

Right lateralized alpha desynchronization increases with the proportion of symmetry in the stimulus

Alexis D. J. Makin¹  | John Tyson-Carr¹ | Giulia Rampone¹ | Amie Morris¹ | Marco Bertamini^{1,2}

¹Department of Psychological Sciences, University of Liverpool, Liverpool, UK

²Department of General Psychology, University of Padova, Padova, Italy

Correspondence

Alexis D. J. Makin, Department of Psychological Sciences, University of Liverpool, Liverpool, UK.
Email: alexis.makin@liverpool.ac.uk

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Abstract

Research into the neural basis of symmetry perception has intensified in the last two decades; however, the functional role of neural oscillations remains unclear. In previous work Makin et al. (2014, *Journal of Vision*, 14, 1–12) and Wright et al. (2015, *Psychophysiology*, 52, 638–647) examined occipital alpha event-related desynchronization (alpha ERD). It was concluded that alpha ERD is right lateralized during active regularity discrimination but not during a secondary task. Furthermore, alpha ERD was unaffected by stimulus properties, such as the type of regularity. These conclusions are refuted by new time-frequency analysis on an electroencephalography (EEG) data set first introduced by Makin et al. (2020, *Journal of Cognitive Neuroscience*, 32, 353–366). We compared alpha ERD across five tasks. First, we found that right lateralization of alpha ERD was evident in all tasks, not just active regularity discrimination. This was caused by hemispheric differences in alpha power during prestimulus baseline (left < right), which equalized after stimulus onset (left = right). Second, we found that Alpha ERD increased with the proportion of symmetric elements in the image (PSYMM). Sensitivity to PSYMM was stronger on the right. These findings suggest that known extrastriate symmetry activations are accompanied by reduced alpha power.

KEYWORDS

EEG, LOC, neural oscillations, regularity, time-frequency analysis

1 | INTRODUCTION

Many animals, including humans, are sensitive to visual symmetry and use it for figure-ground segmentation (Machilsen et al., 2009) and mate selection (Grammer et al., 2003). Psychophysical work has shown that people can detect

symmetry within 100 ms and that they are sensitive to symmetry in noisy displays (Barlow & Reeves, 1979; Treder, 2010).

The neural basis of human symmetry perception has been studied extensively in the last two decades (Bertamini et al., 2018). Functional Magnetic Resonance Imaging (fMRI) experiments have identified a network of

Abbreviations: ANOVA, analysis of variance; EEG, electroencephalography; ERD, event related desynchronization; ERP, event related potential; fMRI, functional magnetic resonance imaging; ICA, independent components analysis; LOC, lateral occipital complex; PSYMM, proportion of symmetry; SPN, sustained posterior negativity; TMS, transcranial magnetic stimulation.

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extrastriate visual areas activated by symmetry, including V4 and the object-sensitive lateral occipital complex (LOC, Keefe et al., 2018; Kohler et al., 2016; Sasaki et al., 2005; Tyler et al., 2005). Conversely, symmetry does not activate V1 or V2. Electroencephalography (EEG) studies have shown that the extrastriate symmetry response generates an event-related potential (ERP) called the sustained posterior negativity (SPN, Höfel & Jacobsen, 2007; Jacobsen & Höfel, 2003; Makin et al., 2012). SPN amplitude scales with the salience of different kinds of visual regularity (Makin et al., 2016) and increases with the proportion of symmetry in symmetry + noise displays (Palumbo et al., 2015). Cattaneo et al. (2011) claimed that the LOC is causally involved in symmetry discrimination based on their transcranial magnetic stimulation (TMS) experiments.

While the symmetry response is broadly bilateral, it is sometimes slightly stronger in the right hemisphere. There is converging evidence from four sources. First, Van Meel et al. (2019) found that the symmetry signal could be decoded more reliably from the right LOC. Second, Bona et al. (2014) found that TMS disruption of the right LOC had a greater impact on symmetry discrimination. Third, the SPN is larger over the right hemisphere, and this lateralization is sometimes significant in single experiments (Bertamini & Makin, 2014). Fourth, behavioral work has found that discrimination is superior when symmetry is presented to the right hemisphere (Verma et al., 2013).

Hemispheric specialization has also been studied with time-frequency analysis. The occipital alpha rhythm (around 8–15 Hz) indicates low activation in the visual cortex, resulting from reduced incoming stimulation (e.g., closed eyes) or increased top-down inhibition (Buzsáki, 2006; Klimesch et al., 2007). Meanwhile, visual onsets generate a reduction in occipital alpha power termed event-related desynchronization (alpha ERD). In sum, occipital alpha ERD is traditionally interpreted as a measure of excitation of the visual cortex (Pfurtscheller & Lopes da Silva, 1999). However, invasive recordings paint a more complex picture (Bollimunta et al., 2008) and it is now understood that both alpha ERD and ERS are under top-down control, while alpha can increase signal to-noise ratio in task-relevant networks (Klimesch, 2012). Many studies have used alpha ERD to examine right hemisphere specialization for spatial attention (Gallotto et al., 2020; Pietrelli et al., 2019). Less often, alpha ERD has been used to examine right hemisphere specialization for visual symmetry processing (Makin et al., 2012, 2014; Wright et al., 2015).

Makin et al. (2012) found that alpha ERD was similar for reflection and random patterns, (although results were not entirely consistent across their three experiments). Makin et al. (2014) examined alpha ERD when participants observed reflectional or translational symmetry. Alpha ERD was evident over both hemispheres and was comparable for reflection and translation. It was, however, stronger over the right hemisphere when participants were discriminating regularity

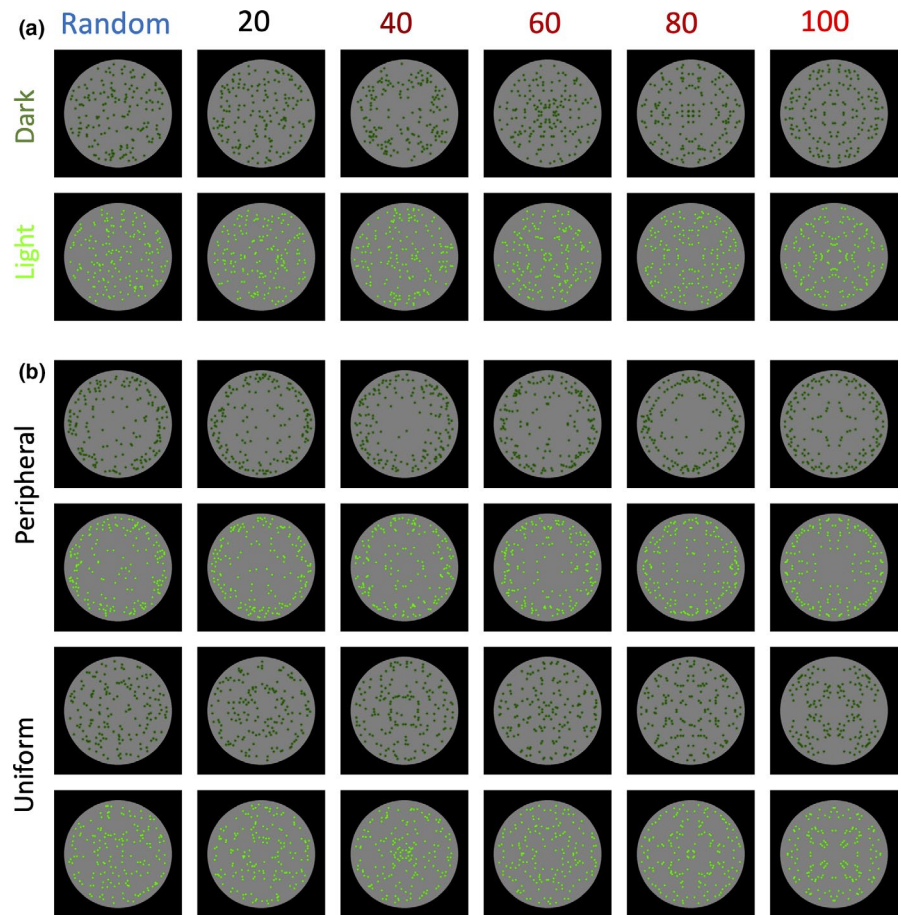
(reflection or translation) but bilateral when they were discriminating the number of objects (one or two). This suggests that active regularity discrimination selectively recruits additional mechanisms in the right hemisphere. In a subsequent study, alpha ERD was again right lateralized for both reflectional and translational symmetry during active regularity discrimination. This was found whether the axis of symmetry was vertical or horizontal (Wright et al., 2015). It was concluded that symmetry discrimination is indeed mediated by neural mechanisms which are right-hemisphere dominant, and those stimulus characteristics, such as regularity type, do not modulate alpha ERD. Stimulus and task manipulations thus have disparate effects on alpha ERD and SPN signals.

These conclusions about alpha ERD are extrapolated from limited published data with small samples. For example, there were 40 participants in the mixed design of Makin et al. (2014), with just 20 participants in the regularity task where the right lateralization was observed (partial $\eta^2 = 0.196$). There were 24 participants in Wright et al. (2015) where this right lateralization was replicated (partial $\eta^2 = 0.260$). The observed power of the hemisphere effect was 0.53 in Makin et al. (2014) and 0.77 in Wright et al. (2015). This suggests that these experiments were underpowered to detect any small effects on alpha ERD, and even the right lateralization may not replicate with the original samples.

To fill these gaps in our understanding of alpha ERD and symmetry perception, we conducted time-frequency analysis on an EEG dataset first introduced by Makin et al. (2020). This data set involved 130 participants across five tasks. This increased sample size has many advantages. For instance, alpha ERD *might be* weakly sensitive to stimulus regularity, and this might not be detected with smaller samples.

In all tasks, we varied the proportion of symmetrical and randomly arranged dots (PSYMM). We presented PSYMM in 20% increments from 0% to 100% (Figure 1). In all tasks, participants made a binary judgment. In the **Regularity task**, they judged whether the patterns contained “Some Regularity” or “No Regularity.” In the **Color task**, the same stimuli were used, but participants judged whether they were light green or dark green. In the **Sound/Color task**, a high- or low-pitched beep was presented simultaneously. The task was to judge the congruence of the relationship between auditory pitch and color (congruent = high pitch and light green or low pitch and dark green, incongruent = high pitch and dark green or low pitch and light green). In the **Direction/Color task**, participants judged the congruence of the relationship between color and the direction of a central triangle (e.g., congruent = upwards triangle and light green, downwards triangle and dark green, incongruent = upwards triangle and dark green or downwards triangle and light green). The two congruence tasks were similar, except that one involved judgment comparing auditory and visual modalities, and the other involved judgments entirely within the visual modality.

FIGURE 1 Stimuli and procedure. (a) Example dark and light green pattern stimuli (rows), with increasing proportion of symmetry (PSYMM) (columns). These pattern types were used in the regularity, color, sound/color and direction/color tasks. (b) Example pattern stimuli used in the distribution task



Participants found the congruence judgments intuitive after some practice (Walker, 2012). Finally, in the **Distribution task** (Figure 1b), participants judged whether the dots were uniformly distributed across the area (Uniform) or disproportionately located around the perimeter (Outside). In this task, participants were attending to an aspect of the configuration but not to regularity itself. An advantage of using multiple levels of PSYMM (rather than just reflection and random) was that it became possible to separate visual responses from binary, decision level responses. Classification is not the same thing as visual representation; the current paradigm makes them dissociable.

SPN waves from this EEG data set have already been reported (Makin et al., 2020). SPN amplitude increased with PSYMM, but the SPN was selectively enhanced in the Regularity task. The parametric SPN response was similar in the other four tasks, despite the different demands.

Based on previous findings (Makin et al., 2014; Wright et al., 2015), we predicted selective right-lateralization of alpha ERD in the Regularity task. We also predicted that alpha ERD would be similar across all levels of PSYMM. However, these predictions were not confirmed. In fact, alpha was right lateralized in all five tasks and increased with PSYMM. Furthermore, we found that the right lateralization can be better described as a cancelation of hemispheric

differences present during the prestimulus baseline, rather than an emergence of hemispheric differences after stimulus onset. It is important to be aware of this when interpreting right lateralization of alpha ERD.

2 | METHOD

Details of the participants, apparatus, stimuli, and procedure are described in Makin et al. (2020). There were 130 participants in total, with 26 in each of the five tasks. The participants gave informed consent before the experiment began. The study had local ethics committee approval (Ref 2,122) and was conducted in accordance with the Declaration of Helsinki (revised 2008).

Sixty-four channel EEG were recorded with a BioSemi Active 2 system (BioSemi, Amsterdam, Netherlands). Experiments were presented using open source *PsychoPy* software (Peirce, 2007). The gray background disk around the elements was 7.7° in diameter. Stimuli were presented for 1.5 s, following a 1.5 s fixation baseline. In all tasks, there were 300 random trials and 60 at each level of PSYMM (20%, 40%, 60%, 80%, and 100%). The other factors in the design were always crossed with PSYMM. Participants entered their binary judgments after stimulus

offset with their left or right index fingers. An ideal observer would press the left and right buttons equally often at each level of PSYMM (so this is unlikely to explain any observed right lateralization effects).

2.1 | EEG analysis

EEG preprocessing was performed using the EEGLAB 13.4.4b toolbox in Matlab 2014b (MathWorks, Natick, USA). Epochs were -1 to 2 s, and EEG a was high pass filtered at 1 Hz, as well as low pass filtered at 25 Hz. Independent components analysis (ICA, Jung et al., 2000) was used to remove high-amplitude artifacts. Component removal was as follows: Regularity task (mean = 5 , min = 1 , max = 12), Color task (mean = 6.85 , min = 1 , max = 20), Sound/Color task (mean = 6.27 , min = 2 , max = 12), Direction/Color (mean = 6.46 , min = 2 , max = 12), Distribution Regularity task (mean = 7.5 , min = 3 max = 12). While there is an element of subjectivity in ICA cleaning, this approach was consistent with previous work: Components which are obviously caused by large blink artifacts or single electrode artifacts can be identified and removed relatively easily. After ICA cleaning, trials were excluded if amplitude was more extreme than ± 100 μV at any electrode. Trial exclusion rates were similar at all levels of PSYMM (Regularity task: 1% , Color task: 2% – 3% , Sound/Color task: 1% – 2% , Direction/Color task: 7% – 8% , and Distribution task: 3% – 4%).

Alpha ERD was examined with the Fieldtrip toolbox (Oostenveld et al., 2011) in Matlab 2014b. Preprocessing was based on our previous studies (Makin et al., 2014; Wright et al., 2015). Frequency bands from 4 to 20 Hz were explored. EEG data at each electrode were convolved with a Hanning-tapered wavelet with four cycles at each frequency. Relative power was measured as proportion change from -500 to 0 ms baseline (so, e.g., -0.4 indicates a 40% reduction in power compared to the baseline interval). Wavelets were positioned at 50 ms increments, so that low-frequency wavelets overlapped to a greater degree than high-frequency ones. We examined frequencies in the 400 to $1,000$ ms window, in 8 – 15 Hz frequency band. These parameters were chosen a priori following Wright et al. (2015). For analysis comparing hemispheres, the electrode clusters were [P7 O1 PO7 PO3] on the left and [P8 O2 PO8 PO4] on the right. We also conducted further analysis on absolute, rather than baseline-relative alpha power. As described below, this revealed that hemispheric differences are better understood as cancelation of baseline lateralization.

For all analysis of variance (ANOVA) analyses, the Greenhouse–Geisser correction factor was used to adjust degrees of freedom when the assumption of sphericity was violated. We report uncorrected degrees of freedom (to facilitate

transparency of the design), the ϵ correction factor (which can be used to adjust reported degrees of freedom), and corrected p values. Large individual variations in alpha power are well documented (Aminoff, 2012). The standard practice of calculating ERD as relative change from the prestimulus baseline removes some of this variation. Outliers are more problematic when analyzing absolute alpha power. We note that 50% of variables violated the assumption of normality in tests of relative alpha power (there were 12 within-subject variables in the Hemisphere X Psymm ANOVA, and 6 were normally distributed across 130 participants according to Kolmogorov–Smirnov test). In contrast, 100% of variables violated the assumption of normality in tests of absolute alpha power (there were 24 within-subject variables in the Time-Window X Hemisphere X PSYMM ANOVA and none were normally distributed). Although ANOVAs are arguably robust to violations of the normality assumption (Blanca et al., 2017), we confirmed that all main effects could be replicated with nonparametric tests (not reported for brevity).

3 | RESULTS

3.1 | Behavioral results

Analysis of behavioral results is reported in Makin et al. (2020). In the Regularity task, participants judged 84% of random trials correctly (by reporting “No Regularity”). Thereafter, correct “Some Regularity” judgments became more frequent as PSYMM increased and plateaued at 80% PSYMM ($\sim 97\%$ correct). In the Color, Sound/Color and Direct/Color tasks, performance was at ceiling throughout ($>98\%$ correct). In the Distribution tasks, performance was above chance but below ceiling ($\sim 87\%$ correct). This shows that the Regularity and Distribution tasks were slightly more difficult than the others.

3.2 | Alpha ERD

Following the conclusions of Makin et al. (2014) and Wright et al. (2015), we predicted right lateralization of alpha ERD in the Regularity task alone. We also predicted that alpha ERD would be similar across all levels of PSYMM. However, the results did not meet these predictions: Alpha ERD was right lateralized in all tasks and increased with PSYMM in all tasks. This can be seen in time-frequency plots in Figure 2 and frequency-top plots in Figure 3.

Alpha ERD effects were then confirmed with a 2 (Hemisphere) X 6 (PSYMM) X 5 (Task) mixed ANOVA (Figure 4a,b). There were main effects of Hemisphere ($F(1, 125) = 23.540$, $p < .001$, partial $\eta^2 = 0.158$) and PSYMM ($F(5, 625) = 8.557$, $p < .001$, partial $\eta^2 = 0.064$, $\epsilon = 0.803$,

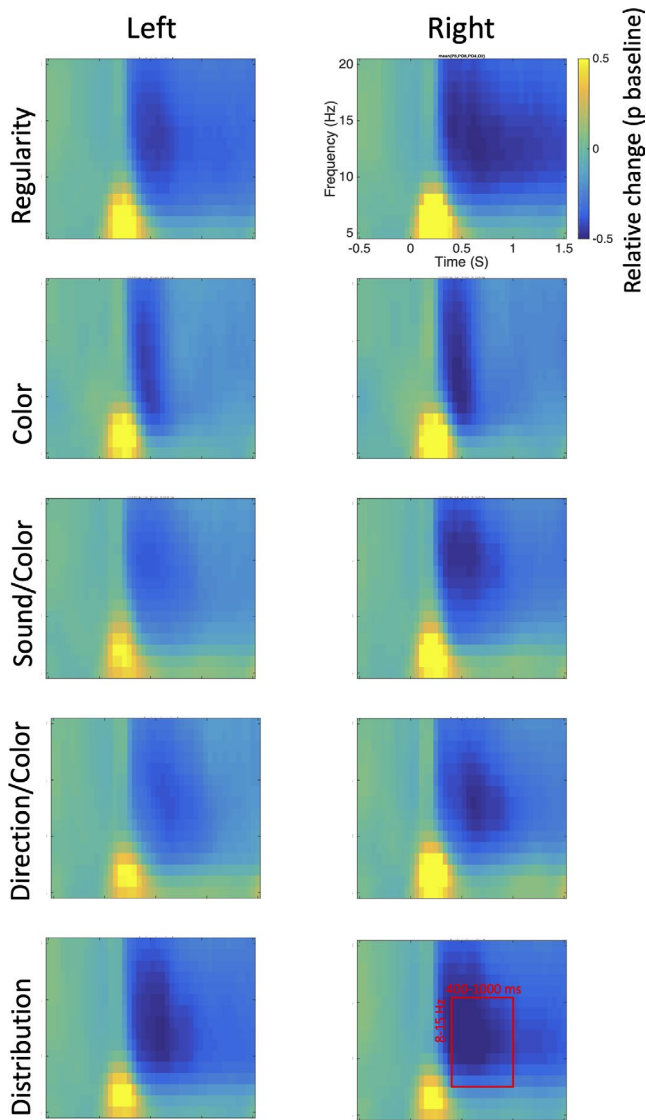


FIGURE 2 Alpha desynchronization results. Time-frequency plots from left and right posterior electrodes (columns) in each task (rows). This data collapses across all levels of proportion of symmetry (PSYMM). The red square on the lower right panel indicates time-frequency window used for statistical analysis

linear contrast $F(1, 125) = 26.700, p < .001$, partial $\eta^2 = 0.176$) and a Hemisphere X PSYMM interaction ($F(5, 625) = 4.892, p < .001$, partial $\eta^2 = 0.038, \epsilon = 0.878$). The linear effect of PSYMM on alpha ERD was significant over both hemispheres but weaker over the left (linear contrast $F(1, 125) = 11.508, p = .001$, partial $\eta^2 = 0.084$) than the right (linear contrast $F(1, 125) = 34.882, p < .001$, partial $\eta^2 = 0.218$). Although ERD was apparently stronger in the Regularity and Distribution tasks (Figures 2 and 3), there were no effects involving Task (the largest was the main effect of Task; $F(4, 125) = 2.075, p = .088$, partial $\eta^2 = 0.062$). Finally, we note that Alpha ERD (as a reduction from baseline) was significant in both hemispheres, at all six levels of

PSYMM (smallest effect; $t(129) = -15.931, p < .001, d_z = -1.397$).^{1,2}

3.3 | Right lateralization of alpha ERD is caused by cancelation of hemispheric differences during the prestimulus baseline

The right lateralization in Figures 2 and 3 could be explained in two alternative ways. First, it could be that alpha power was equal on the left and right during the prestimulus baseline (left = right) and right lateralized emerged after stimulus onset (left > right). Second, it could be that alpha power was greater on the right during the prestimulus baseline (left < right) and equalization was achieved after stimulus onset (left = right). The results presented above are equally consistent with either interpretation. Further analysis confirmed that the second is correct. Absolute alpha power was indeed stronger on the right during the prestimulus baseline, then equal during the originally analyzed effect window (Figure 4a). Furthermore, reanalysis of Makin et al. (2014) and Wright et al. (2015) showed that baseline differences explained the reported right lateralization here as well (Figure 4b,c). In contrast, the main effect of PSYMM and the Hemisphere X PSYMM interaction was not inherited from the prestimulus baseline period.

These impressions were confirmed with repeated measures ANOVAs. The DV was absolute alpha power (rather than relative change from prestimulus baseline). In addition to the original factors, there was an additional factor of Time window (baseline, effect window).

Starting with the current results (Figure 4a), there was a Hemisphere X Time window interaction ($F(1, 125) = 24.721, p < .001$, partial $\eta^2 = 0.165$). There was a main effect of Hemisphere during the baseline ($F(1, 125) = 20.824, p < .001$, partial $\eta^2 = 0.143$) which disappeared during the effect window ($F(1, 125) = 2.996$,

¹It is instructive to report the frequency of these effects across all participants. We recorded bilateral alpha ERD (as a reduction from prestimulus baseline) in 123/130 participants ($p < .001$, binomial test). Alpha ERD right lateralized in 83/130 participants ($p = .002$) and the increased with PSYMM in 88/130 participants ($p < .001$). Finally, 24/130 participants were left-handed. Additional mixed ANOVA found no interaction between Hemisphere and Dominant hand ($F(1,120) < 1, N.S$). The main effect of Hemisphere was still significant in the left-handers ($F(1, 23) = 7.186, p = .013$, partial $\eta^2 = 0.238$).

²In all tasks, half the patterns were light green and half dark green (Figure 1). We term this factor “Greenshade” (although we note that luminance and contrast were not controlled). There was no main effect of Greenshade on Alpha ERD ($F < 1, N.S$). There were no interactions involving Greenshade, although there was a borderline PSYMM X Greenshade effect ($F(5, 625) = 2.302, p = .053$, partial $\eta^2 = 0.018, \epsilon = 0.862$).

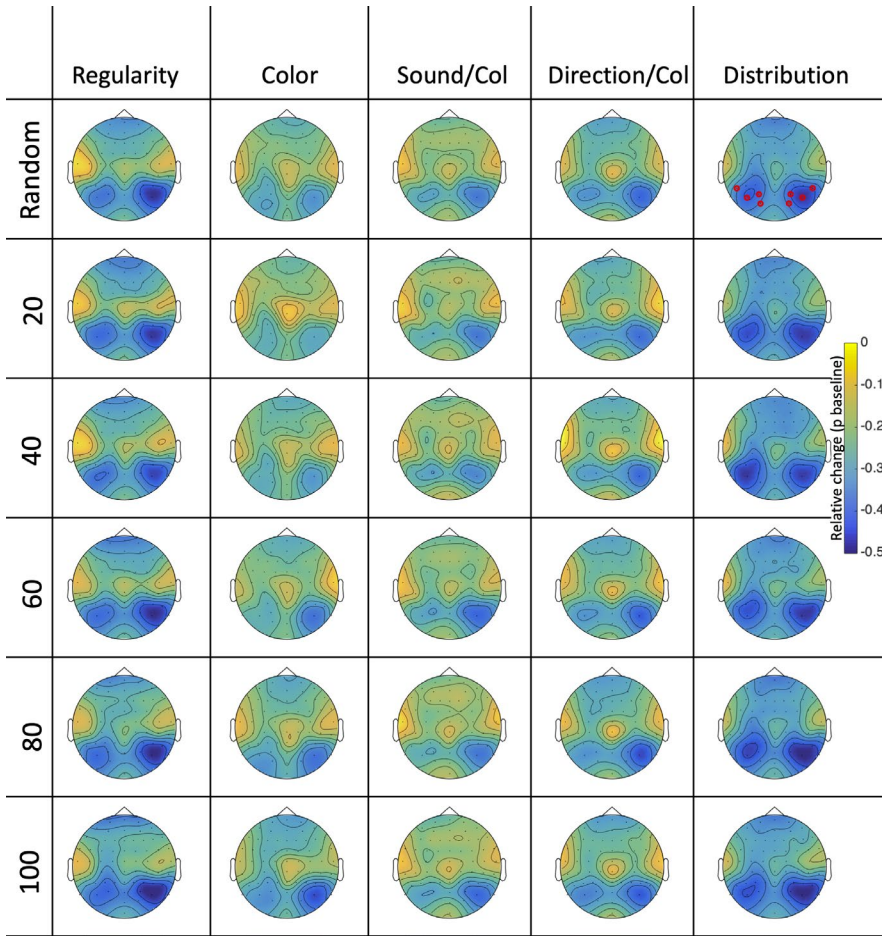


FIGURE 3 Topography of alpha power (Time-frequency window = 8–15 Hz, 400 to 1,000 ms) with increasing proportion of symmetry (PSYMM) (rows) and in the five tasks (columns) electrodes used for analysis are indicated in the top right panel. Note the increase in alpha event-related desynchronization (ERD) with PSYMM

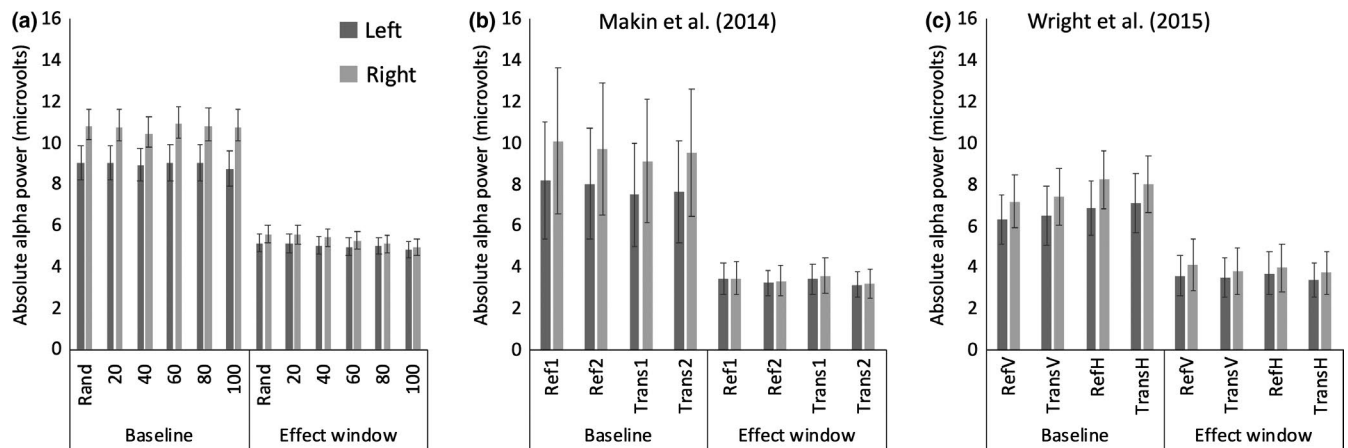


FIGURE 4 Absolute alpha power in baseline and effect windows in (a) current study, (b) Makin et al. (2014), and (c) Wright et al. (2015). During the baseline, alpha is more pronounced on the right (light gray bars). This hemispheric asymmetry in the baseline gives way to hemispheric symmetry during the effect window

$p = .086$). There was also a PSYMM X Time window interaction ($F(5, 625) = 2.636, p = .035, \text{partial } \eta^2 = 0.021, \epsilon = 0.776$). There was no effect of PSYMM during the baseline ($F(5, 625) = 1.008, \epsilon = 0.773$), but one appeared in the effect window ($F(5, 625) = 12.234, p < .001, \text{partial } \eta^2 = 0.089, \epsilon = 0.665$). The PSYMM X Hemisphere

interaction was further modulated by Time Window ($F(5, 625) = 3.639, p = .010, \text{partial } \eta^2 = 0.028, \epsilon = 0.676$). There was no Hemisphere X PSYMM interaction in the baseline ($F(5, 625) = 1.458, p = .222, \epsilon = 0.660$), but one appeared in the effect window ($F(5, 625) = 6.168, p < .001, \text{partial } \eta^2 = 0.047, \epsilon = 0.746$). In the effect window, the

TABLE 1 Pearson's r correlations between different neural signals (averaged over PSYMM)

	Left alpha V right alpha	SPN V left alpha	SPN V right alpha	Gamma V left alpha	Gamma V right alpha	SPN V gamma
Regularity	0.84	0.35	0.29	0.07	0.17	-0.09
Color	0.68	-0.05	0.07	-0.05	0.07	0.21
Sound/color	0.86	-0.20	-0.11	0.17	0.28	-0.01
Direction/color	0.78	0.00	-0.01	0.25	0.29	-0.14
Distribution	0.82	0.09	0.22	-0.22	-0.22	-0.04

Note: Left and right alpha ERD were correlated in all tasks (leftmost column). This means participants who had high alpha ERD in one hemisphere tended to have high alpha ERD in the other. There were no other significant correlations. Bold indicates a significant correlation ($p < .001$).

Abbreviations: ERD, event-related desynchronization; PSYMM, proportion of symmetry; SPN, sustained posterior negativity.

linear effect of PSYMM was weaker on the left ($F(1, 125) = 12.339$, $p = .001$, partial $\eta^2 = 0.090$) than on the right ($F(1, 125) = 35.401$, $p < .001$, partial $\eta^2 = 0.221$).³

Next, we analyzed absolute alpha from Makin et al. (2014, Figure 4b). The Hemisphere X Time window interaction was significant ($F(1, 19) = 4.518$, $p = .047$, partial $\eta^2 = 0.192$). There was a borderline effect of Hemisphere in the baseline ($F(1, 19) = 3.793$, $p = .066$) but not in the effect window ($F < 1$). This suggests that baseline lateralization was the major driver of the reported effects in Makin et al. (2014).

Finally, we analyzed absolute alpha from Wright et al. (2015, Figure 4c). The Hemisphere X Time window interaction was not significant ($F(1, 23) = 3.040$, $p = .095$). However, the effect of Hemisphere was significant during the baseline ($F(1, 23) = 6.106$, $p = .021$, partial $\eta^2 = 0.210$) but not during the effect window ($F(1, 23) = 1.596$, $p = .219$). This again suggests that baseline lateralization was the major driver of the reported effects in Wright et al. (2015).

In summary, alpha power is equivalent in both hemispheres during the effect window. Hemispheric symmetry follows prestimulus hemispheric asymmetry. When alpha power is calculated as a relative change from the asymmetrical prestimulus baseline, it manifests as asymmetrical alpha ERD. This subtlety is an important step beyond the analysis presented in Makin et al. (2014) and Wright et al. (2015).⁴ The effects of PSYMM are not inherited from the baseline in this way.

³We also found another preliminary result in the Regularity task. Alpha was reduced in the prestimulus baseline on 60% PSYMM trials where participants missed the regularity and gave an incorrect response. This suggests a certain amount of prestimulus alpha facilitates perceptual organization.

⁴This is also a challenge to interpretations in our original version of the manuscript. An anonymous reviewer 3 suggested the revealing analysis of baseline alpha.

3.4 | Gamma band analysis

Further analysis revealed a posterior central increase in gamma power (50–100 Hz) during Regularity and Distribution tasks. Gamma did not vary with PSYMM, and gamma was not inversely proportional to alpha. Gamma analysis included supporting information open science framework (<https://osf.io/cru8d/>).

3.5 | Relationship between different brain signals

This data set provided four alternative neural responses. SPN amplitude was reported in Makin et al. (2020). Left and right hemisphere alpha ERD is reported above. Posterior-central gamma is reported in the supporting information. Are these four neural responses related to each other? For instance, do participants with large SPNs also show enhanced alpha ERD? Mean correlation coefficients (collapsed across levels of PSYMM) are shown in Table 1. There was a significant relationship between left and right ERD in all tasks. That is, participants with large alpha ERD on the left tended to have large alpha ERD on the right ($p < .001$). There were no other significant correlations ($p > .05$).

4 | DISCUSSION

This analysis of event-related alpha desynchronization (alpha ERD) during five different tasks provided unexpected results. Our previously published claims require substantial revision. There was a right lateralization of alpha ERD in all tasks, not just Regularity discrimination. However, this is best understood as emergence hemispheric symmetry (left = right) following an asymmetrical baseline (left < right), rather than emergence asymmetry (left > right) following a symmetrical baseline (left = right). Baseline asymmetry also explains right

lateralization effects reported in Makin et al. (2014) and Wright et al. (2015). This baseline hemispheric asymmetry is unlikely to be an artifact of our apparatus: The occipital alpha rhythm can be up to 50% strong over the right hemisphere (Aminoff, 2012). Furthermore, central warning cues are associated with increased right lateralized alpha oscillations before stimulus onset (Gallotto et al., 2020). However, baseline differences cannot explain our most important new result: Namely, Alpha ERD increased with PSYMM, and the effect of PSYMM was stronger on the right.

Despite the all-important caveat regarding baselines, one could maintain that the current results *do* show a right lateralized response, although not in the straightforward way proposed by Makin et al. (2014) and Wright et al. (2015). The relative change from baseline was indeed greater in the right hemisphere, and this is the standard way to analyze alpha ERD (Klimesch, 2012). It is not that right lateralization effects reported by Makin et al. (2014) and Wright et al. (2015) should be dismissed as mere artifacts, but a more subtle understanding of their origins is essential. Furthermore, the effect of PSYMM was stronger on the right, and this cannot be attributed to baseline imbalances. This aspect of our results unambiguously demonstrated that the right hemisphere is specialized for symmetry perception.

It is likely that the PSYMM manipulation used here was stronger than the reflection versus translation comparison used in Makin et al. (2014) and Wright et al. (2015). That partly explains why we now observe a stimulus-driven effect on alpha ERD that was not seen previously. We should also consider increased statistical power. While previous work had similar samples *per task* (20 in Makin et al., 2014, 24 in Wright et al., 2015), we can now combine data over five tasks ($26 \times 5 = 130$ total) rather than just one or two. This allows us to see stimulus effects which may be missed in smaller samples. Post hoc power analysis shows that at least 46 participants are required for a >80% chance of replicating the observed main effect of PSYMM, and 73 participants are required for >80% chance of replicating the observed Hemisphere X PSYMM interaction. If these effect sizes are representative, it is not surprising that previous experiments with smaller samples found no effect of stimulus regularity on Alpha ERD. These are important considerations when designing future experiments.

Alpha ERD partly resembles the SPN waves recorded from the same data set (Makin et al., 2020): The SPN also scaled parametrically with PSYMM. However, the SPN was clearly enhanced in the Regularity task compared to the other four tasks, and this was not found for alpha ERD. Furthermore, there was no correlation between SPN and alpha ERD at the individual subject level (Table 1). We conclude that alpha ERD and the SPN index the same extrastriate symmetry

response. However, the SPN is a more precise measurement and these signals are subject to nonoverlapping sources of interindividual variation.

Precision notwithstanding, it would be interesting to analyze alpha ERD responses to symmetrical 3D objects rather than symmetrical 2D images. Symmetrical 2D images are the most common stimulus in lab experiments. However, in the real world, symmetrical objects only project symmetrical images when viewed from specific viewpoints. Human faces provide an intuitive example: Faces only project a symmetrical image if the person is viewed directly from the front rather than from the side (Chen et al., 2007). Any useful symmetry detection mechanism must be sensitive to symmetrical objects seen from generic viewpoints (Sawada & Pizlo, 2008; Szlyk et al., 1995). The SPN is tuned to object level symmetry when symmetry is task relevant (Makin et al., 2015). Future work could determine whether this is also true of alpha ERD.

In the supporting information (<https://osf.io/cru8d/>), we report high-frequency gamma band oscillations (50–100 Hz). Previous work suggests that alpha and gamma are inversely related (Buzsáki, 2006; Klimesch et al., 2007). Although we found a novel posterior-central gamma band response in Regularity and Distribution tasks, this could have been caused by small eye movement artifacts (Yuval-Greenberg et al., 2008). The gamma results are an interesting exploratory analysis, but they should not be overinterpreted.

5 | CONCLUSIONS

We found that alpha ERD increases with the proportion of symmetry in symmetry + noise displays (PSYMM). The effect of PSYMM on alpha ERD was bilateral but stronger over the right hemisphere. Furthermore, the same pattern of alpha ERD was found across five tasks with different cognitive and perceptual requirements. As with previous studies (Makin et al., 2014; Wright et al., 2015) alpha ERD was right lateralized. New analysis clarified the origins of this effect: It is best understood as hemispheric asymmetry only in relation to an asymmetrical baseline (in the past a symmetrical baseline was assumed). These findings are major step forward in understanding the role of alpha ERD in symmetry processing.

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CONFLICT OF INTEREST

We declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Alexis Makin designed and programmed the experiments, facilitated data collection, analyzed the EEG data, and wrote the manuscript. Giulia Rampone assisted with data analysis and interpretation. Amie Morris collected the EEG data for the Regularity and Color Tasks. John Tyson-Carr conducted the gamma band analysis in the supporting information. Marco Bertamini programmed the stimulus construction algorithm and contributed to data interpretation and manuscript writing.

OPEN SCIENCE POLICY

All materials for rerunning the experiments and re-analyzing the results are available on Open Science Framework (<https://osf.io/cru8d/>). We are happy for others to re-use these materials. All ERP data from our lab, along with user friendly analysis and analysis tools, are now available in one complete SPN catalog also on Open Science Framework (<https://osf.io/2sncj/>).

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ejn.15176>.

ORCID

Alexis D. J. Makin  <https://orcid.org/0000-0002-4490-7400>

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