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Fast unconscious processing of emotional stimuli in early stages of the visual cortex

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Abstract

Several cortical and subcortical brain areas have been reported to be sensitive to the emotional content of subliminal stimuli. However, the timing of these activations remains unclear. Our scope was to detect the earliest cortical traces of visual unconscious processing by recording event-related potentials (ERPs) from 43 participants. Subliminal spiders (emotional) and wheels (neutral), sharing similar low-level visual parameters, were presented at two different locations (fixation and periphery). The differential (peak to peak) amplitude from CP1 (77 milliseconds from stimulus onset) to C2 (100 milliseconds), two early visual ERP components originated in V1/V2 according to source localization analyses, was analyzed via Bayesian and traditional frequentist analyses. Spiders elicited greater CP1-C2 amplitudes than wheels when presented at fixation. This fast effect of subliminal stimulation -not reported previously to the best of our knowledge- has implications in several debates: i) the amygdala cannot be mediating these effects, ii) latency of other evaluative structures recently proposed, such as the visual thalamus, is compatible with these results, iii) the absence of peripheral stimuli effects points to a relevant role of the parvocellular visual system in unconscious processing.

Introduction

Our nervous system unconsciously and continuously monitors the environment so salient stimuli -which are, by definition, emotional- may be detected preattentively or, in other words, without consuming controlled, limited brain resources (Carretié 2014). Such unconscious detection requires the access of the emotional visual input to perceptual brain mechanisms -so it can be identified as a function of its shape, color, motion pattern, etcetera- as well as to evaluative structures -so it is marked as emotional/salient if pertinent-. In this regard, affective neuroscience has revealed several brain areas involved in both evaluation and perception to be modulated by the emotional content of subliminal stimulation. Among the former, the activity of the amygdala increases in response to unconsciously perceived emotional stimuli - mainly faces- as compared to neutral ones (see reviews by Diano et al. 2017; Öhman 2002). Other brain structures often linked to emotional evaluation, such as the insular or the anterior cingulate cortices, have shown a similar behavior as well (see a meta-analysis in Brooks et al. 2012). Among perceptual structures, the sensitivity of different levels of the visual cortex, from striate (or V1) to various extrastriate areas, such as the fusiform face area, has been also reported (e.g., Axelrod et al. 2015; Brooks 2012). Despite the fact that these data have remarkably increased our knowledge on unconscious processing, several key issues remain unexplored.

Due to the low temporal resolution of functional magnetic resonance imaging (fMRI), the most employed methodology in this field, the timing of unconscious affective processing, and particularly the moment in which the structures mentioned above intervene, is poorly understood. Our main scope is exploring this question and, concretely, detecting the first signs of unconscious visual detection of emotional stimuli. Event-related potentials (ERPs), an electrophysiological manifestation of brain activity with maximal temporal resolution, are especially useful for this purpose, but have been scarcely employed yet. Their main drawback is that, contrary to fMRI, they present low sensitivity to subcortical activity. However, and as

explained later, cortical activity may indirectly -but reliably- inform on certain aspects of subcortical activity. Fortunately, most of visual cortex activity is detectable by ERPs so, more specifically, we aim at studying the first visual cortex traces of subliminal emotion detection using this neural recording methodology. Several studies report increased amplitudes in certain ERP visual components around 150-170 ms in response to subliminal facial and non-facial emotional stimuli. As regards facial stimuli, these effects have been reported for the N170 component of the ERPs (e.g., Pegna et al. 2008; Smith 2012; Zotto & Pegna 2015; but see Kiss & Eimer 2008). Face processing areas including the fusiform face area, located in the ventral visual cortex, contribute to the generation of N170 (Deffke et al. 2007; Itier and Taylor 2004; Sadeh et al. 2010). With respect to non-facial emotional subliminal stimuli results are scarcer. However, greater amplitudes to spiders than to non-negative stimuli have been also observed at 150 ms, the extrastriate visual cortex contributing to this activity (Carretié et al. 2005).

Importantly, several ERP components reflecting earlier visual processing take place in short latencies, namely C1, P1p and C2. Whereas their latency varies as a function of the physical characteristics of the stimuli, their spatial location, or the scalp region in which they are recorded, these three components consistently appear before 150ms and two of them, C1 and (often) P1p, before 100ms (Capilla et al. 2016; Di Russo et al. 2012). Their origin also signals these three components as the earliest manifestation of cortical visual processing. Thus, C1 and C2 are mainly originated in the primary visual cortex -or V1- (Capilla et al. 2016; Di Russo et al. 2012; but the contribution of early stages of extrastriate cortex such as V2 and V3 may not be dismissed: Ales et al. 2010). On the other hand, P1p is originated in dorsal areas of the visual extrastriate cortex according to these studies. Although C1 and P1p (C2 has not been explored at this respect) have been reported to be sensitive to the emotional content of supraliminal emotional stimuli (C1: Acunzo et al. 2019; Eldar et al. 2010; Pourtois et al. 2004; P1p: Carretié & Ruiz-Padial 2016; Holmes et al. 2008; Luo et al. 2010), their sensitivity to the

emotional content of subliminal stimuli has not been studied yet, to the best of our knowledge. This issue would be relevant at several cerebral levels. At the cortical level, the timing of unconscious processing is less understood than that of conscious processing. Indeed, the first sign of conscious visual processing is well established in the literature: the visual awareness negativity (VAN), an ERP component ranging from 150 to 300 ms, approximately, and originated in extrastriate ventral areas of the visual cortex (see reviews in Förster et al. 2020; Jiménez et al. 2020). However, first visual cortex traces of unconscious processing remain unexplored.

At the subcortical level, some issues may be also clarified thanks to the temporal resolution of ERPs. One of them is the role of the amygdala in unconscious processing. As indicated, this structure is consistently reported as being sensitive to the emotional content of subliminal stimulation (Brooks et al. 2012; Diano et al. 2017; Öhman 2002). Some studies have reported the amygdala to respond before visual cortex to subliminal emotional faces (e.g., Bayle et al. 2009). In relation to this, the amygdala's role as an early detector or evaluator of emotional stimuli capable of modulating the subsequent activity of the visual cortex has been often postulated (e.g., Framorando et al. 2021; Krolak-Salmon et al. 2004; Sabatinelli et al. 2009; Vuilleumier 2005). Whether this previous evaluation of the amygdala is necessary for the visual cortex activity to be modulated by emotional stimulation is, however, unclear. The shortest response of the amygdala to emotional faces reported so far is produced at 74 ms and more than 100ms later in response to emotional non-facial stimuli, according to intracranial recordings (Méndez-Bértolo et al. 2016). Taking into account conduction velocity in middle-range neurons in humans, information from amygdala would reach V1 or V2 at ~95ms and ~200ms in the case of facial and non-facial emotional stimuli, respectively (Carretié et al. 2021). Indeed, the amygdala has been postulated as a key piece of the neural circuitry involved in social behavior and as especially responsive to facial information (e.g., Amaral 2003; Wang et al. 2014). Therefore, along with time, the facial or non-facial nature of emotional stimuli

seems critical in this field. Non-facial emotional stimuli (e.g., harmful animals, food, etc.) may have similar or even more dramatic evolutionary consequences in some circumstances, so they should also be susceptible to being processed unconsciously. However, up to now neuroscience has provided scarce data on the processing of subliminal non-facial emotional stimuli.

The present study explored the earliest ERP visual components elicited by non-facial emotional and neutral stimuli using a backward masking task. If a modulation in C1, P1p or C2 is observed, several conclusions may be made regarding the visual cortical (when and which striatal and/or extrastriatal areas are involved, if any) and subcortical roles (any significant effect of emotion in these three components would rule out the mandatory involvement of the amygdala, or other evaluation structures with longer latencies, in unconscious processing). Stimuli consisted of (emotionally aversive) spider and (emotionally neutral) wheel silhouettes. This format was selected since presenting Gestalt characteristics such as closed contours or compact shape (as is the case of silhouettes) are optimal to increase the response of contour-sensitive neurons present in V1 and V2 (e.g., Ko & von der Heydt 2018). Additionally, spiders are among the top five most feared animals (Gerdes et al. 2009), and they cause the most prevalent phobia related to animals (Jacobi et al. 2004). Subliminal stimuli were presented both at fixation and in the periphery in order to detect possible biases of unconscious processing towards the magnocellular visual processing system (more involved than parvocellular in peripheral processing) activity, as previously proposed (Crick & Koch 2003). Additionally, this foveal or peripheral presentation helped us to identify C1, C2 and P1p, since they behave differently as a function of the spatial location of stimulation (Capilla et al. 2016).

Methods

Participants

Forty-six individuals participated in this experiment, although data from only 43 of them could eventually be analyzed¹ to guarantee an optimal minimum number of trials per condition, as explained later (40 women, age range of 18 to 25 years, mean=19.58, SD=1.33). The study had been approved by the Universidad Autónoma de Madrid's Ethics Committee. All participants were students of Psychology, provided their informed consent according to the Declaration of Helsinki, and received academic compensation for their participation. They reported normal or corrected-to-normal visual acuity.

Stimuli and procedure

Participants were placed in an electrically shielded, sound-attenuated room. They were asked to place their chin on a chinrest maintained at a fixed distance (40 cm) from the screen (VIEWpixx®, 120 Hz) throughout the experiment. A backward masking experimental paradigm was employed (Figure 1). Twenty emotional (spiders) and 20 neutral silhouettes (wheels), all in black color over a grey background, were employed as probe stimuli. Spiders are assessed as negatively valenced stimuli by relatively large samples in emotional picture databases (e.g., IAPS: Lang et al. 2005; EmoMadrid: Carretié et al. 2019). In order to test whether spider silhouettes were also efficient as negatively valenced stimuli, and wheels as neutral, these stimuli were previously evaluated by an independent sample of 447 participants (397 women, mean age=19.51, SD=1.46) who rated their emotional valence through a 7-point Likert scale that ranged from “very negative” (1) to “very positive” (7). Spiders were rated as negative (mean=1.704, standard error of means [SEM]=0.038) and wheels as neutral (i.e., in the intermediate values of the scale: mean=3.918, SEM=0.030). Differences between both stimuli were strongly significant ($F(1,446)=2557.289$, $p<0.001$, $\eta^2_p=0.852$).

¹ This sample size was enough to reach a statistical power of 0.8 for each of the three factors to be introduced in the foreseen frequentist ANOVA ($\alpha=0.05$) expecting medium-low effect sizes - see footnote 2- (computations were carried out using the applet developed by Lenth 2009).

As indicated in the introduction, stimuli presenting Gestalt characteristics such as closed contours or compact shape, as is the case of silhouettes, are optimal to increase the response of contour-sensitive neurons present in V1 and V2 (Ko & von der Heydt 2018). Moreover, the use of black silhouettes over grey background inherently equalizes color and contrast, which may influence the ERP temporal window we are interested in (color: Paulus et al. 1987; contrast: Foxe et al. 2008), across experimental categories. Luminosity (i.e., figure surface against background) and spatial frequency of silhouettes, which may also influence ERP components of interest (spatial frequency: Nakashima et al. 2018; luminosity: Johannes et al. 1995), were manipulated so they did not significantly differ between categories (spiders vs. wheels). Details on these two low-level characteristics and statistical contrasts are provided in EmoMadrid (psicologiauam.es/CEACO/EmoMadrid.htm). In sum, the only visual parameter besides their emotional meaning differing among spiders and wheels was their shape, in any case sharing certain key characteristics (e.g., wheel spokes may resemble spider legs and viceversa). More importantly, shape has been reported to firstly affect ERPs in latencies longer than those explored in this study (Bradley et al. 2007; Hillyard et al. 1998; Van Strien et al, 2016).

The size of probe stimuli (figure + ground) was $14^{\circ} \times 14^{\circ}$ width. Each spider and wheel appeared 4 times in random order in one of the two locations depicted in Figure 1: at fixation or at the lower visual field. This resulted in 80 trials per emotional category and location, and the total number of trials was 320 (80 x 2 categories x 2 locations). Each probe stimulus, whatever its location, was displayed on the screen for 8.33 ms. We selected this peripheral location since early ERP visual components have previously shown to be more sensitive to emotional stimuli similar to those employed here when they appear in the lower visual field than when presented in other locations of the visual scene (Carretié et al. 2020). Additionally, the lower field is anatomically overrepresented in V1 (Burkhalter et al. 1986), so stimuli in this area tend to elicit greater amplitudes in these components (Capilla et al. 2016).

*** Figure 1 about here ***

Immediately after the offset of the probe, a mask appeared for 83.33ms. It consisted of two adjacent squared boxes, each with the same size of probes. The boxes were presented over both possible locations of the probes whatever the actual location of the just presented probe was (Figure 1). The two boxes forming the mask were always the same and consisted of random, colored and unrecognizable composites of small squared fragments of two of the probe pictures. Since both boxes appeared contiguously, they formed a rectangular, perceptually unitary mask. One of the boxes (or mask halves) included a vertical black line ($7.7^\circ \times 1.15^\circ$, centered in that box: Figure 1). The line appeared 50% of trials at the upper box/half and another 50% at the lower in each experimental condition (spider fixation, spider periphery, wheel fixation, wheel periphery). To ensure active, endogenous attention to both locations, participants were asked to press a button if the line appeared in the upper half and a different button if it appeared in the lower. The intertrial interval (i.e., between the mask offset and the next probe onset) was 1500ms. Participants were instructed to look at the fixation dot at the center of the screen all the time, which was marked with a grey circle (0.3° radius) during the interstimulus intervals. The stimulus sequence was divided into two blocks of four minutes approximately with a brief rest period in between.

Recording and pre-processing

Electroencephalographic (EEG) activity was recorded using an electrode active cap (Biosemi) with Ag-AgCl electrodes. Sixty-four electrodes were placed at the scalp following a homogeneous distribution and the international 10-20 system. The EEG signal was pre-amplified at the electrode. Following the BioSemi design, the voltage at each active electrode was recorded with respect to a common mode sense (CMS) active electrode and a Driven Right Leg (DRL) passive electrode, replacing the ground electrode. All scalp electrodes were referenced offline to the nosetip. Electrooculographic (EOG) data were recorded supra- and

infraorbitally (vertical EOG) as well as from the left versus right orbital rim (horizontal EOG) to detect blinkings and ocular deviations from the fixation point. An online analog low-pass filter was set to 104 Hz (5th order, CIC filter). Recordings were continuously digitized at a sampling rate of 512 Hz. An offline digital Butterworth bandpass filter of 0.3 to 30 Hz (4th order, zero phase forward and reverse –twopass- filter) was applied to continuous (pre-epoched) data using the Fieldtrip software (<http://fieldtrip.fcdonders.nl>; Oostenveld et al. 2011). The continuous recording was divided into 1000 ms epochs for each trial, beginning 200 ms before the probe stimulus onset. The inevitable lag between the marks signaling stimuli onsets (or ‘triggers’) in EEG recordings and its actual onset in the screen was measured employing a photoelectric sensor as described in <https://www.youtube.com/watch?v=0BPwcciq8u8>, and corrected during pre-processing.

EEG epochs corresponding to trials in which participants responded erroneously or not responded in the task (see the previous section) were eliminated. Blinking-derived artifacts were removed through an independent component analysis (ICA)-based strategy (Jung et al. 2000), as provided in Fieldtrip. After the ICA-based removal process, a second stage of visual inspection of the EEG data was conducted to manually discard trials in which any further artifact, ocular (horizontal or vertical motion) or other type, was present. This automatic and manual rejection procedure led to the average admission of 60.674, 60.279, 60.046, 58.279 (respectively for spider fixation, spider periphery, wheel fixation, wheel periphery; SDs: 6.823, 6.445, 7.101, 6.185). The minimum number of trials accepted for averaging was 50 trials per participant and condition (i.e., each category presented in each location). Data from three participants were eliminated since they did not meet this criterion.

Data analysis

Behavioral analyses comprised the performance in the line detection task as well as tests of subliminality (both subjective and objective). Regarding performance in the task, errors and

reaction times (after removing outliers: ± 3 standard deviations) were submitted to repeated-measures ANOVAs introducing Emotion of the probe (spiders, wheels) and its Location (fixation, periphery) as factors. The subjective test of subliminality consisted in asking participants whether they saw “anything apart from the mask and the line”. This question was asked verbally and participants were free to respond whatever they considered. The objective test of subliminality consisted in an additional presentation of the same stimuli at the end of the experimental session. The 20 exemplars of spiders and wheels were randomly presented using the same backward masking setting as in the experimental run (the same exposure times of probes and masks, intertrial interval, and screen locations). In this case, however, the line did not appear in any of both mask boxes, and the task consisted in pressing a key if participants saw a wheel or another key if not (spiders were never mentioned across the experiment to avoid any supraliminal information on the emotional probe and to prevent “contamination” of other potential participants by transmitting this information). The sensitivity index (d') was computed on the performance of this final task.

As regards ERPs, the first analytic task was identifying and quantifying relevant ERP components (C1, P1p, C2). As later described and discussed, P1p and C1 overlapped in time and manifested as a single “fused component” that shared typical characteristics of both (probably reflecting overlapped processing of probe and mask), so it will be labeled CP1 hereafter. CP1 and C2 were quantified by measuring their peak amplitudes (positive and negative, respectively) within their corresponding windows of interest (72 to 82ms and 95-105ms, respectively). Additionally, and in order to better characterize these components and to localize the processes underlying them within the visual cortices, the Loreta localization algorithm (eLoreta version: Pascual-Marqui 2007) was computed on these amplitudes.

The experimental effects on these peak amplitudes were analyzed following a two-step procedure. First step was of exploratory nature due to the absence of previous data on

the behavior of the earliest ERP visual components in response to subliminal emotional (non-facial) stimulation. It consisted of Bayesian paired samples T-tests using JASP software (JASP Team 2020) with the default Cauchy prior distribution (scale 0.3, which represents a medium-low effect size in T-tests²). Importantly in this regard, Bayesian analyses might not require multiple comparison corrections during statistical tests (Gelman et al. 2012), even when running over 500,000 contrasts (fMRI voxels: Han & Park 2018). Bayes factors (BF) were computed in relevant scalp channels (i.e., those actually presenting CP1 and C2 components) in order to contrast spider vs wheel amplitudes when presented at fixation, on one hand, and when presented at the periphery, on the other. BFs allowed assessing the strength of evidence in favor of the alternative hypothesis (H1: S>W in the case of CP1 or S<W in the case of C2, which had positive and negative polarity, respectively) over the null hypothesis (H0: S=W) in all analyses. A BF_{10} (i.e., informing on the $H1>H0$ probability) over 3 represents substantial evidence supporting H1 over H0, and less than 1/3, a substantial evidence in the opposite direction: H0 over H1 (Jeffreys 1939; see also Dienes 2014).

The second analytical step, of confirmatory nature, consisted of traditional frequentist repeated-measures ANOVAs introducing Emotion of the probe (spiders, wheels), its Location (fixation, periphery) and Electrode as factors. Electrodes introduced in this analysis were those detected in the previous Bayesian analyses to present the strongest evidence in favor of H1. Effect sizes in these ANOVAs were computed using the partial eta-square (η^2_p) method. Post-hoc comparisons to determine the significance of pairwise contrasts in potential interactions were performed using the Bonferroni correction procedure. This second step was complemented by a Bayesian repeated-measures ANOVA on these same factors and their

² The average effect sizes of the only three studies (to the best of our knowledge) reporting them and exploring both C1 and P1 amplitudes to emotional stimuli (supraliminal, in all cases) is medium-low as regards factor Emotion (or equivalent label) and its interactions (Acunzo et al., 2019; Eldar et al., 2010; Weymar et al., 2014). As indicated in the main text, C2 has not been explored in response to emotional stimuli yet.

levels, using a Cauchy probability as prior (scale fixed effects=0.2, which in ANOVA corresponds to medium-low effect sizes: see footnote 1). Post-hoc Bayesian T-tests used the same prior distribution as the exploratory T-tests.

Results

Individual behavioral and ERP data, as well as supplemental information mentioned below, are openly available at <https://osf.io/afq5r/>. In the case of ERPs, data are provided in the form of a four-dimension matrix with a size of 43 participants x 4 conditions x 513 data points x 64 EEG recording channels. Table 1 shows means and standard error of means of behavioral and neural parameters in each of the experimental conditions.

*** Table 1 around here ***

Behavioral analyses

As shown in Table 2, ANOVAs on both the error rates and the reaction times in the line detection task did not yield and significant main effects of the probe's emotional content, its location, or of their interaction (all $p \geq 0.082$).

The subjective test of subliminality consisted, as indicated, in asking participants -at the end of the experimental session- whether they saw something apart from the mask. Thirty-seven out of the 43 participants responded “no”, and six reported seeing some element unrelated to spiders: “circles” ($n=2$), “something dentate” ($n=1$), “maybe a wheel” ($n=1$), “something black” ($n=1$), and “a helix” ($n=1$). This subjective test was complemented by the objective test, which consisted in the forced-choice task described in Data Analysis and the resulting sensitivity index (d'). Average d' in the whole sample³ was close to zero ($8.123 \cdot 10^{-17}$,

³ Two out of the 43 participants responded an insufficient number of trials (1 and 6 out of 40) due to their misunderstanding of the forced-choice task instructions (they avoided pressing any button whenever they ignored the response), so their d' was not computed. In any case, their blank response rates objectively confirm, in an alternative way, the subliminal condition of probes also for these two participants. The rest of participants responded in more than 75% of trials.

SD=0.5911). As may be appreciated in the supplemental link provided above, except in one case which presented moderate sensitivity ($d'=2.300$), all d' were below 1.

*** Table 2 around here ***

ERPs: identification and characterization of components

Figure 2 shows a selection of grand averages after subtracting the baseline (prestimulus) activity from each ERP. These grand averages correspond to medial and lateral parieto-occipital areas, where the relevant visual components were most prominent. As may be appreciated, the two most conspicuous components in early latencies are a positive deflection peaking at 77 ms average (± 3) and a negative one at 100ms (± 5). Figure 3 shows the topographical distribution of both peak amplitudes as well as their neural origin as revealed by eLoreta. This origin was located in V1/V2 in both components (Table 3). As may be appreciated in these figures, the positive deflection presents characteristics of P1p such as the (slightly, in this case) greater amplitude in response to foveal than to low periphery stimulation (C1 is typically characterized by the opposite pattern), or its bilateral distribution (rather than at midline, as usual in C1; see Capilla et al. 2016; Di Russo et al. 2012 regarding C1 and P1p characteristics). But it also presents attributes of C1 as its latency (slightly shorter than typical P1p) and its origin (V1/V2, whereas P1p is originated in dorsal extrastriate visual areas: Capilla et al. 2016; Di Russo et al. 2012). This overlapping is relatively frequent, but it has probably been enhanced by the rapid probe-mask flip and the concurrence of their respective neural effects. Therefore, and as previously advanced, it is being labeled CP1. As regards the negative deflection, its topographical distribution, its polarity, its latency, and its neural origin (V1/V2) converge to identify it as C2 (Capilla et al. 2016; Di Russo et al. 2012).

*** Table 3, Figures 2, Figure 3 around here ***

ERPs: analyses on the experimental effects

A relevant pattern of present ERPs, already visible in the grand averages, is that CP1 to C2 peak-to-peak amplitude appears to be especially sensitive to the experimental manipulation (Figure 4, right). Bayesian, exploratory T-test analyses (see Data Analysis) were carried out on these CP1-C2 peak to peak amplitudes (additional exploratory analyses on CP1 and C2 amplitudes by separate found no evidence to support H1 -Spider>Wheel- since all $BF_{10} < 1.05$; see “supplementary information” at <https://osf.io/afq5r/>). Since CP1 and/or C2 were absent at 10 recording sites (mainly at, or near, temporal locations), this peak-to-peak amplitude was incomputable in them. Figure 4 (left) graphically shows the magnitude of Bayesian factors (BF_{10}), and Table 4 summarizes the main outputs of all tests, in the remaining (computable) 54 scalp locations. As may be appreciated, strong evidence in favor of H1 (greater CP1-C2 amplitude for spiders than for wheels) is observed in lateral parietal areas, but only when probes were presented at fixation. Concretely, CP1-C2 peak to peak amplitudes in response to probe stimuli presented at fixation yielded $BF_{10} > 5$ in electrodes at C6, CP4, P6, and P8 ($BF_{10} = 5.605, 5.507, 10.699, 10.144$, respectively). Spider vs wheel amplitudes yielded $BF_{10} < 0.6$ in all electrodes (Figure 3 and Table 4).

*** Figure 4 and Table 4 around here ***

Exploratory analyses were followed by confirmatory analyses, as explained in Data Analysis. To this aim, repeated-measures ANOVAs were computed on CP1-C2 peak to peak amplitudes introducing Emotion of the probe (spiders, wheels), its Location (fixation, periphery) and Electrode (C6, CP4, P6, P8) as factors. The distribution of these amplitudes across participants and conditions is shown in Figure 5, as well as the average and the 95% confidence interval for each condition. Importantly to our scopes, the Emotion x Location interaction resulted significant ($F(1,42) = 5.016$, $p = 0.030$, $\eta^2_p = 0.107$). Post-hoc comparisons showed significant spider > wheel differences when presented at fixation ($p = 0.006$), but not when presented peripherally ($p = 0.656$). These and other less relevant ANOVA results are

shown in Table 5. As may be appreciated, interactions with Electrode were all non-significant pointing to a homogeneous behavior of this group of electrodes. The Bayesian repeated-measures ANOVA on these same factors (Emotion x Location x Electrode) yielded similar results and, as regards the Emotion x Location interaction, they pointed to a greater probability of H1 over H0 ($BF_{10}=3.200$). Post-hoc Bayesian T-tests, as frequentist analyses, specified that the spider>wheel effects are observed in fixation conditions ($BF_{10}=7.037$), but not in periphery ($BF_{10}=0.328$). Figure 5 illustrates the robustness checks on these post-hoc tests.

*** Figure 5 and Table 5 around here ***

Discussion

The present study explored the earliest traces of unconscious processing of emotion in the visual cortex by recording ERPs, a temporally rapid neural signal. The relatively large sample size ensured an adequate statistical power. Two different analytical strategies (Bayesian and frequentist) revealed a short-latency sensitivity (72-105ms) of early stages of the visual cortex (V1/V2) to the emotional content of non-facial stimuli presented subliminally. These results are especially valuable since they were obtained using a backward masking paradigm, in which EEG and MEG have more difficulty to manifest unconscious processing effects (as compared to other paradigms such as binocular rivalry; Axelrod et al. 2015). Additionally, they were obtained using a relatively short probe duration, since spiders and wheels were exposed only for 8ms. Several characteristics of the experimental design may have helped to obtain these early effects for the first time -to the best of our knowledge-. First, the use of spiders, an emotionally potent stimulus, as explained in the Stimuli and Procedure section, may intensify emotion detection mechanisms as compared to other stimuli (including faces). Second, the use of black silhouettes over a lighter background increases the response of contour-sensitive neurons present in V1 and V2, thus also augmenting the signal-to-noise ratio of the activity

detected at the scalp level. And third, the relatively large number of trials (~60 average per condition, 50 minimum) also contributes to increase the signal-to-noise ratio.

These results have important implications not only at the cortical level, but also at the subcortical. Regarding the former, they reveal certain parallelism with what occurs in response to supraliminal emotional stimulation, since early visual ERP components also show sensitivity to emotional stimuli (C1: Acunzo et al. 2019; Eldar et al. 2010; Pourtois et al. 2004; P1p: Carretié & Ruiz-Padial 2016; Holmes et al. 2008; Luo et al. 2010). However, the effects are more difficult to detect in this case and, along with the implementation of the issues mentioned in the previous paragraph, have required the quantification of differential CP1-C2 amplitudes (rather than individual component amplitudes), a classical way of computing amplitudes that seems useful in this field (e.g., Begleiter et al., 1980; Hillyard & Picton, 1978; Verleger & Cohen, 1978). Also at the cortical level, these results contribute to balance the knowledge on the temporal characteristics of unconscious vs conscious visual processing. On the conscious side of the coin, there is a relatively broad consensus that the earliest traces of conscious processing are reflected in VAN (~150 to 300 ms), as indicated in the Introduction (Förster et al. 2020; Jiménez et al. 2020). Whereas from this it would follow that earlier visual activity remains in the unconscious domain -although consequent processes may become conscious-, data from further studies directly exploring the effects of subliminal information are necessary for this temporal characterization.

Subcortical implications of these results are also relevant, mostly in the emotional field. As also indicated in the Introduction, any early effect of subliminal emotional stimuli, especially if they are non-facial, automatically rules out the involvement of the amygdala in this phase (its involvement in later phases of emotional processing -conscious and unconscious- is clear in the light of existing data). Even if stimuli were faces, the latency of the observed effects (72-105ms) would also be incompatible with the involvement of the

amygdala in visual cortex modulation. Indeed, the earliest response of amygdala reported so far is produced at 74 ms, and more than 100 ms later in the case of non-facial emotional stimuli (Méndez-Bértolo et al. 2016). This amygdalar activity would require ~20-25 additional milliseconds to reach the visual cortex, as explained in the Introduction. The probability that the amygdala may be found in future studies to respond significantly earlier than this to visual stimuli is remote due to anatomical and functional reasons detailed elsewhere (Carretié et al. 2021). Relatedly, the probability that other structures postulated as evaluative, such as ventral prefrontal, insular or anterior cingulate cortices intervene at this latency in visual cortex modulation is even more remote, due to their even longer latencies in response to emotional stimuli (Adolphs et al. 2006; Willenbockel et al. 2012).

Indeed, present results point to alternative hypotheses regarding brain areas responsible for initial stimulus evaluation, particularly to first and second order structures (i.e., retinal ganglion cells directly reach them, or only after one synapsis, respectively), due to their short processing latency. This is the case of the visual thalamus, which includes the lateral geniculate nucleus (LGN), the pulvinar, and the visual portion of the thalamic reticular nucleus (TRN), but also of other non-thalamic first order visual nuclei, such as the superior colliculus (SC). These nuclei have been revealed as active processors rather than passive relays in the visual ascending route towards visual cortices, as traditionally considered, and increase their response to attended stimuli (LGN: McAlonan et al. 2008; TRN: Crick 1984; pulvinar: Robinson & Petersen 1992; SC: Krauzlis et al. 2013), an increase that would be reflected in the activity of visual cortices, to which they project. The capability of emotional stimuli to capture attention (see a review in Carretié 2014) would therefore enhance the activity of these thalamic and extra-thalamic early evaluation nuclei, as recently proposed (Carretié et al. 2021). This preferential processing of emotional stimuli by early evaluation structures would be also mediated by arousal-related neural systems. Two examples are the midbrain reticular formation, whose activity affects the processing of low level visual parameters at early stages

of visual processing, probably even at the retinal ganglion cells level (Frizzi 1978; Granit 1956), and the histamine brain system (originated in the tuberomammillary nucleus), which projects to the LGN (among other structures) and boosts its transfer ratio towards visual cortices upon threatening stimuli or other arousing situations (Casagrande et al. 2005). The attentional nature of the observed effects would be reinforced by the right-hemisphere localization of the observed effects, given that certain attention modalities, such as spatial, have been reported to show a right-hemisphere advantage (e.g., Bartolomeo & Malkinson 2019; Müri et al. 2002; but see meta-analyses by Cona & Scarpazza 2019; Toro et al. 2008).

Two additional results are worth discussing. On one hand, only spiders presented at fixation elicited enhanced amplitudes as compared to neutral stimuli. Retinal projections to parvocellular and magnocellular layers of the lateral geniculate nucleus decline to a greater extent in the former case with eccentricity (Brown et al. 2005), resulting in a magnocellular bias for peripheral vision. This is a relevant issue since some traditional postulates defend a preferential involvement of the parvocellular system in conscious visual processing and the magnocellular in unconscious processing (Crick & Koch 2003; Milner & Goodale 1995). Present results point against this sort of segregation in line with more recent views (Breitmeyer 2014). On the other hand, although both CP1 and C2 originated in the cuneus (V1/V2), the CP1-C2 peak to peak effects were observed more laterally and extending towards the parietal cortex. The fact that the experimental effects are not reflected where amplitudes are more prominent is relatively frequent, however. This phenomenon has been scarcely studied, but probably reflects the involvement of additional, secondary sources being responsible for the observed effects. This is even more probable when, as in our study, multiple overlapping are produced: CP1 presents mixed characteristics of C1 and P1, and the peak to peak amplitude further involves the processes underlying C2. Although source reconstruction was not possible for the experimental effects, since not all electrodes were analyzed (those not actually showing CP1 and C2 were discarded), we hypothesize -at the light of the scalp distribution of effects: Figure

4) that dorsal extrastriate areas are probably involved. Some dorsal extrastriate areas, such as MT, receive rapid and direct inputs from the visual thalamus which, as mentioned, has been recently proposed as an early evaluation structure (e.g., from the inferior pulvinar, from lateral geniculate nucleus and from the visual portion of the thalamic reticular nucleus: Carretié et al. 2021).

In sum, present results show the short-latency sensibility of early stages of the visual cortex to the emotional content of unconsciously perceived stimulation. This finding confirms the particular (and adaptive) relevance of emotional stimuli for our nervous system. Several implications derived from this result have been discussed throughout this section. They go beyond the visual cortex level and also beyond emotional processing and would require further research to be confirmed. At this respect, ERPs demonstrate to be a valuable tool in this scarcely explored field, although several manipulations to increase the signal-to-noise ratio of recordings, such as those mentioned previously, seem necessary.

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References

- Acunzo D, MacKenzie G, van Rossum, Mark CW. 2019. Spatial attention affects the early processing of neutral versus fearful faces when they are task-irrelevant: A classifier study of the EEG C1 component. *Cogn Affect Behav Neurosci.* 19:123-137.
- Adolphs R, Kawasaki H, Oya H, Howard MA. 2006. Intracranial electrophysiology of the human orbitofrontal cortex. In: Zald DH, Rauch SL, editors, *The orbitofrontal cortex*. Oxford: Oxford University Press. p 355-375.
- Ales JM, Yates JL, Norcia AM. 2010. V1 is not uniquely identified by polarity reversals of responses to upper and lower visual field stimuli. *Neuroimage.* 52:1401-1409.

- Amaral DG. 2003. The amygdala, social behavior, and danger detection. *Ann N Y Acad Sci.* 1000:337-347.
- Axelrod V, Bar M, Rees G. 2015. Exploring the unconscious using faces. *Trends Cogn Sci.* 19:35-45.
- Bartolomeo P, Malkinson TS. 2019. Hemispheric lateralization of attention processes in the human brain. *Curr Opin Psychol.* 29:90-96.
- Bayle DJ, Henaff MA, Krolak-Salmon P. 2009. Unconsciously perceived fear in peripheral vision *alerts the limbic system: a MEG study.* *PLoS One.* 4(12): e8207.
- Begleiter H, Porjesz B, Tenner M. 1980. *Neuroradiological and neurophysiological evidence of brain deficits in chronic alcoholics.* *Acta Psychiat Scand.* 62:3-13.
- Bradley MM, Hamby S, Löw A, Lang PJ. 2007. *Brain potentials in perception: picture complexity and emotional arousal.* *Psychophysiology.* 44:364-373.
- Breitmeyer BG. 2014. *Contributions of magno-and parvocellular channels to conscious and non-conscious vision.* *Philos Trans R Soc Lond B Biol Sci.* 369(1641):20130213.
- Brooks SJ, Savov V, Allzén E, Benedict C, Fredriksson R, Schiöth HB. 2012. Exposure to subliminal arousing stimuli induces robust activation in the amygdala, hippocampus, anterior cingulate, insular cortex and primary visual cortex: a systematic meta-analysis of fMRI studies. *NeuroImage.* 59:2962-2973.
- Brown LE. 2005. Peripheral vision for perception and action. *Exp Brain Res.* 165:97-106.
- Burkhalter A, Felleman DJ, Newsome WT, Van Essen DC. 1986. Anatomical and physiological asymmetries related to visual areas V3 and VP in macaque extrastriate cortex. *Vision Res.* 26:63–80.
- Capilla A, Melcón M, Kessel D, Calderón R, Pazo-Álvarez P, Carretié L. 2016. Retinotopic mapping of visual event-related potentials. *Biol Psychol.* 118:114-125.
- Carretié L, Hinojosa JA, Mercado F, Tapia M. 2005. Cortical response to subjectively unconscious danger. *Neuroimage.* 24: 615-623.
- Carretié L, Méndez-Bértolo C, Bódalo C, Hernández-Lorca M, Fernández-Folgueiras U, Fondevila S, et al. 2020. Retinotopy of emotion: Perception of negatively valenced stimuli presented at different spatial locations as revealed by event-related potentials. *Hum Brain Mapp.* 41:1711-1724.
- Carretié L, Ruiz-Padial E. 2016. Ambient light modulation of exogenous attention to threat. *Brain Topogr.* 29:847-855.
- Carretié L, Tapia M, López-Martín S, Albert J. 2019. EmoMadrid: An emotional pictures database for affect research. *Motiv Emot.* 43:929-939.
- Carretié L, Yadav RK, Méndez-Bértolo C. 2021. The Missing Link in Early Emotional Processing. *Emot. Rev.* 13:225–244.
- Carretié L. 2014. Exogenous (automatic) attention to emotional stimuli: A review. *Cogn Affect Behav Neurosci.* 14:1228-1258.

- Casagrande VA, Royal DW, Sary G. 2005. Extraretinal inputs and feedback mechanisms to the lateral geniculate nucleus (LGN). In: Kremers J, editor, *The primate visual system: A comparative approach*. Hoboken, NJ: Wiley Online Library. p 191-211.
- Cona G, Scarpazza C. 2019. Where is the “where” in the brain? A meta-analysis of neuroimaging studies on spatial cognition. *Hum Brain Map*, 40:1867-1886.
- Crick F, Koch C. 2003. A framework for consciousness. *Nat Neurosci*. 6:119–126.
- Crick F. 1984. Function of the thalamic reticular complex: the searchlight hypothesis. *P Natl Acad Sci USA*. 81:4586-4590
- De Cesarei A, Mastria S, Codispoti M. 2013. Early spatial frequency processing of natural images: an ERP study. *PloS one*. 8(5), e65103.
- de Gelder B, Pourtois G, Weiskrantz L. 2002. Fear recognition in the voice is modulated by unconsciously recognized facial expressions but not by unconsciously recognized affective pictures. *Proc. Natl. Acad. Sci. U.S.A.* 99:4121–4126.
- Deffke I, Sander T, Heidenreich J, Sommer W, Curio G, Trahms L, et al. 2007. MEG/EEG sources of the 170-ms response to faces are co-localized in the fusiform gyrus. *NeuroImage*. 35:1495-1501.
- Di Russo F, Pitzalis S, Spitoni G, Aprile T, Patria F, Spinelli D, Hillyard SA. 2005. Identification of the neural sources of the pattern-reversal VEP. *Neuroimage*. 24:874-886.
- Di Russo F, Stella A, Spitoni G, Strappini F, Sdoia S, Galati G et al. 2012. Spatiotemporal brain mapping of spatial attention effects on pattern-reversal ERPs. *Hum Brain Mapp*. 33:1334-1351.
- Diano M, Celeghin A, Bagnis A, Tamietto M. 2017. Amygdala response to emotional stimuli without awareness: facts and interpretations. *Front Psychol*. 7:2029.
- Dienes Z. 2014. Using Bayes to get the most out of nonsignificant results. *Front Psychol*. 5:781.
- Eldar S, Yankelevitch R, Lamy D, Bar-Haim Y. 2010. Enhanced neural reactivity and selective attention to threat in anxiety. *Biol Psychol*. 85:252-257.
- Förster J, Koivisto M, Revonsuo A. 2020. ERP and MEG correlates of visual consciousness: The second decade. *Conscious Cogn*. 80:102917.
- Foxe JJ, Strugstad EC, Sehatpour P, Molholm S, Pasiaka W, Schroeder CE, McCourt ME. 2008. Parvocellular and magnocellular contributions to the initial generators of the visual evoked potential: high-density electrical mapping of the “C1” component. *Brain Topogr*. 21:11-21.
- Framorando D, Moses E, Legrand L, Seeck M, Pegna AJ. 2021. Rapid processing of fearful faces relies on the right amygdala: evidence from individuals undergoing unilateral temporal lobectomy. *Sci Rep*. 11:426.
- Frizzi JT. 1979. Midbrain reticular stimulation and brightness detection. *Vision Res*. 19:123-130.
- Gelman A, Hill J, Yajima M. 2012. Why we (usually) don't have to worry about multiple comparisons. *J Res Educ Eff*. 5:189-211.
- Gerdes AB, Uhl G, Alpers GW. 2009. Spiders are special: Fear and disgust evoked by pictures of arthropods. *Evol Hum Behav*. 30:66-73.

- Granit R. 1956. Receptors and sensory perception. New Haven: Yale University Press.
- Han H, Park J. 2018. Using SPM 12's second-level bayesian inference procedure for fMRI analysis: Practical guidelines for end users. *Front. Neuroinformatics*. 12:1.
- Hillyard SA, Picton TW. 1978. On and off components in the auditory evoked potential. *Percept Psychophys*. 24:391-398.
- Hillyard SA, Teder-Sälejärvi WA, Münte TF. 1998. Temporal dynamics of early perceptual processing. *Curr Opin Neurobiol*. 8:202-210.
- Holmes A, Nielsen MK, Green S. 2008. Effects of anxiety on the processing of fearful and happy faces: An event-related potential study. *Biol Psychol*. 77:159-173.
- Itier RJ, Taylor MJ. 2004. Source analysis of the N170 to faces and objects. *Neuroreport*. 15:1261-1265.
- Jacobi F, Wittchen HU, Höltling C, Höfler M, Pfister H, Müller N, et al. 2004. Prevalence, comorbidity and correlates of mental disorders in the general population: Results from the German Health Interview and Examination Survey (GHS). *Psychol Med*. 34:597-611.
- JASP Team. 2020. JASP (Version 0.14.1) [Computer software].
- Jeffreys H. 1939. *Theory of probability* (1st ed.). Oxford, England: Oxford University Press.
- Jiménez M, Hinojosa JA, Montoro, PR. 2020. Visual awareness and the levels of processing hypothesis: A critical review. *Conscious Cogn*. 85:103022.
- Johannes S, Münte TF, Heinze HJ, Mangun GR. 1995. Luminance and spatial attention effects on early visual processing. *Cogn Brain Res*. 2:189-205.
- Kiss M, Eimer M. 2008. ERPs reveal subliminal processing of fearful faces. *Psychophysiology*. 45:318-326.
- Ko HK, von der Heydt. 2018. Figure-ground organization in the visual cortex: does meaning matter?. *J Neurophysiol*. 119:160-176.
- Krauzlis RJ, Lovejoy LP, Zénon A. 2013. Superior colliculus and visual spatial attention. *Annu Rev Neurosci*. 36:165-182.
- Krolak-Salmon P, Hénaff MA, Vighetto A, Bertrand O, Mauguière F. 2004. Early amygdala reaction to fear spreading in occipital, temporal, and frontal cortex: a depth electrode ERP study in human. *Neuron*. 42:665-676.
- Lang PJ, Bradley MM, Cuthbert BN. 2005. *International affective picture system (IAPS): Affective ratings of pictures and instruction manual*. Gainesville, FL: University of Florida.
- Lenth RV. 2009. *Java Applets for Power and Sample Size* [Computer software]. Retrieved February 2010 from <http://www.stat.uiowa.edu/~rlenth/Power>.
- Luo W, Feng W, He W, Wang N, Luo Y. 2010. Three stages of facial expression processing: ERP study with rapid serial visual presentation. *Neuroimage*. 49:1857-1867.
- McAlonan K, Cavanaugh J, Wurtz RH. 2008. Guarding the gateway to cortex with attention in visual thalamus. *Nature*. 456:391-394.
- Méndez-Bértolo C, Moratti S, Toledano R, López-Sosa F, Martínez-Alvarez R, Mah YH, et al. 2016. A fast pathway for fear in human amygdala. *Nat Neurosci*. 19:1041.
- Milner AD, Goodale MA. 1995. *The visual brain in action*. Oxford: Oxford University Press.

- Müri RM, Böhler R, Heinemann D, Mosimann UP, Felblinger J, Schläpfer TE, Hess CW. 2002. Hemispheric asymmetry in visuospatial attention assessed with transcranial magnetic stimulation. *Exp Brain Res.* 143:426-430.
- Nakashima T, Kaneko K, Goto Y, Abe T, Mitsudo T, Ogata K, ... Tobimatsu S. 2008. Early ERP components differentially extract facial features: evidence for spatial frequency-and-contrast detectors. *Neurosci Res.* 62:225-235.
- Öhman A. 2002. Automaticity and the amygdala: Nonconscious responses to emotional faces. *Curr Dir Psychol Sci.* 11:62-66.
- Oostenveld R, Fries P, Maris E, Schoffelen JM. 2011. FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Comput Intell Neurosci.* 2011:1.
- Pascual-Marqui RD. 2007. Discrete: 3D distributed, linear imaging methods of electric neuronal activity. Part 1: exact, zero error localization. *arXiv.* 0710.3341.
- Paulus WM, Hömberg V, Cunningham K, Halliday AM, Rohde N. 1984. Colour and brightness components of foveal visual evoked potentials in man. *Electroenceph Clin Neurophysiol.* 58:107-119.
- Pegna AJ, Landis T, Khateb A. 2008. Electrophysiological evidence for early non-conscious processing of fearful facial expressions. *Int J Psychophysiol.* 70:127-136.
- Pourtois G, Grandjean D, Sander D, Vuilleumier P. 2004. Electrophysiological correlates of rapid spatial orienting towards fearful faces. *Cereb Cortex.* 14:619-633.
- Robinson DL, Petersen SE. 1992. The pulvinar and visual salience. *Trends Neurosci.* 15:127-132.
- Sabatinelli D, Lang PJ, Bradley MM, Costa VD, Keil A. 2009. The timing of emotional discrimination in human amygdala and ventral visual cortex. *J Neurosci.* 29:14864-14868.
- Sadeh B, Podlipsky I, Zhdanov A, Yovel G. 2010. Event-related potential and functional MRI measures of face-selectivity are highly correlated: a simultaneous ERP-fMRI investigation. *Hum Brain Mapp.* 31:1490-1501.
- Smith ML. 2012. Rapid processing of emotional expressions without conscious awareness. *Cereb Cortex.* 22:1748-1760.
- Tapia E, Breitmeyer BG. 2011. Visual consciousness revisited: magnocellular and parvocellular contributions to conscious and nonconscious vision. *Psychol Sci.* 22:934-942.
- Toro, R., Fox, P.T.,y Paus, T. 2008. Functional coactivation map of the human brain. *Cereb Cortex.* 18:2553-2559.
- Van Strien JW, Christiaans G, Franken IH, Huijding J. 2016. Curvilinear shapes and the snake detection hypothesis: an ERP study. *Psychophysiology.* 53:252-257.
- Verleger R, Cohen R. 1978. Effects of certainty, modality shift and guess outcome on evoked potentials and reaction times in chronic schizophrenics. *Psychol Med.* 8:81-93.
- Vuilleumier P. 2005. How brains beware: Neural mechanisms of emotional attention. *Trends Cogn Sci.* 9:585-594.

- Wang XD, Chen C, Zhang D, Yao H. 2014. Cumulative latency advance underlies fast visual processing in desynchronized brain state. *Proc Natl Acad Sci USA*. 111:515-520.
- Weymar M, Keil A, Hamm AO. 2014. Timing the fearful brain: unspecific hypervigilance and spatial attention in early visual perception. *Soc Cogn Affect Neurosci*, 9:723-729.
- Willenbockel V, Lepore F, Nguyen DK, Bouthillier A, Gosselin F. 2012. Spatial frequency tuning during the conscious and non-conscious perception of emotional facial expressions – an intracranial ERP study. *Front Psychol*. 3:237.
- Zotto MD, Pegna AJ. 2015. Processing of masked and unmasked emotional faces under different attentional conditions: an electrophysiological investigation. *Front Psychol*. 6:1691.

Table 1. Means and standard error of means (in italics) of error rate, reaction times and CP1-C2 peak to peak amplitude (average of recordings at C6, CP4, P6, P8, PO8 electrodes). See the main text for more details.

	Spider fixation	Spider periphery	Wheel fixation	Wheel periphery
Error rate (0 to 1)	3.95E-04	4.17E-04	4.84E-04	4.75E-04
	<i>5.84E-05</i>	<i>5.46E-05</i>	<i>7.02E-05</i>	<i>5.73E-05</i>
Reaction time (ms)	403.610	405.113	404.732	404.721
	<i>7.691</i>	<i>8.274</i>	<i>8.108</i>	<i>8.094</i>
CP1-C2 amplitude (μV)	2.539	1.668	1.935	1.755
	<i>0.631</i>	<i>0.594</i>	<i>0.575</i>	<i>0.603</i>

Table 2. Main outputs of ANOVAs on errors and reaction times (RTs) in the line detection task for both analyzed factors: Emotion of the probe (neutral, negative), Location of the probe (fixation, periphery) and their interaction. Df=degrees of freedom.

	Emotion				Location				Interaction			
	F	df	p	η^2_p	F	df	p	η^2_p	F	df	p	η^2_p
Errors	3.169	1,42	0.082	0.07	0.021	1,42	0.884	0.001	0.268	1,42	0.607	0.006
RTs	0.19	1,42	0.665	0.005	0.419	1,42	0.521	0.01	0.549	1,42	0.463	0.013

Table 3. Main source provided by eLoreta for CP1 and C2 amplitudes.

ERP component	X,Y,Z (MNI coordinates)	Brodmann area	Subregion
CP1	-20 , -100 , 0	BA18 (0 mm)	V2
		BA17 (7 mm)	V1
C2	-10 , -100 , -5	BA17 (0 mm)	V1
		BA18 (5 mm)	V2

Table 4. Bayesian factors regarding the likelihood of data on H1 (spider>wheel) over H0 (spider=wheel) - BF_{10} - computed through Bayesian Paired Samples T-Test using JASP (Jasp Team, 2020) on the CP1-C2 peak to peak amplitude both when the probe stimuli were presented at fixation and in the periphery. Missing electrodes (n=10) are those not presenting any deflection corresponding to CP1 and C2 components (peak to peak amplitude being incomputable).

Electrode	Fixation	Periphery	Electrode	Fixation	Periphery
Fp1	1.689	0.247	AF8	0.607	0.196
AF7	0.672	0.417	AF4	0.381	0.235
AF3	0.675	0.252	AFz	0.591	0.225
F1	1.079	0.208	Fz	0.505	0.231
F3	0.748	0.173	F2	0.617	0.218
F5	0.676	0.222	F4	1.027	0.268
F7	0.232	0.237	F6	0.603	0.257
FC5	1.259	0.224	F8	0.543	0.139
FC3	0.818	0.182	FT8	2.399	0.587
FC1	0.657	0.18	FC6	1.674	0.316
C1	0.831	0.181	FC4	1.898	0.235
C3	0.639	0.164	FC2	0.853	0.26
CP3	0.504	0.143	FCz	0.698	0.219
CP1	0.775	0.17	Cz	0.737	0.211
P1	0.49	0.183	C2	1.639	0.245
P3	0.507	0.144	C4	3.759	0.284
P5	0.547	0.136	C6	5.605	0.29
PO7	0.344	0.154	CP6	3.321	0.303
PO3	0.484	0.178	CP4	5.507	0.229
O1	0.639	0.145	CP2	2.098	0.23
Iz	1.355	0.144	P2	1.607	0.219
Oz	0.756	0.197	P4	2.602	0.279
POz	1.335	0.224	P6	10.699	0.239
Pz	0.654	0.208	P8	10.144	0.321
CPz	0.914	0.216	PO8	4.408	0.361
Fpz	1.386	0.153	PO4	2.414	0.298
Fp2	1.264	0.188	O2	2.512	0.23

Table 5. Main outputs of ANOVA on CP1-C2 peak to peak amplitudes for both analyzed factors: Emotion of the probe (neutral, negative), Location of the probe (fixation, periphery), Electrode (C6, CP4, P6, P8, PO8), and their interactions. Df=degrees of freedom. BF_{10} =Bayes factor (likelihood of data on H1 over H0).

	F	df	p	η^2_p	BF_{10}
Emotion	2.08	1, 42	0.157	0.047	0.450
Location	4.862	1, 42	0.033	0.104	6.856
Electrode	18.675	4, 168	<0.001	0.308	4.597 E+28
Emo x Locat	4.878	1, 42	0.033	0.104	3.200
Emo x Electr	0.585	4, 168	0.543	0.014	0.102
Locat x Electr	0.788	4, 168	0.451	0.018	0.117
Emo x Locat x Electr	0.406	4, 168	0.813	0.006	0.179

Figure legends

Figure 1. Schematic representation of the stimulus sequence. One of the exemplars of spider and wheel probes are depicted, as well as on mask showing the line in the upper half and another in the lower.

Figure 2. Grand averages (only the -200 to 500 portion of the epoch is depicted) corresponding to five representative sites of the parietal-occipital region, where relevant visual components (CP1 and C2) are prominent.

Figure 3. Topographical distribution of CP1 and C2 peak amplitudes (left), and their source as provided by eLoreta (right).

Figure 4. Left: representation, in the form of scalp maps, of Bayesian factors describing the likelihood of data on H1 (spider>wheel) over H0 (spider=wheel) (BF_{10}) computed through Bayesian Paired Samples T-Test on the CP1-C2 peak to peak amplitude both when the probe stimuli were presented at fixation and in the periphery. Missing electrodes (see Table 3) were removed and interpolated for this representation. Right: grand averages at one representative electrode of the region showing the greatest BF_{10} values, with the portion involving CP1 and C2 enlarged to illustrate the peak to peak amplitude quantification procedure.

Figure 5. A: Violin plots of CP1-C2 peak-to-peak amplitudes across participants and conditions. **B:** average and 95% confidence intervals of CP1-C2 peak-to-peak amplitudes in each condition. **C:** robustness checks of post-hoc Bayesian T-tests on the H1 (spider>wheel) over H0 (spider=wheel) likelihood; left: when presented at fixation, right: when presented at periphery.

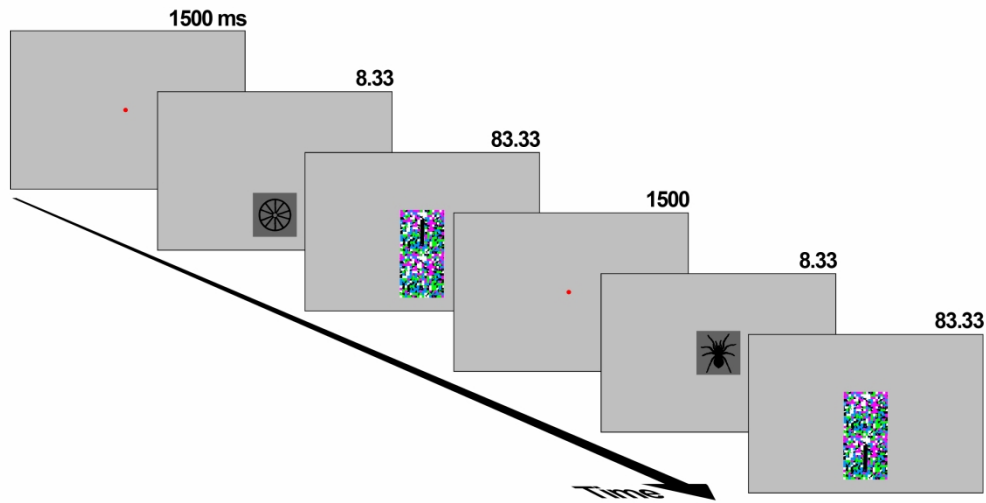


Figure 1. Schematic representation of the stimulus sequence. One of the exemplars of spider and wheel probes are depicted, as well as on mask showing the line in the upper half and another in the lower.

800x409mm (96 x 96 DPI)

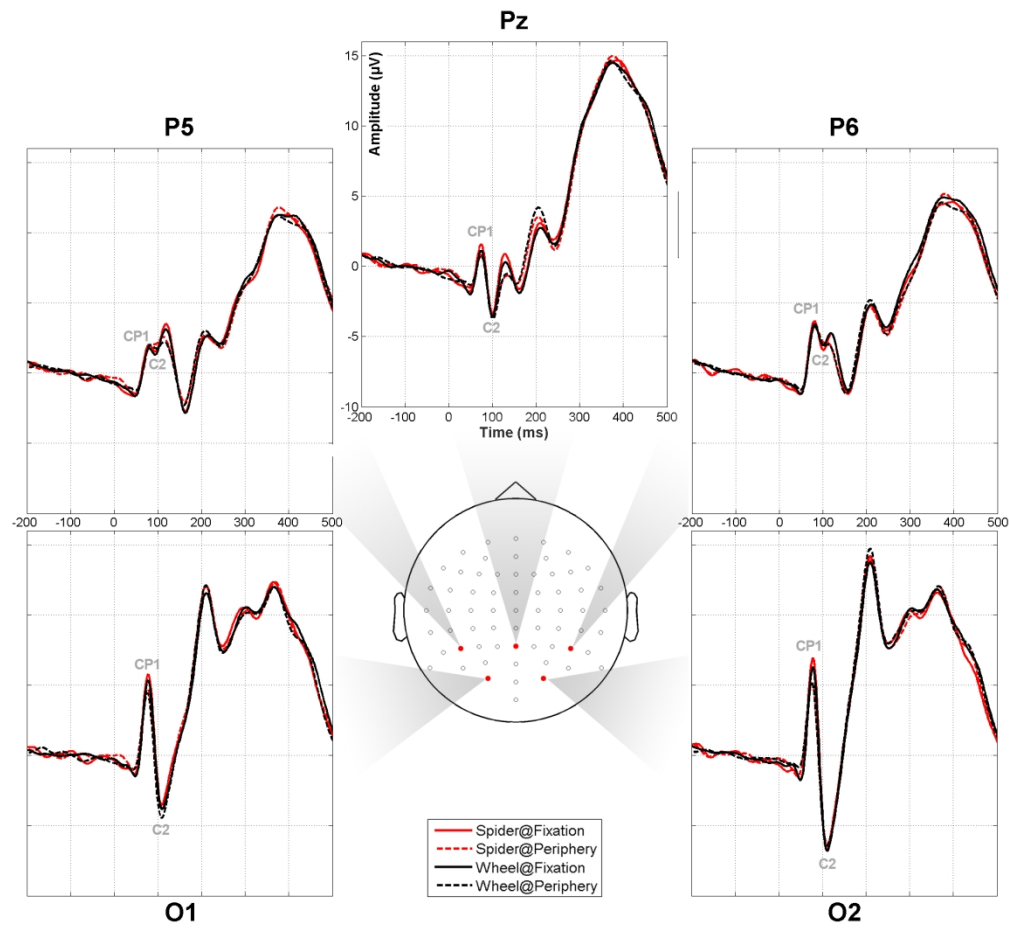


Figure 2. Grand averages (only the -200 to 500 portion of the epoch is depicted) corresponding to five representative sites of the parietal-occipital region, where relevant visual components (CP1 and C2) are prominent.

338x314mm (150 x 150 DPI)

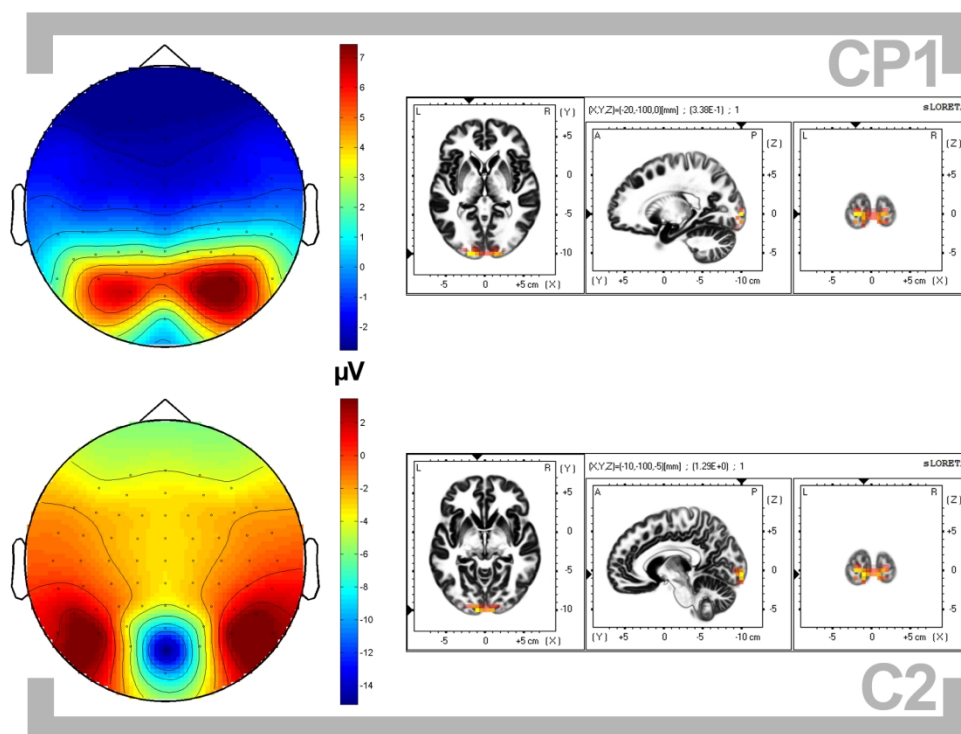


Figure 3. Topographical distribution of CP1 and C2 peak amplitudes (left), and their source as provided by eLoreta (right).

325x251mm (150 x 150 DPI)

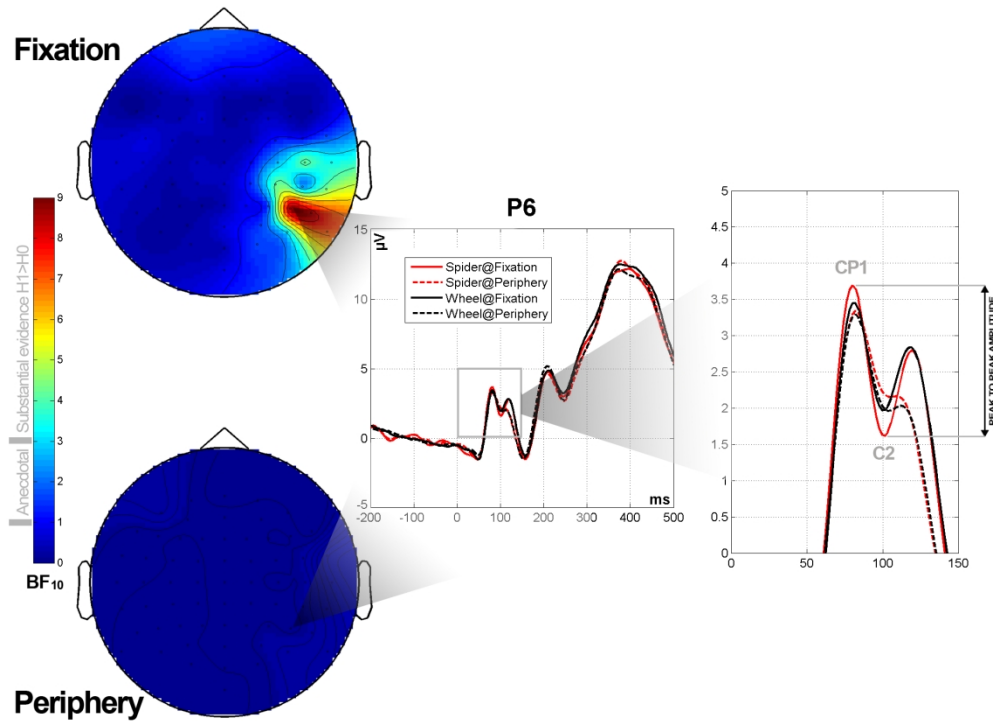


Figure 4. Left: representation, in the form of scalp maps, of Bayesian factors describing the likelihood of data on H1 (spider>wheel) over H0 (spider=wheel) (BF₁₀) computed through Bayesian Paired Samples T-Test on the CP1-C2 peak to peak amplitude both when the probe stimuli were presented at fixation and in the periphery. Missing electrodes (see Table 3) were removed and interpolated for this representation. Right: grand averages at one representative electrode of the region showing the greatest BF₁₀ values, with the portion involving CP1 and C2 enlarged to illustrate the peak to peak amplitude quantification procedure.

340x247mm (150 x 150 DPI)

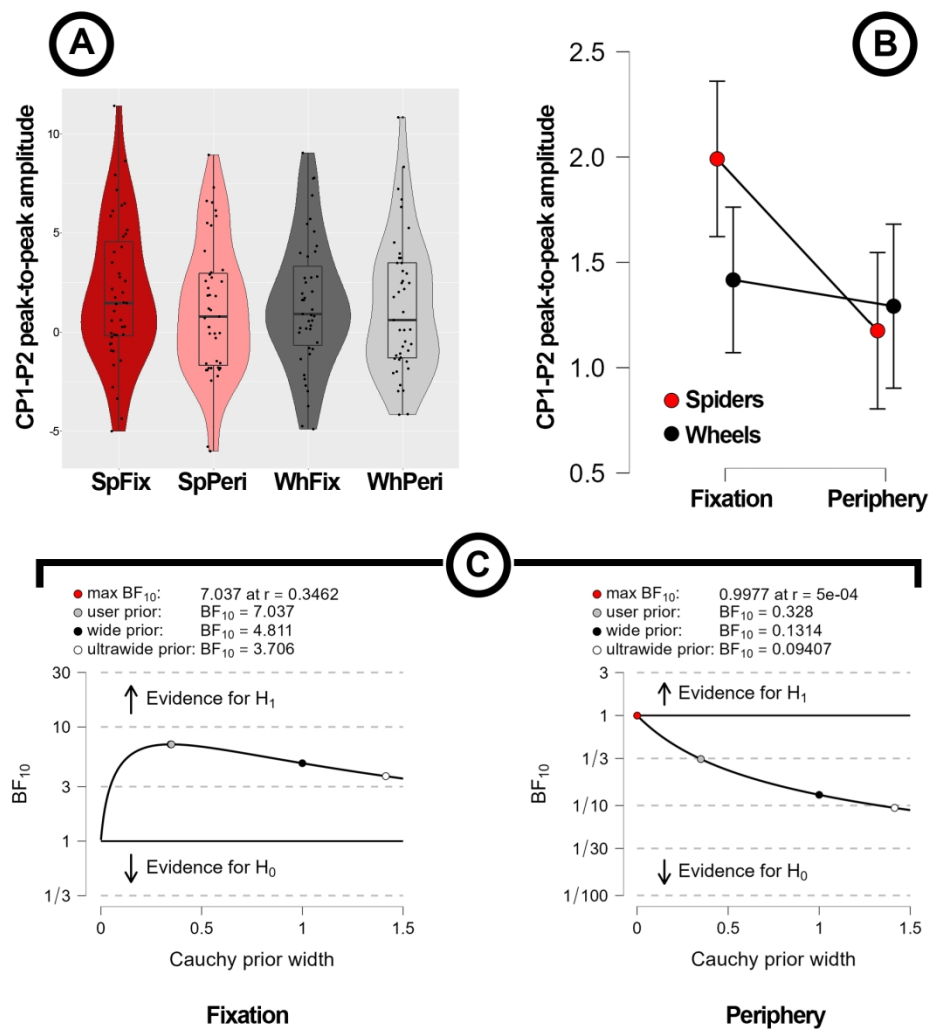


Figure 5. A: Violin plots of CP1-C2 peak-to-peak amplitudes across participants and conditions. B: average and 95% confidence intervals of CP1-C2 peak-to-peak amplitudes in each condition. C: robustness checks of post-hoc Bayesian T-tests on the H1 (spider > wheel) over H0 (spider = wheel) likelihood; left: when presented at fixation, right: when presented at periphery.