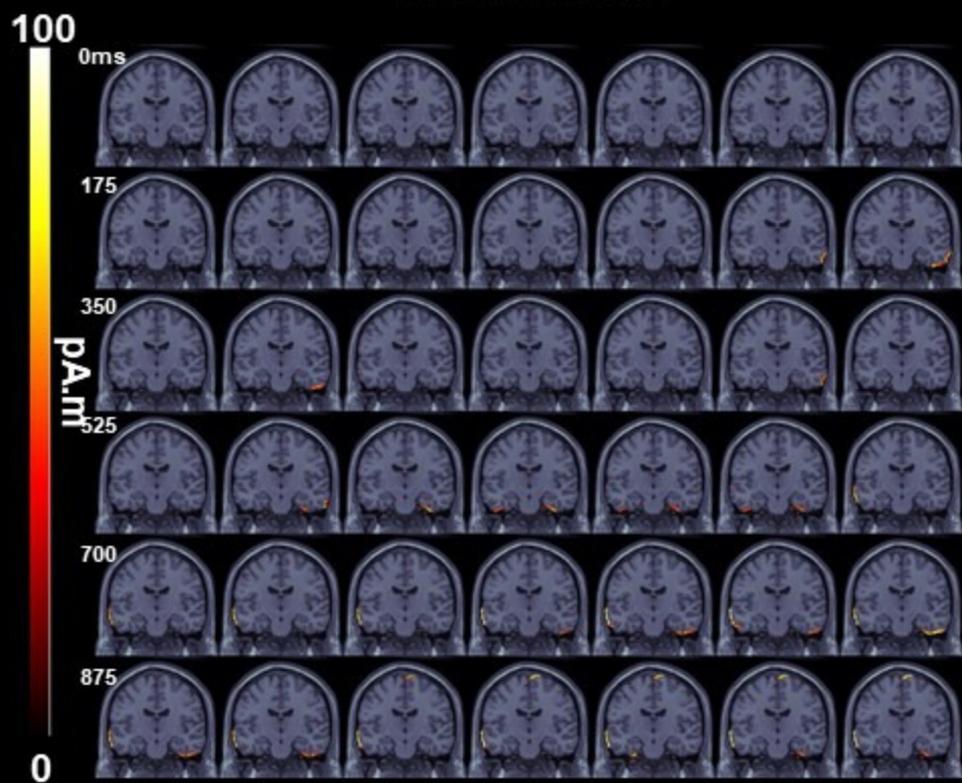
c.



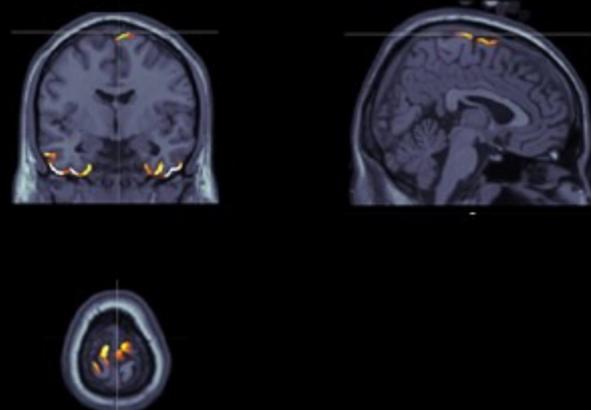
Masked CNV

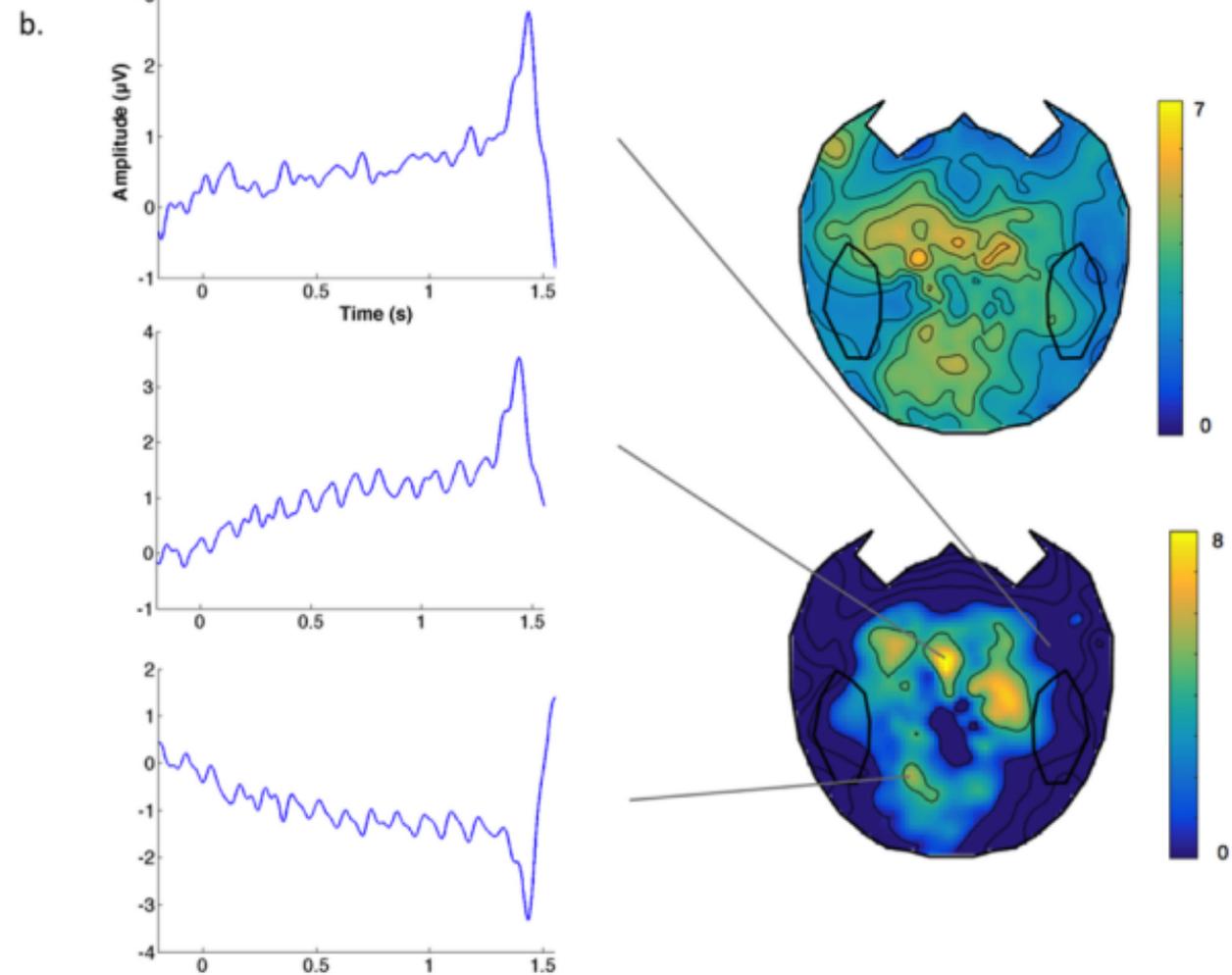
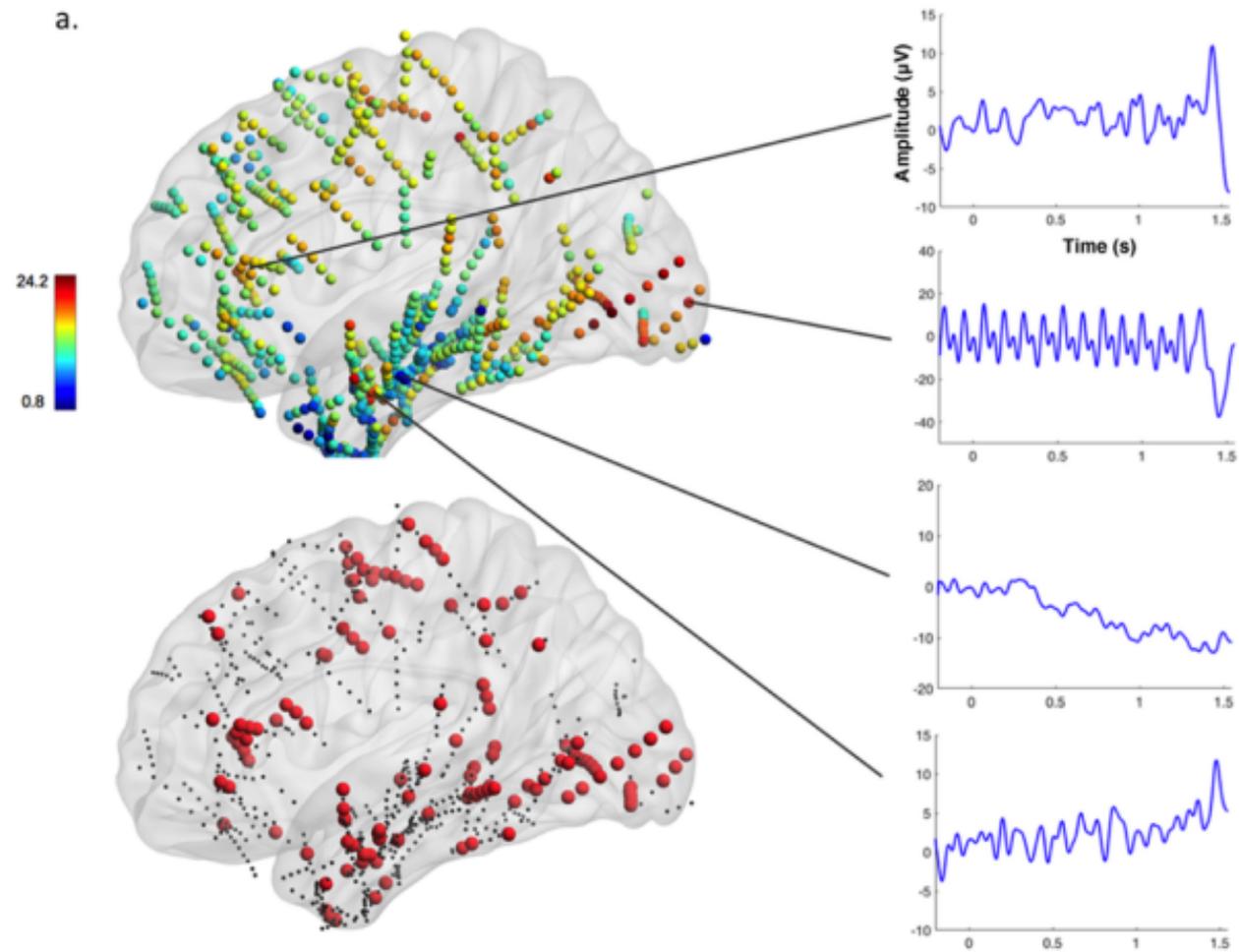


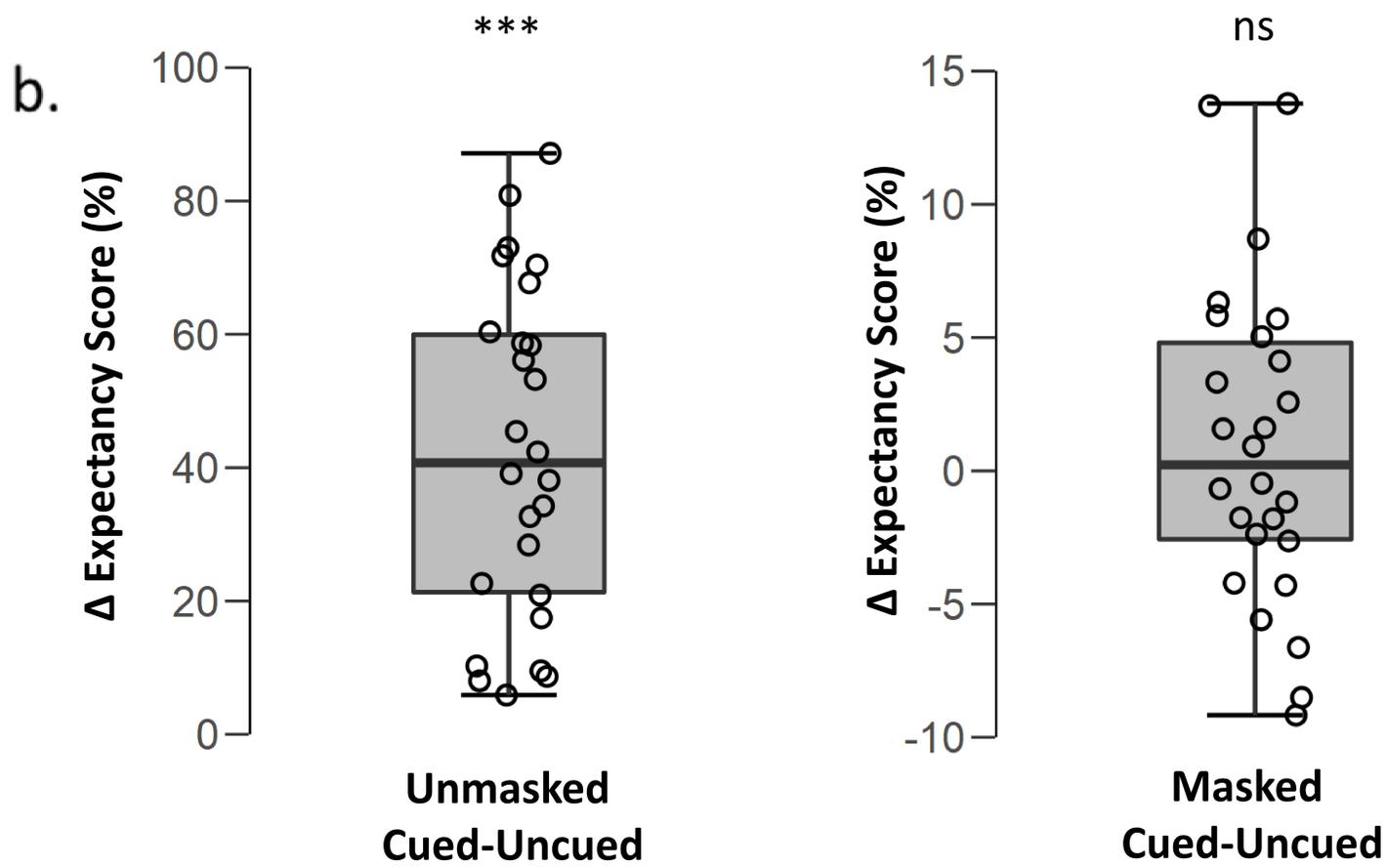
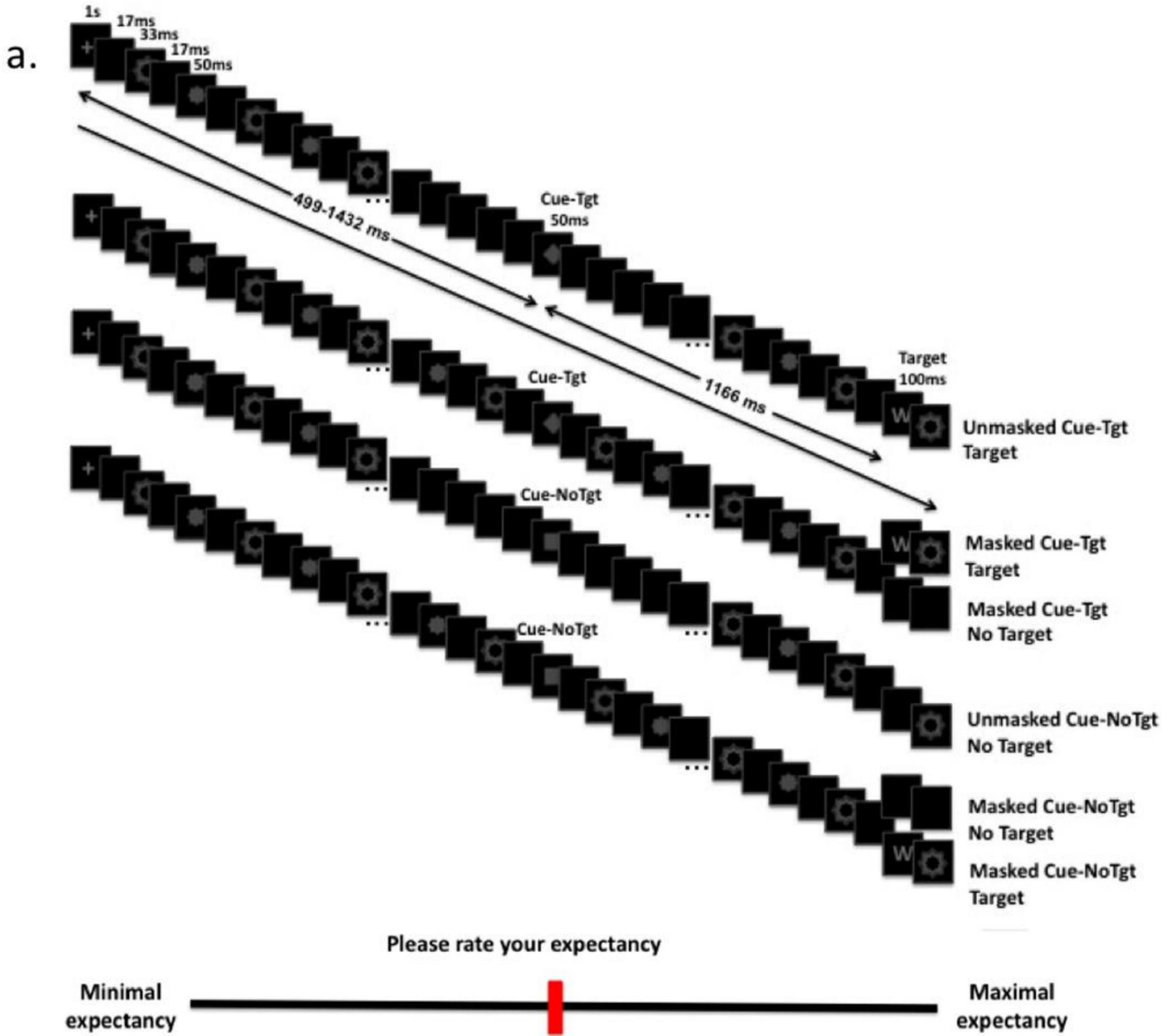
Unmasked CNV



MNI: 3 -13 82
1000ms







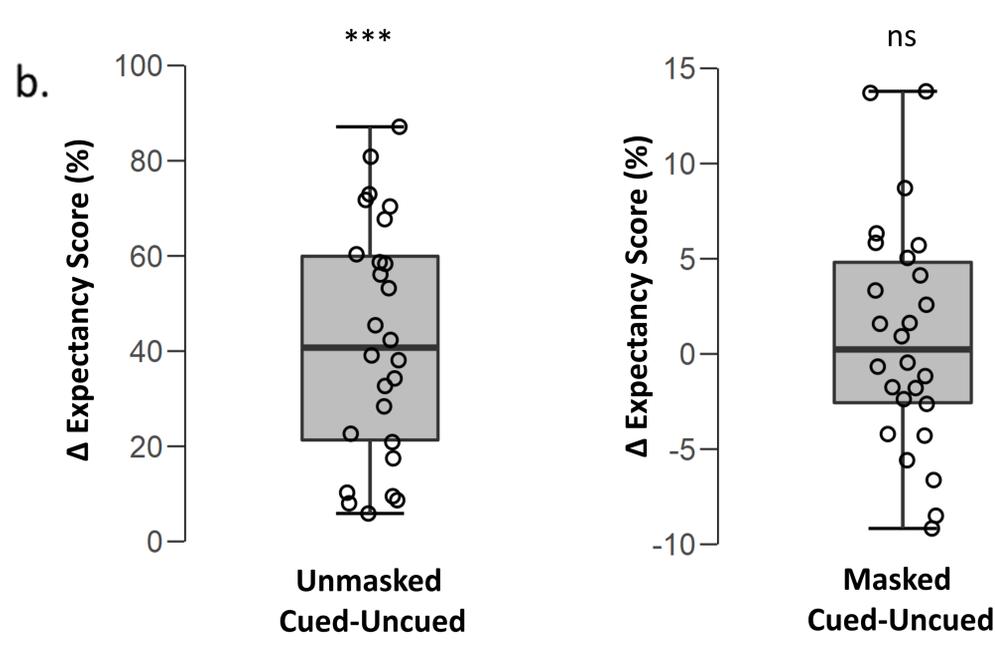
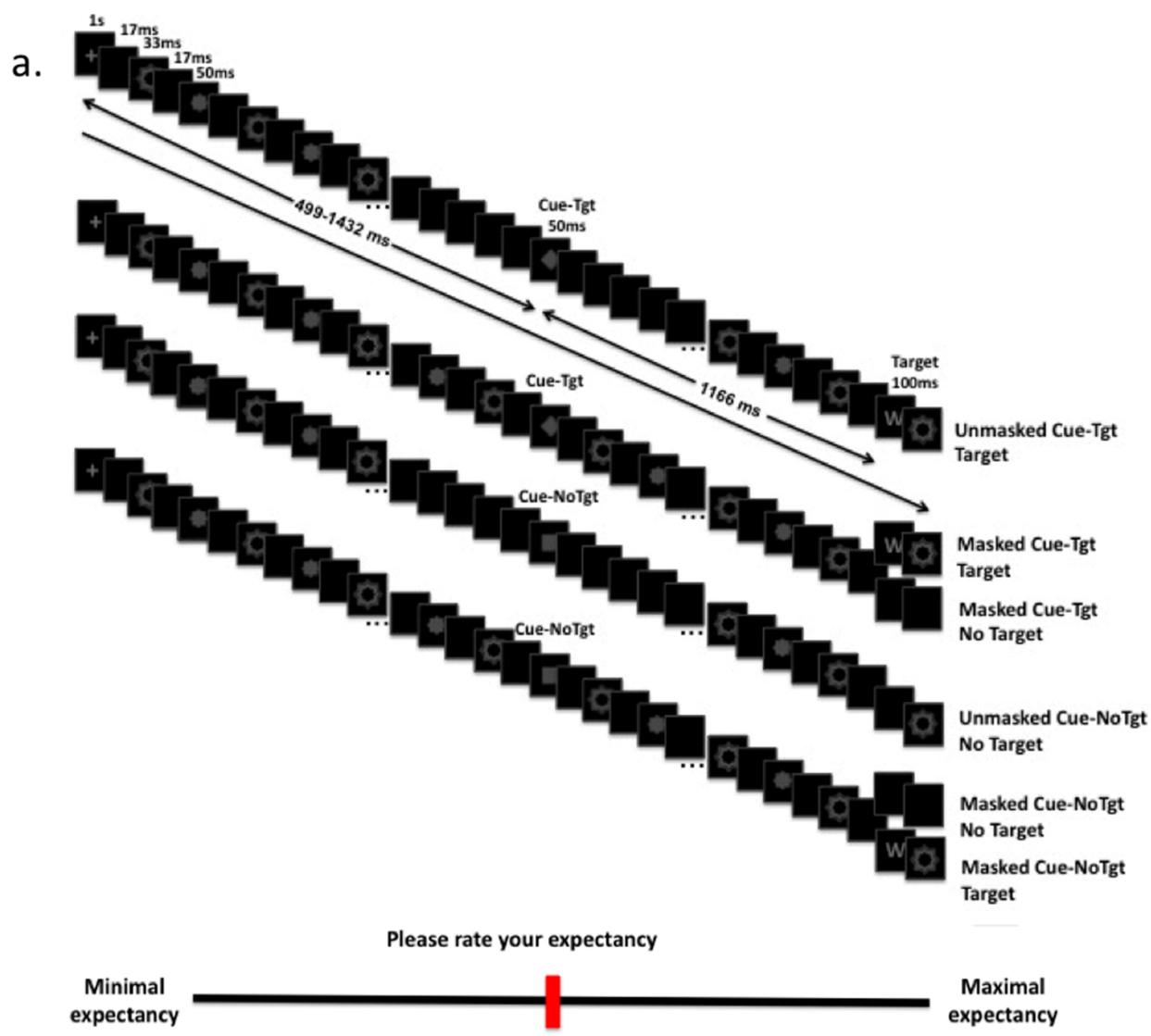


Table 1. Individual behavioral results of iEEG patients.

Patient Nb	d prime		Unmasked priming effect		Masked priming effect	
	Value	Chi2	Effect size (ms)	p value	Effect size (ms)	p value
1	-0.40	0.11	123.77	1E-10	-2.77	0.86
2	0.30	0.23	-24.98	0.21	-55.31	0.03
3	0.09	0.78	0.53	0.97	-24.57	0.09
4	0.30	0.23	24.74	0.10	-1.89	0.91
5	0.00	1.00	96.81	2E-05	27.35	0.19
6	0.46	0.07	49.94	0.10	46.71	0.09
7	-0.05	0.84	108.11	0.01	24.80	0.56
8	0.20	0.42	-24.53	0.48	-13.53	0.71
9	0.15	0.54	16.17	0.20	-28.64	0.13
10	0.20	0.42	110.96	3E-03	43.99	0.23
11	0.05	0.84	119.33	2E-13	5.90	0.73
12	-0.10	0.69	40.81	0.02	-2.93	0.87
13	-0.11	0.67	-10.85	0.47	-12.08	0.45
14	-0.42	0.10	73.77	3E-09	13.71	0.28

Table 2. Anatomical location of iEEG effects.

Unmasked effects				
Coordinates			Subject Number	Anatomical Labels
x	y	z		
53,6	-42	-9,6	14	posterior middle temporal gyrus
-17,1	-21,1	69,5	11	dorsal precentral gyrus
52,2	-18,9	-3,65	14	banks of superior temporal sulcus
58,2	-18,6	-24,65	14	medial inferior temporal gyrus
-21,2	-18,5	72,05	11	dorsal precentral gyrus
-8,1	-15,5	68,7	11	posterior paracentral lobule
-4,85	-15,2	64,55	11	posterior paracentral lobule
-14,8	-15,1	77,6	11	dorsal precentral gyrus
-12,6	-12,6	40	11	posterior cingulate cortex
-16,8	-10,2	42,6	11	white matter near posterior-cingulate cortex
-20,9	-8	46,05	11	dorsal precentral gyrus
30,9	-7,35	-39,95	14	anterior fusiform gyrus
-36,7	-6,4	57,9	11	dorsal precentral gyrus
-25,5	-5,65	49,55	11	dorsal precentral gyrus
12	-5,05	58,6	7	sma
-31,4	-4	55	11	dorsal precentral gyrus
-39,8	-3,7	-21,35	2	white matter near amygdala
-30,2	-3	52,2	11	dorsal precentral gyrus
-26,2	-1,8	52,2	11	dorsal precentral gyrus
34,35	-1,35	55,3	1	dorsal precentral gyrus
-34,3	-1	55	11	caudal middle frontal gyrus
37,6	-0,5	60,45	1	dorsal precentral gyrus
13,8	0,1	62,6	1	sma
40,3	0,3	65,35	1	dorsal precentral gyrus
-38,5	0,9	57,85	11	caudal middle frontal gyrus
13,7	1,2	41,1	7	caudal anterior cingulate cortex
-7,95	3,6	43,9	11	median cingulate cortex
-7,15	4,5	64,4	11	sma
-10,5	8,8	65,45	11	sma
-13,9	13	65,95	11	sma
35	27,9	32,15	14	white matter near dlpc
49,45	-51,7	-14,15	13	medial inferior temporal cortex
-1,65	-14,5	59,4	11	sma
-59,6	-15	-22,45	10	anterior middle temporal gyrus
-8,4	-15	37,35	11	Posterior cingulate cortex
19,7	-0,8	65,65	7	sma
11,65	28,4	-30,25	14	medial orbital frontal cortex
Masked effects				
Coordinates			Subject Number	Anatomical Labels
x	y	z		
33,45	-80,7	21,45	13	middle occipital gyrus
-44,9	-33,6	53,95	12	dorsal postcentral gyrus
37,55	-15,6	-32,9	4	parahippocampal gyrus
16,05	-3	61,85	7	sma
48,2	37,05	-7,2	6	pars orbitalis
-24,3	-3,05	-23,35	2	amygdala
52,15	48,85	-5	5	ventrolateral prefrontal cortex
44,1	-18,5	-19,5	4	parahippocampal gyrus
48,3	-14,6	-29,4	4	anterior fusiform gyrus
-34,4	-6,8	-26,15	4	parahippocampal gyrus
-54,9	6,35	-34,75	3	anterior middle temporal gyrus

Electrodes are sorted according to the Y (posterior-anterior) axis of the MNI system. Grey shaded lines correspond to: p -values ≤ 0.05 ; and non-shaded lines to $0.05 < p$ -values ≤ 0.1 .

Table 3. Individual iEEG results.

Patient Nb	Nb of electrodes				Nb of electrodes showing an unmasked effect ($p \leq 0.1$)				Nb of electrodes showing an masked effect ($p \leq 0.1$)				Nb of electrodes showing an unmasked effect ($p \leq 0.05$)				Nb of electrodes showing an masked effect ($p \leq 0.05$)			
	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other	All	Frontal	Temporal	Other
1	42	42	0	0	4	4	0	0	0	0	0	0	4	4	0	0	0	0	0	0
2	50	30	20	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0	1	0
3	51	7	44	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0
4	68	7	61	0	0	0	0	0	4	0	4	0	0	0	0	0	1	0	1	0
5	37	21	14	2	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
6	66	7	59	0	0	0	0	0	1	1	0	0	0	0	0	0	1	1	0	0
7	49	49	0	0	3	3	0	0	1	1	0	0	2	2	0	0	1	1	0	0
8	48	0	48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	26	0	9	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	39	0	20	19	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
11	45	45	0	0	21	21	0	0	0	0	0	0	19	19	0	0	0	0	0	0
12	37	22	6	9	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	1
13	51	0	8	43	1	0	1	0	1	0	0	1	0	0	0	0	1	0	0	1
14	65	20	45	0	6	2	4	0	0	0	0	0	6	2	4	0	0	0	0	0
All	674	250	334	90	37	30	7	0	11	3	6	2	32	27	5	0	6	2	2	2
L/R	286/388	120/130	147/187	30/60	23/14*	21/9*	2/5*	0/0	4/7	0/3	3/3	1/1	20/12*	19/8*	1/4	0/0	2/4	0/2	1/1	1/1

Number of electrodes in the left (L) and right (R) hemispheres is indicated, as well as significant L/R asymmetry (* for Fisher's exact test with a p -value ≤ 0.05).

Table 4. Synthesis of the four experiments.

Exp. #	Nb of subjects	Contrasts	Electrophysiology	Main results
1	28	CueTgt vs CueNoTgt	no	Masked and unmasked behavioral cueing effects
2a	16	<u>Bhv</u> : CueTgt vs NoCue <u>Cue-Tgt ERPs</u> : CueTgt vs CueNoTgt	HD-EEG	Masked and unmasked CNVs
2b	14	<u>Bhv</u> : CueTgt vs NoCue <u>Cue-Tgt ERPs</u> : CueTgt vs CueNoTgt	iEEG	<u>Temporal cortex</u> : masked and unmasked CNV <u>SMA</u> : only for unmasked CNV
3	26	CueTgt vs CueNoTgt	No	Introspection of unmasked cues trials No introspection of masked cues trials