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Tactile expectancy modulates occipital alpha oscillations in early blindness

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ABSTRACT

Alpha oscillatory activity is thought to contribute to visual expectancy through the engagement of task-relevant occipital regions. In early blindness, occipital alpha oscillations are systematically reduced, suggesting that occipital alpha depends on visual experience. However, it remains possible that alpha activity could serve expectancy in non-visual modalities in blind people, especially considering that previous research has shown the recruitment of the occipital cortex for non-visual processing. To test this idea, we used electroencephalography to examine whether alpha oscillations reflected a differential recruitment of task-relevant regions between expected and unexpected conditions in two haptic tasks (texture and shape discrimination). As expected, sensor-level analyses showed that alpha suppression in parieto-occipital sites was significantly reduced in early blind individuals compared with sighted participants. The source reconstruction analysis revealed that group differences originated in the middle occipital cortex. In that region, expected trials evoked higher alpha desynchronization than unexpected trials in the early blind group only. Our results support the role of alpha rhythms in the recruitment of occipital areas in early blind participants, and for the first time we show that although posterior alpha activity is reduced in blindness, it remains sensitive to expectancy factors. Our findings therefore suggest that occipital alpha activity is involved in tactile expectancy in blind individuals, serving a similar function to visual anticipation in sighted populations but switched to the tactile modality. Altogether, our results indicate that expectancy-dependent modulation of alpha oscillatory activity does not depend on visual experience.

Significance statement: Are posterior alpha oscillations and their role in expectancy and anticipation dependent on visual experience? Our results show that tactile expectancy can modulate posterior alpha activity in blind (but not sighted) individuals through the engagement of occipital regions, suggesting that in early blindness, alpha oscillations maintain their proposed role in visual anticipation but subserve tactile processing. Our findings bring a new understanding of the role that alpha oscillatory activity plays in blindness, contrasting with the view that alpha activity is task unspecific in blind populations.

1. Introduction

Since the first electroencephalographic (EEG) recordings, a close relationship has been suggested between visual processes and posterior (parieto-occipital) alpha oscillatory activity (Berger, 1929). Although at first alpha oscillatory activity was considered to reflect cortical idling (Adrian and Matthews, 1934; Pfurtscheller et al., 1996), alpha oscillations are now thought to play an important role in shaping the state of sensory regions that direct the flow of information and allocating resources (Jensen and Mazaheri, 2010). Even if some studies consider the role of alpha band activity to be the same across slower and faster frequencies (Foxe et al., 1998; Foxe and Snyder, 2011; Fu et al., 2001; Haegens et al., 2010, 2011), other studies distinguish different subbands and assign them different functions. Alpha oscillations below 10 Hz have been associated with attention, expectation and encoding (Doppelmayr et al., 2002; Klimesch, 1997; Klimesch et al., 1993), while

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alpha activity above 10 Hz has been related to expectation, memory or semantics (Doppelmayr et al., 2002; Klimesch et al., 1994; Klimesch, 1997; Schubert et al., 2019). Specifically, alpha activity is thought to reflect anticipatory states of sensory processing in vision (Foxe et al., 1998; Fu et al., 2001; Mayer et al., 2016; Rihs et al., 2009; Thut, 2006; Worden et al., 2000), but also in other sensory modalities (Deng et al., 2019; Haegens et al., 2011a, 2011b; Hartmann et al., 2012). Anticipation of a specific stimulus leads to a desynchronization of alpha oscillations in areas involved in the processing the upcoming stimulus (Klimesch, 2012; Thut, 2006), facilitating its processing via the enhancement of the neural signal-to-noise ratio (Hanslmayr et al., 2016; Mitchell et al., 2009). Likewise, decreased alpha power during periods preceding a target's appearance has been related to improved task performance (Feng et al., 2017). On the other hand, alpha synchronization has been associated with distractor suppression (Kelly et al., 2006; Rihs et al., 2007, 2009). Importantly, alpha activity was found to correlate with the amplitude of early sensory electrophysiological components, suggesting its implication in the selective amplification of predicted information (Mayer et al., 2016). However, it is still unknown to what extent posterior alpha oscillations and their role in prediction depend on visual experience.

One effective way for assessing whether expectancy could modulate alpha oscillations independent of visual experience is to investigate posterior alpha oscillations in early blind (EB) people. In EB populations, it has been consistently shown that posterior occipito-parietal regions reorganize to engage in the processing of non-visual inputs, both in the tactile (Amedi et al., 2003; Jiang et al., 2015; Sadato et al., 1998, 2004; van Kemenade et al., 2014) and auditory (Collignon et al., 2011; Dormal et al., 2016; Mattioni et al., 2020; Poirier et al., 2006; Rezk et al., 2020) modalities. If alpha activity is tightly linked to vision, it should therefore be altered in congenitally blind individuals. Several studies have suggested that this might be the case by showing that in early blindness, posterior alpha oscillations are decreased while participants are at rest (Adrian and Matthews, 1934; Hawellek et al., 2013; Noebels et al., 1978; Novikova, 1973), dreaming (Bertolo et al., 2003) or during haptic tasks (Kriegseis et al., 2006; Schepers et al., 2012; Schubert et al., 2015). The variety of tasks in which EB participants showed these reductions led to the suggestion that alpha rhythms did not play a role in sensory/cognitive functions in the reorganized occipital cortex of blind people (Kriegseis et al., 2006). In contrast, other studies suggest that alpha-band activity reflects spatial coding during tactile processing both in sighted and blind populations (Schubert et al., 2019). However, no study so far has directly tested whether predictions (e.g., expectancy matched or mismatched trials) can modulate posterior alpha activity in the blind, a key signature of alpha oscillations in sighted people for visual processing (Foxe et al., 1998; Kizuk and Mathewson, 2017; Rihs et al., 2007, 2009; Thut, 2006).

Given the prominent role of posterior alpha oscillations in visual expectation and considering that in early blind people occipito-parietal regions reorganize to engage in the processing of tactile stimuli (Beauchamp et al., 2007; Blake et al., 2004; Jiang et al., 2015; van Kemenade et al., 2014), in the present study we assessed whether tactile expectancy modulated alpha oscillations in visually deprived people. To do so, we compared alpha band activity between expected and unexpected conditions in two separate haptic tasks (texture and shape discrimination), both at the sensor-level and in source space. Since occipital and occipito-parietal regions in visually deprived populations may maintain their computational specialization in the absence of vision (Dormal and Collignon, 2011), we expected to find expectancy-induced alpha modulations in the early blind group. In contrast to our previous Event-Related Potential (ERP) study on the same data set (Gurtubay-Antolin and Rodríguez-Fornells, 2017), where we investigated the time-course of haptic shape vs texture discrimination, this study is focused entirely on the role that tactile expectation may play in modulating occipital oscillations.

2. Materials and methods

2.1. Participants

14 congenitally blind (7 women, mean ±SD, age = 35.7 ± 10.9 years) and 15 sighted participants (9 women, mean age = 29.3 ± 9.0 years) took part in the experiment. Both groups were matched for age and years of education. The inclusion criteria for the EB group included right handedness, less than 3% of visual residual abilities, blindness onset before 5 years of age, no recollection of visual memories and the ability to avoid blinks and control eye movements for 3 s. Blindness of cerebral origin was an exclusion criterion. Three congenitally blind participants were excluded from the analysis. EB4 was removed due to excessive muscular artifacts. EB10 was rejected due to residual abilities to read with a very high contrast and magnifiers, despite reporting 3% of residual visual abilities. EB14 was removed because he did not perform the shape discrimination task for timing reasons. The experiment was undertaken with the understanding and written consent of each participant and was approved by the local ethics committee in accord with the declaration of Helsinki. Demographic characteristics of early blind and sighted control participants can be seen in Table 1.

2.2. Procedure

Participants performed haptic shape and texture discrimination tasks with their right hand. In the texture task, ten textures were used (cotton, cork, sackcloth, sandpaper, sponge, scourer, corduroy, suede, paper and velvet). In the shape-task, ten 2D wooden geometrical shapes were used (racket, circle, square, triangle, arrow, flower, crown, heart, star and lightning). An opaque screen was placed between sighted participants and the items to ensure vision was obstructed during the entire experimental session.

The texture- and shape-discrimination tasks followed the same procedure (see Fig. 1). To minimize individual differences in haptic exploration, all participants conducted the same constrained, guided exploration which allowed them to contact the object with three fingertips for ~3 sec. In the texture experiment, all three fingers were tied together and participants touched the textures with their fingertips, after sliding their fingers down a vertical pole. In the shape discrimination task, participants touched the shapes at three specific locations (*contact points*), bringing their three fingers together by sliding them through three grooves that were carved into the table.

Each trial began with the fingers in the initial position. Then, participants heard the name of an expected stimulus through headphones. An auditory cue (a beep) indicated that the fingers could start moving towards the figure. In half of the trials the presented stimuli matched the previous name (congruent condition), and in the other half it did not (incongruent). A second auditory cue indicated that a response had to be made, requesting the participants to press (with their left hand) one of two different keyboard buttons to report whether the stimulus that they were touching corresponded to the previous expectancy. There was a 3000 ms delay before this auditory cue in order to avoid contamination of the EEG signal by motor related EEG-components.

The experimental session consisted of 180 trials conducted in 4 blocks, with resting periods in between. Each block consisted of three series of 15 trials. To measure the time at which subjects contacted the object (contact time) the position and velocity of the fingers was recorded using an infrared motion capture system (CMS-30P, Zebris, Isny, Germany). The spatial resolution of the motion tracking system was 0.1 mm and a sampling frequency of 200 and 66 Hz was used in the texture and shape discrimination task, respectively. The difference in the sampling frequency between tasks was because the three fingers moved as one entity in the texture experiment (hence a single sensor was needed), whereas they moved separately in the shape task (therefore three sensors were needed).

Table 1
Demographic characteristics of participants. The ‘LP’ column indicates whether the subjects have light perception. The ‘onset’ and ‘duration’ columns refer to the age of blindness onset and the duration of blindness until present (years). ‘Education’ represents the years of education. ‘Braille duration’ refers to the years spent reading Braille. ‘Hrs/ week Braille’ details how many hours a week the subjects dedicate to Braille reading (at present). EB = Early Blind, SC = Sighted Controls. M = Male, F = Female.

	Age & Gender	Cause of blindness	LP	Onset	Duration	Education	Braille duration	Hrs/week Braille
EB 1	24 M	Congenital glaucoma & retinal detachment	No	0	24	14	19	0
EB 2	30 F	Microphthalmia & Congenital cataracts	Yes	0	30	15	25	1
EB 3	28 F	Premature retinopathy	Yes	0	28	22	24	1
EB 4	30 F	Congenital glaucoma	Yes	0	30	12	26	0
EB 5	31 F	Leber’s congenital amaurosis	Yes	0	31	19	25	3
EB 6	46 F	Atrophy of the optic nerve	No	1.5	44.5	23	41	6
EB 7	29 M	Bilateral retinoblastoma	No	4	25	24	24	10
EB 8	53 M	Atrophy of the optic nerve	No	0	53	7	37	1
EB 9	35 F	Bilateral retinoblastoma	No	4	31	20	30	1
EB 10	35 F	Bilateral retinoblastoma	Yes	1	34	19	-	-
EB 11	23 M	Premature retinopathy	No	0	23	20	19	0
EB 12	52 F	Bilateral retinoblastoma	No	0	50	36	47	14
EB 13	43 M	Premature retinopathy	Yes	0	43	19	38	40
EB 14	19 M	Bilateral retinoblastoma	No	0	19	16	15	1
SC	29 (±9) 9F	-	-	-	-	20 (±4)	-	-

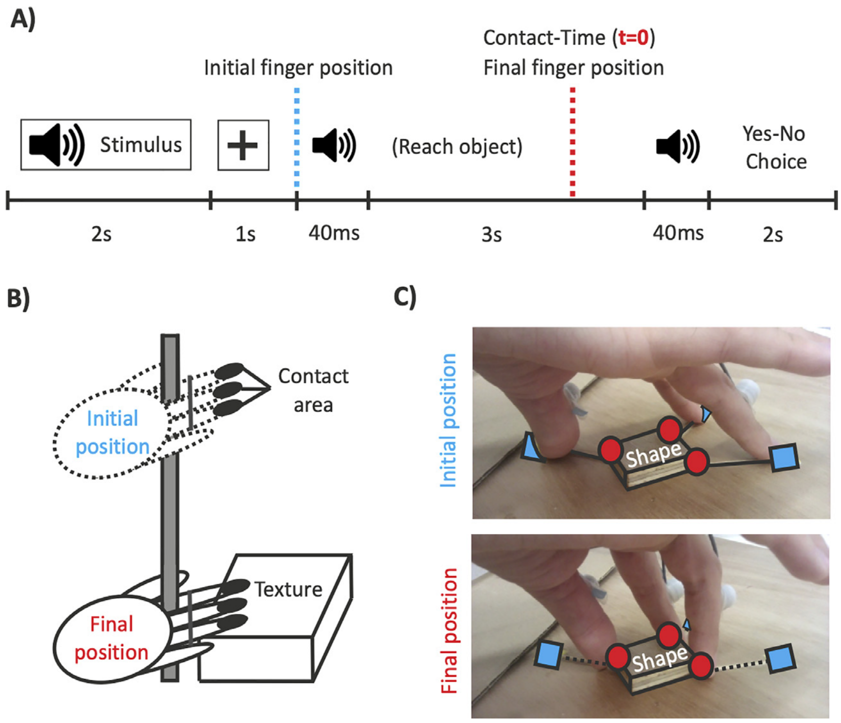

Fig. 1. A. Trial procedure. B. Exploratory procedure in the texture discrimination task: all three fingers were tied together and participants touched the textures with their fingertips, after sliding their fingers down a vertical pole. No movement was allowed after the Contact Time. C. Exploratory procedure in the shape discrimination task: participants touched the shapes at three specific locations (Contact Points), bringing their three fingers together by sliding them through three grooves that were carved into the table.

The instant when the participant first touched the object was labeled as Contact-Time (CT). CT was defined as the time when the absolute velocity of the first finger to contact the object was lower than 5% of its peak velocity. In the texture discrimination task, the arrival of the three fingers to the stimulus happened simultaneously. Whereas in the shape discrimination task, the fingers moved separately so CT was based on the first finger only. No further movement was allowed after Contact-Time, isolating the somatosensory processing from the previous motor execution. Trials with an incorrect Yes-No response (incorrect trials) or with a response-time slower than 2000 ms were removed from the analysis.

2.3. Behavioral analysis

To give an overview of participants’ performance in each task, we reiterate the results of the two-way repeated measures ANOVA on the discriminability index with the within-subject factor ’group’ (Sighted Controls vs. Early Blinds) and the between-subject variable ’task’ (texture vs. shape) (Gurtubay-Antolin and Rodríguez-Fornells, 2017). No new analyses were conducted regarding behavioral measures.

2.4. EEG acquisition

EEG recordings were acquired from 64 scalp electrodes (Electro-Cap International) using Brain-Vision Recorder software (version 1.3; Brain Products, Munich, Germany). Electrode positions were based on the standard 10/20 positions: Fpz/1/2, AF3/4, Fz/1/2/3/4/5/6/7/8, Fcz/1/2/3/4/5/6, Cz,/1/2/3/4/5/6, T7/8, Cpz/1/2/3/4/5/6, Tp7/8, Pz/1/2/3/4/5/6/7/8, POz/1/2/3/4/5/6, Oz/1/2. An electrode placed at the lateral outer canthus of the right eye served as an online reference. EEG was re-referenced offline to the average of the reference electrodes

(Offner, 1950). Electrode impedances were kept below 5 kΩ. The EEG signal was sampled at 250 Hz and filtered with a bandpass of 0.03–45 Hz (half-amplitude cut-offs). Trials with base-to-peak electrooculogram (EOG) amplitude of more than 100 μV, amplifier saturation, or a baseline shift exceeding 200 μV/s were automatically rejected. These criteria removed electrocardiogram (ECG) contamination in most of the participants. After visually inspecting all the trials and in order to remove trials with remaining ocular artifacts, independent component analysis (ICA) (Delorme et al., 2007) was conducted on three subjects' data where the previous rejection was not enough to remove ECG contamination.

2.5. EEG analysis

In contrast to our previous ERP study on the same data set (Gurtubay-Antolin and Rodríguez-Fornells, 2017), we focused our analysis entirely on brain oscillatory activity. Data was analyzed using MATLAB (The Mathworks, Inc., Munich, Germany), EEGLAB (Delorme and Makeig, 2004) and FieldTrip (Oostenveld et al., 2011). The epoch was defined from 2000 ms prior to the Contact-Time to 2500 ms after it, and time-frequency activity was evaluated using a 7-cycle complex Morlet function.

2.5.1. Sensor-level analysis

Replication on pre-stimulus activity: Following previous reports on reduced alpha waves in blind populations (Adrian and Matthews, 1934; Noebels et al., 1978; Novikova, 1973), we first conducted a replication analysis focusing on the pre-stimulus activity, measuring overall alpha activity (8-12 Hz) at occipital sites between -500 and 0 ms before touching the stimulus. We calculated the total alpha power between 8 and 12 Hz as the sum of the power in the frequencies of the alpha range during the -500 - 0 ms interval and compared it between groups:

$$S(\alpha) = \sum_{f=8}^{12} S(f) = S(f = 8) + S(f = 10) + S(f = 12)$$

We expected to replicate previous results that found decreased posterior alpha activity in the EB group. A 500 ms interval was chosen for this analysis since 200 ms is not enough for a good estimation of the Fourier spectrum. As the frequency is the inverse of time, with an interval of 200 ms, we would get a value every 5 Hz (f = 1/t = 1/0.2s = 5Hz). This means that we would only have a value in the alpha range (8-12Hz).

Task effects: We then assessed task effects quantifying event-related power modulations on alpha band in epochs between -200 and 1000 ms, in steps of 20 ms, and between 1 and 40 Hz, in linear steps of 1 Hz. Trials of the same condition [congruent, incongruent and all (congruent + incongruent)] were averaged for each subject and baseline corrected using the relative change before performing a grand average across all individuals. The baseline was defined as 200 ms prior to the Contact-Time (−200 to 0 ms).

2.5.2. Source reconstruction

Following a similar procedure as in previous studies (Crespo-García et al., 2022; Waldhauser et al., 2015), we identified source activity for the obtained EEG power effects in the alpha band in order to gain a deeper understanding of their significance. Since sensor-level analyses reflect a mixture of different neural sources, they cannot isolate the effect of distinct sources of activity. Hence, sensor-level analysis and source reconstruction are complementary analyses that provide different types of information. We performed a source reconstruction analysis using a template head model. We used the New York head (Huang et al., 2016, p. 201), extracted the brain, skull, and scalp masks, and created a three-layer boundary elements model with their interfaces. Lastly, we combined this model with the electrode positions provided by the manufacturer of the EEG system and created a lead field using OpenMEEG (Gramfort et al., 2010). As the source model we used a homogeneous volumetric grid, with 1 cm of spacing between sources, and labeled the sources according to the automated anatomical labeling (AAL) atlas (Tzourio-Mazoyer et al., 2002). Only the 1210 source positions labeled as cortical were used.

As an inverse method we used dynamic imaging of coherent sources (DICS) beamformer (Gross et al., 2001), an adaptive spatial filter based on the cross-spectral density (CSD) matrix. To maximize the quality of the reconstruction, we tuned the filter using the average CSD matrix for the frequencies and latencies where we found differences in the sensor-level analysis. We performed the source reconstruction separately for each participant and condition, using a participant-specific spatial filter created from the "all" condition (common filter approach). Finally, we reconstructed the average power at each source position for the frequencies and latencies of interest, and corrected by the average power in the same source position during baseline, using the relative change.

2.6. Statistical analysis

We performed statistical analyses on three levels, each feeding from the information obtained in the previous one. Firstly, we compared the sensor-level activity between groups (Sighted Control vs. Early Blind) and between conditions (Congruent vs. Incongruent) using a nonparametric cluster-based analysis (Maris and Oostenveld, 2007), defining clusters based on their frequential, temporal and spatial adjacency. To note, in this type of analysis the data is evaluated as a whole, and the correction for multiple comparisons is performed by the comparison of the whole data with a null distribution designed from random partitions of the original data set. The result of this first analysis is a range of frequencies and latencies at which the activity between groups or conditions differs. As done in previous studies where source reconstruction was conducted to further investigate effects found at the sensor-level (Crespo-García et al., 2022; Waldhauser et al., 2015), we reconstructed the source-level activity for the effects found at the sensor-level, that is, limiting our reconstruction to those frequencies and latencies, and repeated the nonparametric analysis in source space, defining clusters from their spatial adjacency. The result of this analysis is a spatial set of adjacent source positions where there are significant differences in frequencies and latencies. Lastly, we computed post-hoc analyses to assess the effect of the task in each group in the source space. We defined a region of interest (ROI) based on the source showing maximal group differences and introduced its average activity into a mixed-effects ANOVA model with one between-subjects factor (the group), one within-subjects factor (the condition) and their interaction. We hypothesized that generators of maximal between-group differences in alpha activity could reflect the distinct role of alpha oscillations in each group, with alpha activity being related to visual expectation in sighted populations and tactile expectation in blind individuals. Therefore, we expected the source driving maximal group differences would show tactile expectancy effects in the EB group.

2.6.1. Nonparametric cluster-based statistics

The nonparametric statistics used in this work are based on the selection of clusters of adjacent elements (that is, frequencies, latencies, or positions) with a consistent behavior not due to chance. The procedure is as follows: 1) a statistical contrast, in this case either a one sample or two samples t-test, is performed for each data bin (frequency, latency, and position); 2) the significant results ($p < 0.01$) are clustered by adjacency, and the resulting cluster receives a value (the cluster statistic) equal to the sum of the t-statistic of all its members; 3) the data is resampled into random partitions, and 1 and 2 are repeated, generating a null distribution of cluster statistics; and 4) the statistic obtained in the original cluster is compared to this null distribution, and a *p*-value is assigned to it accordingly. In this work we used 10,000 permutations for the sensor-level statistics and 100,000 permutations for the source-level statistics.

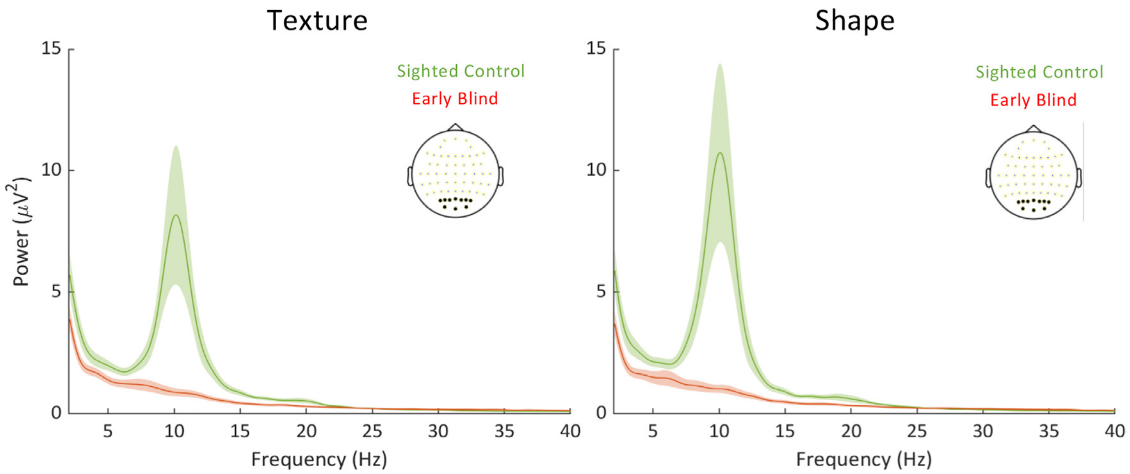

Fig. 2. Replication focusing on the pre-stimulus activity (-500,0 ms). Average power spectral density in the posterior electrodes (marked in the electrode plot) for each group in the texture (left) and shape (right) discrimination tasks. The solid line represents the group average, while the shaded area represents the standard error of the mean. The EB group shows reduced alpha activity in posterior sites in both discrimination tasks.

3. Results

3.1. *Behavioral results*

Detailed behavioral results were reported previously (Gurtubay-Antolin and Rodríguez-Fornells, 2017). Here, we reiterate the main findings to give an overview of participants' performance in each task, but no new analyses were conducted. Overall, participants performed better in the shape discrimination task. The control group showed a lower discrimination index for textures than for shapes, whereas no differences between tasks were observed in the EB group. In the texture discrimination task, a higher discriminability index was found for EBs when compared to sighted but no differences between groups were observed for the shape discrimination task.

3.2. *Sensor-level analysis*

Replication on pre-stimulus activity: We first replicated previous reports on reduced alpha waves in blind populations (Adrian and Matthews, 1934; Noebels et al., 1978; Novikova, 1973). We calculated the total alpha power between 8 and 12 Hz during the -500 - 0 ms interval in occipital and parieto-occipital electrodes and compared it between groups. The results showed that the Early Blind group had significantly lower alpha power during both texture ($t(25) = 2.76$, $p = 0.0109$, Cohen's $d = 1.18$) and shape discrimination ($t(25) = 2.70$, $p = 0.0124$, Cohen's $d = 1.16$) tasks than the Sighted Control group (see Fig. 2).

Task effects: We then assessed task effects on alpha band activity in epochs between -200 and 1000 ms and between 1 and 40 Hz. From here on, all the power estimates will be relative to the baseline (-200 to 0 ms).

In the texture discrimination task, the comparison between groups (Sighted Control vs. Early Blind) showed a significant cluster ($p = 0.0274$) in the alpha band (10 -12 Hz) between 260 and 560 ms after contact time, where the Sighted Control group showed lower alpha power compared to the Early Blind group (see Fig. 3A). In these frequencies and latencies we found that both groups presented a desynchronization relative to baseline, with the control group showing significantly larger values of desynchronization (EB group $t(10) = -2.30$, $p = 0.0443$, Cohen's $d = -0.69$; Controls $t(14) = -8.00$, $p < 0.0001$, Cohen's $d = -2.07$). The effect appeared in occipital, left temporal, and frontal electrodes. The comparison between conditions (Congruent vs. Incongruent) showed no statistically significant differences at this level.

In the shape discrimination task we found similar results. The comparison between groups (Sighted Control vs. Early Blind) showed a significant cluster ($p = 0.0284$) in the alpha band (9 - 12 Hz) between 360 and 660 ms after contact time, where again the Sighted Control group showed lower alpha power (see Fig. 3B). Both groups showed a desynchronization respect to baseline, with the Sighted Control group presenting significantly higher values of desynchronization (EB group $t(10) = -3.88$, $p = 0.0030$, Cohen's $d = -1.17$; Controls $t(14) = -11.51$, $p < 0.0001$, Cohen's $d = -2.97$) . Again, the effect appeared in occipital, temporal, and frontal areas. We did not find any significant difference in the comparison between conditions.

3.3. *Source reconstruction analysis*

In parallel to the sensor-level analysis which represents a mixture of different neural sources, we reconstructed in source space the average power between 10 and 12 Hz in the latencies between 260 and 560 ms for the texture discrimination task, and between 9 and 12 Hz in the latencies between 360 and 660 ms for the shape discrimination task. We then calculated the between-groups comparisons in the source space. As we expected a lower power relative to baseline in the Sighted Control group, we performed a one-tailed t-test.

In the texture discrimination task, the results showed a significant cluster ($p = 0.0156$) where the Sighted Control individuals showed a higher desynchronization than the Early Blind individuals. The comparison between both groups in the shape discrimination task showed similar results, with one significant cluster ($p = 0.0174$). As depicted in Fig. 4, in both cases the largest differences between groups were located in occipital areas, especially the bilateral middle occipital lobe, according to the AAL atlas. Therefore, we selected these areas for the post-hoc analyses.

3.4. *Post-hoc analyses*

We computed post-hoc analyses to assess the effect of task in each group in the source space. As previously indicated, the post-hoc analyses consisted of an ANOVA contrast in which the average power in the middle occipital lobe, relative to baseline, was compared between groups and conditions.

When evaluating the texture discrimination task, the ANOVA contrast revealed both a significant effect of group ($F_{1,24} = 12.9$, $p = 0.0015$) and condition ($F_{1,24} = 12.3$, $p = 0.0018$), together with a marginally significant interaction between both factors ($F_{1,24} = 4.23$, $p = 0.0509$). When considering both groups separately, the effect of condition appeared in the Early Blind individuals ($p = 0.0007$), where the Congruent condition showed significantly higher desynchronization values

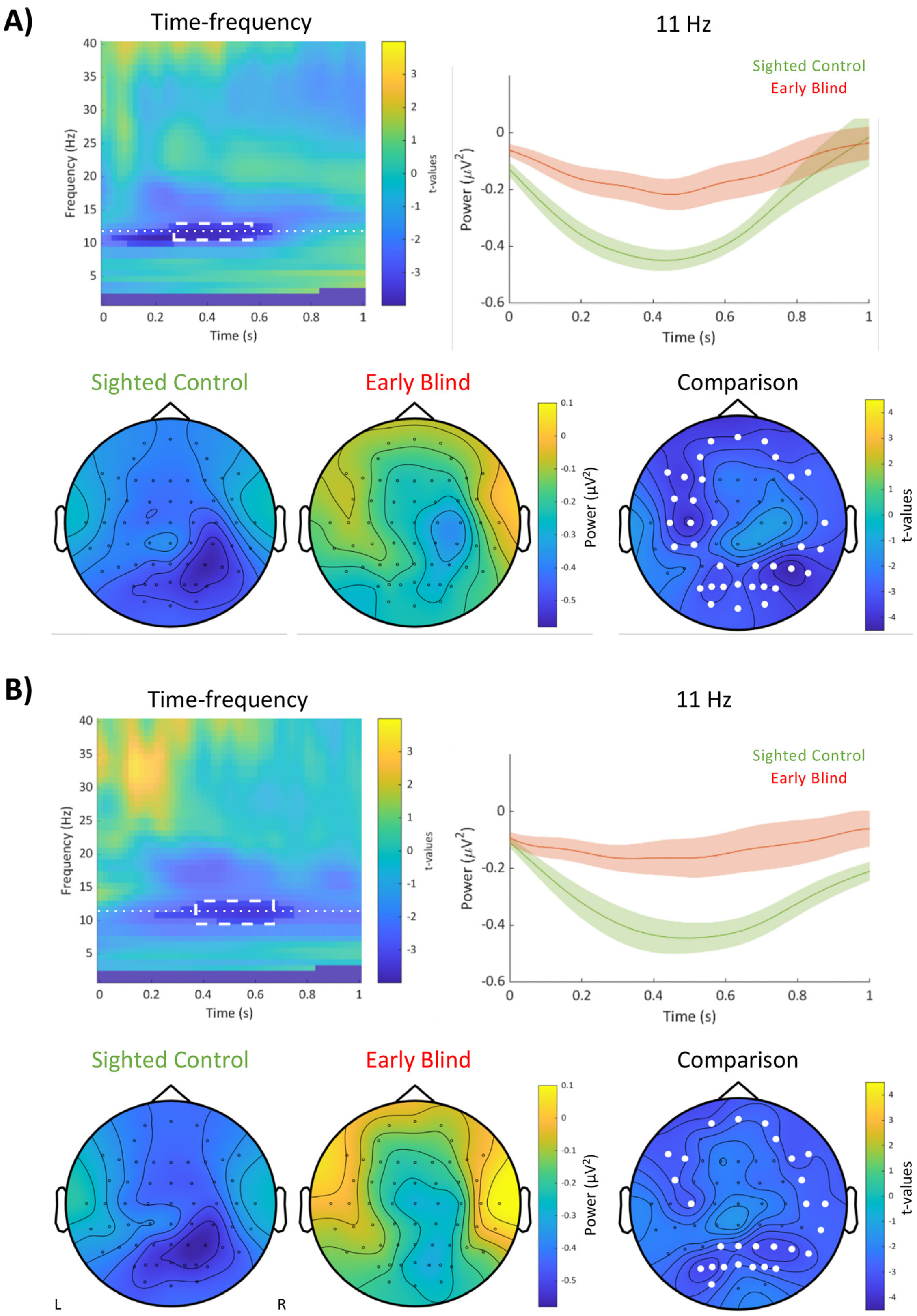

Fig. 3. Results of the sensor-level analyses for the texture (A) and shape (B) discrimination tasks. In both panels A and B, the upper-left image shows the average time frequency over all electrodes, with the significant cluster marked in opaque colors and the nonsignificant data in semi-transparent colors. The upper-right image shows the evoked-related synchronization/desynchronization, separately for the Sighted Control (green) and the Early Blind (red) groups for the wavelet centered at 11 Hz (the center of the significant cluster, represented by a dotted line in the time-frequency graph). Results are shown relative to baseline. The lower-left image shows the topographic representation of the power for the frequencies and times of interest (represented by a dashed rectangle in the time-frequency graph), separately for the Sighted Control and the Early Blind groups. The lower-right image shows the topographic representation of the differences between groups (t-statistic) for the frequencies and times of interest. Notice the reduced alpha desynchronization in the Early Blind group -compared to the Sighted Control group- and the suppression relative to baseline in both groups (in both tasks).

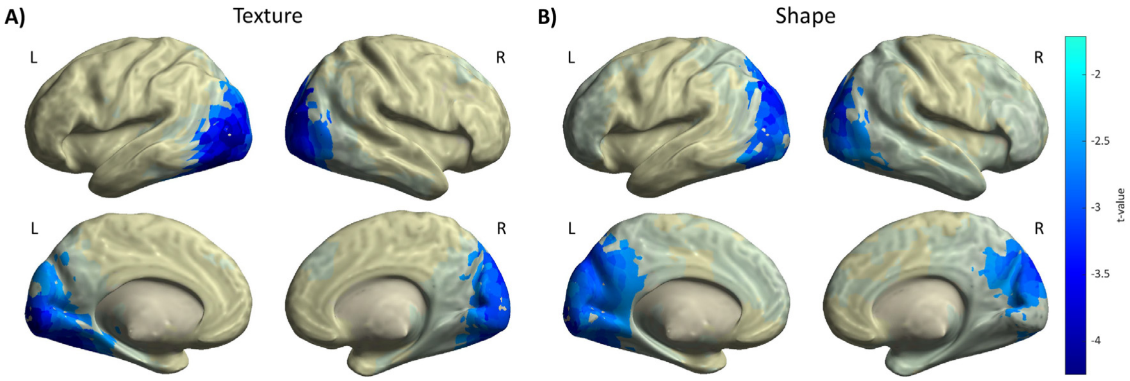

Fig. 4. Topographic representation of the differences between groups (t-statistic) for the frequencies and times of interest in source space for the texture (A) and shape (B) discrimination tasks. The largest differences between groups were located in occipital areas, especially in the bilateral middle occipital lobe. L: Left, R: Right.

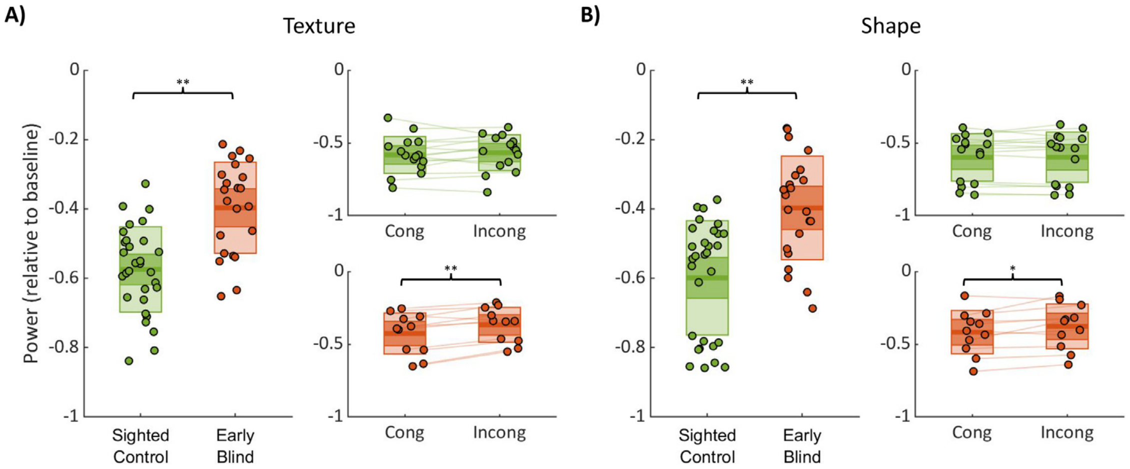

Fig. 5. Power values for the frequencies and times of interest at the middle occipital cortex for the texture (A) and shape (B) discrimination tasks. In both panels A and B, the images on the left show the (baseline-corrected) power for all the trials (congruent and incongruent) separately for the Sighted Control (green) and Early Blind (red) groups. The upper-right images show the (baseline-corrected) power for the Sighted Control group, separately for congruent and incongruent conditions. The lower-right graphs show the same information for the Early Blind group. Notice that alpha activity is modulated by the congruency/expectancy of the trial in the Early Blind (but not in the Sighted Control) group in both tactile tasks. $^{*}p < 0.005$, $^{**}p < 0.01$.

than the Incongruent one, but not in the Sighted Control individuals. These results are shown in Fig. 5A.

Similarly, when evaluating the shape discrimination task the ANOVA showed significant effects of group ($F_{1,24} = 10.1$, $p = 0.004$), condition ($F_{1,24} = 5.8$, $p = 0.024$), and a significant interaction between them ($F_{1,24} = 5.1$, $p = 0.0332$). The effect of condition appeared again in the Early Blind individuals only ($p = 0.0303$), where a larger desynchronization was observed in the Congruent condition. We did not find any differences between conditions in the Sighted Control individuals. These results are shown in Fig. 5B.

4. Discussion

The present study investigated whether posterior alpha oscillations and their role in anticipation depend on visual experience by assessing whether different expectations could modulate alpha activity in visually deprived people in two haptic tasks (texture and shape discrimination). Confirming previous observations, alpha rhythms in parieto-occipital areas were significantly reduced in EB individuals in both haptic tasks. Notably, the source reconstruction analysis revealed that the origin of group differences was in the middle occipital lobe. Interestingly, alpha oscillatory activity in that region was modulated by the expectancy of the condition only in the EB group, with congruent trials evoking higher alpha desynchronization than incongruent ones.

Our observation that alpha oscillatory activity (10-12 Hz) in the middle occipital lobe was modulated by the expectancy of the trial only in the EB group -where a higher alpha suppression was evoked by congruent trials compared to incongruent trials in both discrimination tasks- suggests that the predictive role of alpha oscillations does not depend on visual experience and converges with prior research reporting alpha desynchronizations in the range of 10-12 Hz during the processing of sensory-semantic information in parieto occipital areas (Klimesch et al., 1993, 1994, 1997). Posterior alpha band activity has been systematically associated with visual expectation in sighted people. Specifically, parieto-occipital alpha desynchronization reflects anticipatory states of visual processing (Foxe et al., 1998; Rihs et al., 2009), enhancing the excitability of these areas to facilitate upcoming visual processing (Rihs et al., 2007). On the contrary, alpha synchronization can serve as an active suppressor of unexpected input (Rihs et al., 2007). Of note, pre-stimulus alpha activity was proposed to lead to a later (post-stimulus) amplification of the predicted information since it was correlated with the amplitude of early sensory electrophysiological components (Mayer et al., 2016). In post-stimulus periods, the congruence between expected and actual information has been found to elicit alpha desynchronizations in studies using meaning-trained Mooney images or affective picture processing tasks (Samaha et al., 2018; Strube et al., 2021). In line with the proposed role of alpha oscillations in sighted people, our results show for the first time that alpha oscillations are also modulated by predictions in blind people, and they may play an important role in tactile expectancy. Therefore, we hypothesize that in the case of early blindness, alpha oscillations have a similar function to that related to visual expectancy in sighted populations but switch to the tactile domain (Dormal and Collignon, 2011). This idea is reminiscent of the observation that occipital regions maintain their computational specialization following the loss of vision, but shift their preferred input modality (e.g., from vision to touch), taking advantage of the underlying computational specialization of that area. For instance, the human visual motion-selective area hMT+ has been found to respond to tactile (Beauchamp et al., 2007; Blake et al., 2004; Jiang et al., 2015; van Kemenade et al., 2014) and auditory motion (Battal et al., 2022; Dormal et al., 2016; Poirier et al., 2006; Wolbers et al., 2011) in case of early blindness. Similarly, ventral occipital regions typically showing category-selective responses to specific domains of vision in sighted people were found to respond to analogous categories in non-visual modalities in congenitally blind people (Mattioni et al., 2020; Pietrini et al., 2004; Striem-Amit and Amedi, 2014).

The suggestion that alpha activity may be involved in tactile expectancy in the case of early blindness contrasts with previous suggestions regarding the role that alpha activity plays in this population. Alpha reductions -compared to sighted controls- have been systematically observed while EB individuals were at rest (Adrian and Matthews, 1934; Hawellek et al., 2013; Noebels et al., 1978; Novikova, 1973), dreaming (Bertolo et al., 2003), during haptic tasks (Kriegseis et al., 2006; Schubert et al., 2015) and during mental imagery tasks (Kriegseis et al., 2006). Consequently, posterior alpha oscillations were considered to depend on structured visual input (Bottari et al., 2016; Kriegseis et al., 2006; Novikova, 1973). Additionally, even minimal visual experience (e.g., congenital but incomplete cataracts) was shown to establish the neural mechanisms for alpha generation, whereas the total lack of vision immediately after birth seems to result in permanent impairments (Bottari et al., 2016; Innocenti et al., 1985; Novikova, 1973). Other studies conclude that despite weaker alpha activity during the first three years of life, the main differentiation in terms of alpha activity between sighted and blind subjects happens between 3 and 6 years of life (Campus et al., 2021). These reductions were proposed to reflect a decrease of inhibitory processes as a result of reduced thalamic connectivity (Shimony et al., 2006; Singer and Tretter, 1976) and the reduced activity of pyramidal cells, which are modulated by fast-spiking inhibitory interneurons (Buffalo et al., 2011; Jensen et al., 2012). Importantly, the variety of tasks showing reduced alpha activity in visually deprived populations led to the suggestion that alpha rhythms were not task-specific and did not depend on ongoing sensory or cognitive processes (Kriegseis et al., 2006). Although the overall reduction of alpha activity that we observe in the EB group fits well with this view, our results showing that tactile expectancy can modulate the posterior alpha band activity challenge the idea that alpha rhythms are insensitive to task-dependent factors in congenitally blind people. This converges with previous findings suggesting that alpha band activity may have a functional role in blind populations during tactile processing (Schubert et al., 2019). Of note, the modulation of alpha activity by expectancy was only observed at the source (but not sensor) space, which could be due to the contribution of different neural generators at the sensor-level. Since sensor-level analyses represent the contribution of a mixture of neural sources, it is not possible to disentangle the effect of specific sources of activity. Therefore, we might expect that task expectancy-effects are only visible when isolating the effects of discrete regions driving the largest differences between groups. We predicted that regions responsible for maximal group differences would show tactile expectancy effects in the EB group, because we hypothesized that generators of maximal between-group differences in alpha activity represented the distinct role of alpha oscillations in each group, with alpha activity being related to visual expectation in sighted populations and tactile expectation in blind individuals. The time window where between-group differences emerge in alpha activity (starting at 260 ms for textures and at 360 ms for shapes) is also consistent with the idea, based on the results of our previous ERP study (Gurtubay-Antolin and Rodríguez-Fornells, 2017). We speculate that alpha activity in the EB group may reflect the integration of perceived haptic information with the expected input since the maximum difference between the amplitudes of the ERPs of the congruent and incongruent conditions happened in the 200–400 ms interval for the texture discrimination task and in the 300–500 ms interval for the shape discrimination task. Therefore, alpha activity differences begin 60 ms after the maximal ERP differences between conditions.

Even if the sighted group does not show a modulation of the alpha activity based on tactile expectancy, it presents a prominent alpha desynchronization in both congruency conditions. This result is reminiscent of the parieto-occipital suppression observed in previous studies showing that tactile attention modulates alpha-band activity in parieto-occipital areas (Schubert et al., 2019). We speculate that this suppression may be related to the selection of a hand configuration based on prior studies that locate the source of hand-movement related alpha-band activity in the parietal cortex (Buchholz et al., 2011, 2013), and which activity is likely to extend to occipital areas.

Moreover, the observed increased alpha desynchronization in the congruent condition is consistent with the notion that the iterative checking of the expected features requires higher resources than the detection of a mismatch, and that such resources may be allocated via the engagement of task-relevant regions, in this case, the middle occipital cortex of early blind individuals for processing haptic information. The recruitment of middle occipital areas for the processing of tactile attention is not surprising, given that the involvement of posterior parieto-occipital regions in blind people during tactile processing -due to crossmodal plasticity- has been previously described (Amedi et al., 2003; Jiang et al., 2015; Sadato et al., 1998, 2004; van Kemenade et al., 2014). Interestingly, the recruitment of posterior brain regions is usually reflected in a relatively higher metabolic activity or blood flow in the occipital cortex, which in turn is negatively correlated with alpha power (Sadato et al., 1998). Regarding the higher desynchronization in the congruent condition, we hypothesize that the iterative checking of the expected features elicits a higher alpha suppression as it requires additional resources compared to the incongruent condition (where a single unexpected feature is enough to discard the expected object). This idea is in line with studies conducted in the visual domain (Foxe et al., 1998; Rihs et al., 2009; Samaha et al., 2018; Thut, 2006) and previous work showing that alpha power decreased as stimulus-specific information increased (Griffiths et al., 2019). Likewise, additional resources have been associated with greater alpha band reductions with increasing task difficulty (Pfurtscheller and Lopes da Silva, 1999) or in older (compared to young) participants during haptic object recognition tasks, suggesting a higher cognitive effort needed to perform the task (Pineda, 2005; Sebastián et al., 2011).

It is also important to bear in mind several potential limitations. First, the sample used in this experiment was limited in size, and that could limit the outreach of our results. Increasing the sample would likely reveal differences between conditions at the sensor level. Nevertheless, the source-level analysis helped to increase the signal-to-noise ratio, showing these differences in specific cortical areas. Second, the use of EEG and source reconstruction is not without limitations. While our results are consistent between tasks and with the literature, the spatial resolution of EEG is moderate, and a blurring effect is expected. This may reduce the sensitivity to activity coming from small areas, hiding some interesting effects. A confirmation study using fMRI, with a much higher spatial resolution, or magnetoencephalography, could be helpful to further confirm and extend our findings.

Altogether, our results bring a new understanding of the role that alpha oscillatory activity plays in describing plasticity mechanisms in blindness, indicating that alpha activity is modulated by tactile expectancy in blind individuals through the engagement of task-relevant regions such as the middle occipital cortex.

Data sharing

Processed data and scripts are publicly available on the OSF website (https://osf.io/65bge/).

Declaration of Competing Interest

The authors have no conflicts of interest to declare.

Data availability

Processed data and scripts are publicly available on the OSF website (https://osf.io/65bge/).

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