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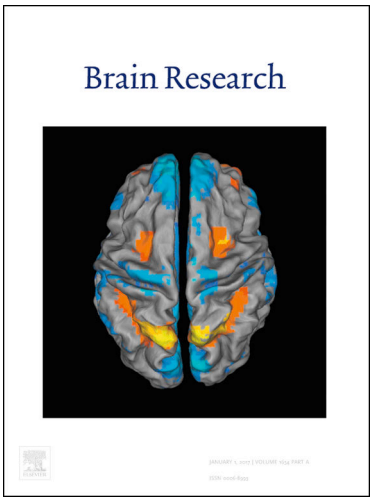

Research report

The relationship between visual discomfort and cortical excitability in cone-opponent stimuli

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Running Head: Visual discomfort in cone-opponent stimuli

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Abstract

Increased colour contrast can induce visual discomfort, but there is little research on the effect of hue. Colour is processed via one or more information streams or channels. We hypothesized that hues which activate more than one channel would induce greater visual discomfort, as they will demand greater neural resources. Normally-sighted young observers made discomfort judgments of isoluminant stimuli of varying hue and contrast whilst EEG was recorded. As predicted, stimuli recruiting more than one channel were more uncomfortable, and this increased with contrast. Uncomfortable stimuli showed increased N2 event-related potentials and decreased alpha-band oscillations, potentially indicating increased neural excitability. This is evidence that increased neural responses are related to visual discomfort for chromatic stimuli. Furthermore, it suggests that the origins of visual discomfort are in early visual areas, when colour is represented in a cone-opponent space, rather than later areas where colour representation is determined by perceptual similarity.

Highlights

Chromatic visual discomfort is related to contrast, but there is less research on hue

Cone-opponent, isoluminant stimuli were used to measure discomfort and EEG

Intercardinal axes were more uncomfortable and showed higher ERP amplitude

Lower alpha power suggests increased excitability for uncomfortable stimuli

1. Introduction

Visual discomfort is an aversive subjective experience which occurs when viewing certain stimuli, such as striped patterns and flickering lights, and can elicit symptoms such as eyestrain, headache, diplopia and blurring (Sheedy et al., 2003). Specific populations can be particularly susceptible to visual discomfort, including those with migraine (e.g. Marcus and Soso, 1989). Visual discomfort has been shown to vary with the spatial characteristics of stimuli. For example, high-contrast monochromatic gratings (e.g. Marcus and Soso, 1989) and filtered noise patterns with particular spatial frequency content (e.g. O'Hare and Hibbard, 2011) make particularly uncomfortable viewing.

Visual discomfort may stem from inefficient processing of visual stimuli that results in increased neural activity (e.g. Hibbard and O'Hare, 2015; Huang et al., 2003; Penacchio and Wilkins, 2015). The theory of inefficient coding predicts that sensory systems in general, and the human visual system in particular, create parsimonious representations of commonly encountered stimuli (i.e., natural scenes) based on their statistical regularities. The theory predicts that these efficient representations will optimise information, whilst limiting metabolic cost (Olhausen and Field, 1996). There is an association between increased discomfort and increased neural activity in both greyscale images (O'Hare et al., 2015; O'Hare, 2017) and chromatic images (Haigh et al., 2013; Haigh et al, 2019; Lindquist et al., 2021). This association has also been found with complex stimuli, Le et al. (2017) found that urban scenes with statistics that deviated from those found in nature were more uncomfortable and create a larger haemodynamic response. In addition to increased neural activity, chromatic contrast is also associated with greater alpha suppression, which is thought to be indicative of increased cortical excitability (Haigh et al., 2018).

There is evidence that chromatic properties of an image can affect discomfort, specifically the relative hues of colours presented together. This began in 1997 when a cartoon was shown on Japanese television which consisted of a large area of the screen flashing deep blue to red at around 12Hz, this induced seizures in over 600 children (Ishida et al., 1998). Although, it is unclear whether the precipitating factor was the flicker, the chromatic content or both. However, greater chromatic contrast corresponds to higher levels of discomfort (Haigh et al., 2018), suggesting that chromatic contrast may increase neural activity independent of flicker. Recently, Penacchio et al. (2021) averaged the local differences in chromaticity within abstract art images and found that this average was a good predictor of visual discomfort. Furthermore, the chromaticity differences in uncomfortable stimuli were significantly greater than those found in natural scenes, except those which depicted fruit and foliage.

Chromaticity separation, how different colours are, has been found to modulate discomfort. Greater chromaticity separation in CIE space results in greater ERP responses and greater reported discomfort in migraine and control groups (Haigh et al., 2019). Similarly, greater chromaticity separation in CIE space results in greater electrophysiological response to 5Hz flicker (Lindquist et al., 2021). However, this effect was not found for 3Hz flicker, suggesting that a certain amount of exposure may be required to elicit the effect (Lindquist et al., 2021).

Research into the influence of chromatic contrast on visual discomfort has mostly used CIE space which plots colour based on perceptual similarity (e.g. Haigh et al., 2013; Haigh et al., 2018).

However, there may also be a relationship between visual discomfort and the relative stimulation of different cone photoreceptors in the eye (red/long wavelength – L, green/medium – M, blue/short – S). This can be investigated by considering position in a cone-opponent colour space such as MB-DKL space (Macleod and Boynton, 1979; Derrington, Krauskopf and Lennie, 1974). MB-DKL space is spherical and describes colours according to the following parameters: luminance or L+M (elevation from the azimuth), contrast (distance from the origin), and hue (position on the azimuth). The cardinal directions across the azimuth (0-180° and 90-270°) are shown in Figure 1, and represent the two colour channels; parvocellular (L-M or salmon/turquoise) and koniocellular (S-(L+M) or violet/lime). Haigh et al. (2013) did transform their stimuli into cone-opponent space, but did not find a relationship to discomfort judgements. However, this was a post-hoc calculation and stimuli were not necessarily cone-opponent for each observer.

**********Figure 1 here **********

Early cortical areas, for example V1, have been shown to respond strongly to contrast in the cardinal directions of cone-opponent colour space, but less strongly to colours on the intercardinal axes (Mullen et al. 2007). Importantly, most of the chromatic information in natural scenes is along the cardinal directions, with relatively little information along the intercardinal axes (Ruderman et al., 1998), suggesting that the early visual system may be optimised for natural scenes. Conversely, it has been suggested that sensitivity in later areas, such as V4, might be associated with perceptual colour similarities (e.g. Brouwer and Heeger, 2009; McKeefry and Zeki, 1997). To give an example, blue (S-(L+M)) and green (L-M) would have entirely separate mechanisms in areas sensitive to cone-opponency (V1), but could have similar mechanisms in perceptual space (V4). Therefore, if stimuli defined by the cardinal and intercardinal directions in cone-opponent space induce different amounts of discomfort, this could suggest that the sensation is generated in early visual anatomy. This would be in contrast to Haigh's (2018) suggestion that perceptual colour space was a better predictor of discomfort.

The current study will investigate visual discomfort using cone-opponent stimuli. According to the principles of inefficient coding, the cardinal axes should create less discomfort compared to the intercardinal axes. The intercardinal axes require both colour mechanisms (L-M *and* S-(L+M) and therefore should demand greater recruitment of neural resources, compared to the cardinal directions which require processing by only one mechanism (L-M *or* S-(L+M)). In accordance with Goddard et al. (2010) it is understood that the intercardinal directions induce the same magnitude of activation in the L-M and S-(L+M) channels as stimuli that only activate one pathway.

Gain control of S cone information means that despite initial imbalances in the number of S cones, the cardinal chromatic channels are largely equivalent by the time information reaches V1 (Mullen et al., 2008). However, to further complicate matters, whilst this is true for 8Hz stimuli it is not the case for stimuli presented at 2Hz, demonstrating differences in gain control depending on the speed of presentation (Mullen et al., 2008). This may relate to the finding by Lindquist et al. (2021) that slower flicker rates do not induce increases in neural activity in the same way as faster ones. Given the possible interaction between flicker and chromatic content in visual discomfort, sustained stimulus presentations will be used in the current study. It should also be noted that the absolute amount of activation is less relevant that the number of brain areas that are active. Lennie (2003) showed that as there are so many neurons in the brain, having even a small proportion active at one time, even at relatively low levels, will result in a large metabolic cost. They conclude that task difficulty is related to 'how much cortex is active', and not the rate of firing.

2. Experimental Procedure

2.1 Apparatus

Experiments were conducted in a quiet, darkened room. Observers were seated 1m from the display. Head movements were restricted using a chinrest. Stimuli were presented using MATLAB (2015a) and the Psychtoolbox (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). Stimuli were presented using a MSI (MS-7788) computer with i7-3990CPU Intel processor, NVida GeForce GTX 650 graphics card, running Windows 7 using Matlab 2014 (The Mathworks, Natick, MA, USA) and the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). The display was 22" Illyama Vision Master Pro 514 monitor set to a resolution of 1024 x 768 with a refresh rate of 85Hz, using a Bits# stimulus processor (Cambridge Research Systems, Cambridge, UK). The display was calibrated using a JETI Specbos 1211 spectroradiometer (JETI, Jena, Germany).

2.2 Observers

19 observers were recruited through opportunity sampling at the University of Lincoln. Participants were screened for normal colour vision using the Ishihara colour vision test (Clark, 1924). Individuals with a personal or close family history of epilepsy were excluded from participation. All experiments adhered to the Declaration of Helsinki (2013) guidelines for experiments with human participants. Ethical approval was sought from the University of Lincoln, School of Psychology Ethics Committee. All participants gave their written informed consent before taking part in the study. Data from six participants was lost due to technical issues during the recording, leaving thirteen participants with EEG data of sufficient quality to analyse. The stimuli consisted of 160 trials per participant (see below) and there were 13 participants in the final analysis, this leads to 2080 trials, which is greater than the recommended number of trials for linear mixed effects models (Brysbaert & Stevens, 2018).

2.3 Stimuli

Stimuli consisted of four isoluminant gratings presented in MB-DKL colour space using the Psychtoolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007). The two cardinal axes representing the two cone-opponent channels and examples of the four stimulus types are shown in Figure 1, in DKL space these were 0-180 degrees (salmon to turquoise), 90-270 degrees (lime to violet) and the two intercardinal axes were 45-225 degrees (pink to green) and 135-315 degrees (blue to orange) in DKL colour space. To account for individual variation in isoluminant point, this was measured for each participant (see below for details) and elevation in DKL space was adjusted accordingly.

A luminance grating (black and white) was used as a comparison pattern in the main EEG experiment. Contrast of the luminance grating was set to 0.1. Due to individual variation in detection thresholds, multiples of individual detection thresholds were used for chromatic stimuli so that they were matched for visibility (see below for details). All gratings appeared as squares against a mid-grey background and subtended 6.5° of visual angle. Stimuli had a spatial frequency of 0.54 cpd. Spatial frequency content is important, as there is spatial frequency tuning between isoluminant and luminance gratings, which equalises around 5 or 6 cycles per degree for stimuli subtending 6 degrees (Adjamian et al., 2008).

2.4 Procedure

2.4.1 Measuring Individual Isoluminant Points

Each participant's psychophysical isoluminant point was measured using the minimum motion paradigm, and stimulus presentation was adjusted accordingly to prevent luminance artefacts (Anstis & Cavanagh, 1983). In this method, two chromatic gratings are interleaved with two low-contrast achromatic gratings. The phase of the four gratings is arranged in quadrature (e.g. chromatic gratings at 0 and π phase, and achromatic gratings at π/2 and 3π/2). When the chromatic gratings are isoluminant the stimulus simply counterphases. However, if a luminance artifact is present in the chromatic channel then a phase advance (i.e. directional motion) will be perceived. Participants reported, in a 2AFC task, the perceived direction of the stimulus while the actual direction of phase advanced was randomised. The elevation of the chromatic stimulus in MB-DKL space was then adjusted in accordance with a one-up-one-down staircase until no coherent motion was perceived and response accuracy was at chance. Previous work comparing photometric and psychophysical isoluminance showed no differences (Sharman et al., 2013). It should be noted that if luminance artefacts remained despite our efforts, this would result in a reduction of any difference between conditions, as the luminance artefacts would dominate the response, making the two conditions more similar rather than less.

2.4.2 Determining Contrast Detection Threshold

The detection thresholds for each of the four stimuli were measured for each individual observer using a 2AFC task. Contrast (distance from the origin in DKL space) was controlled using a staircase procedure (Minimum Expected Entropy; Sanders and Backus, 2006), with 4 interleaved conditions of 40 trials each. In this staircase method, stimuli are chosen from a subset of possible values provided at the start by the experimenter. The stimulus level for a particular trial is chosen as the one that will provide the most information, based on the most unambiguous probability distribution (the minimum entropy). The initial trial can be set based on a prior distribution, but in this case the first trial was set to be 75%. Stimuli were presented for 506ms in each interval, with a fixation cross of radius 0.15 degrees and duration 0.2 seconds between each, presented for 0.5 seconds. After the presentation of the second stimulus, observers indicated which of the two intervals contained the grating using the arrow keys on the keyboard, the left arrow key to indicate the first interval and the right arrow key to indicate the second interval. The contrast detection threshold was extracted by fitting a cumulative Gaussian function to the data from these staircases.

2.4.3 Main EEG experiment

A two-interval forced choice paradigm was used, comparing the isoluminant stimuli to a greyscale control stimulus. Observers were asked to choose the interval containing the most uncomfortable stimulus out of the pair, using the left arrow key to indicate the first interval, and the left arrow key to indicate the second interval. Presentation order was randomised. Stimuli were displayed for 506ms each. During the interstimulus interval a fixation cross was presented for 700ms with a jitter of up to 300ms to prevent phase locking.

2.4.4 EEG Data Acquisition

EEG data were recorded using a 64-channel Biosemi Active Two system, and the 10-20 electrode placement system. There were eight additional facial electrodes placed on the left and right mastoids, outer canthi, suborbital and supraorbital locations. The Biosemi system uses a common mode sense electrode and driven right leg electrode to create a feedback loop to act as the ground electrode during recording, improving the impedance, for details please see

https://www.biosemi.com/faq/cms&drl.htm. In addition, conductive gel was used to improve impedance. Data were initially sampled at 2048Hz, and decimated to 256Hz offline.

Data were exported to MATLAB 2017 (The Mathworks, Natick, MA, USA), using the EEGLAB extensions for data cleaning and analysis (Delorme and Makeig, 2004). Data were band-pass filtered between 0.1Hz and 40Hz, to remove artefacts such as drift and line noise. Extreme bad channels were removed via visual inspection, prior to re-referencing data to the average of all channels (excluding the facial electrodes). Any remaining bad channels were removed using the automatic channel rejection procedure, estimating the joint probability and rejecting channels exceeding a threshold of 5 standard deviations. Data were divided into epochs of -200 to 1000ms around stimulus onset, removing a 200ms baseline prior to stimulus onset. Epochs containing extreme artefacts were rejected using an automated procedure, any epoch exceeding a threshold of ±500μV was excluded from analysis. Finally, a Gratton-Coles procedure (Gratton et al., 1983) was used to correct for eye movement artefacts, using a threshold of ±200μV in a time range of 20ms for blink detection. This procedure uses a regression-based method to estimate propagation factors based on the ocular channels and applied a correction to the remaining channels based on this. Electrodes of interest were those over early visual areas, O1, O2 and Oz. As these showed a similar pattern of results, data were averaged over the three channels.

2.5 Statistical Analysis

The peak ERP response was estimated as the mean value in a time period post stimulus onset: P1 was taken as the mean value between 70 and 100ms, the N2 component between 150 and 230ms, and the P3 component was estimated as the mean value between 250 and 400ms. Relatively wide time-windows were chosen as ERP responses to cardinal axes have different latencies compared to intercardinal axes (Forder et al., 2017). These values were extracted for each observer for each epoch. Linear mixed effect models were used to estimate the effect for data on a trial-by-trial basis.

Linear mixed effect models allow for the analysis of non-independent observations, in this case multiple trials from the same observer, by accounting for the variance of each individual as a random effect. Three linear mixed effects models were fitted to the ERP data (one for P1, one for N2, and one for P3) for each individual trial using the MATLAB function "fitglme". Fixed effects were chromatic axis (cardinal or intercardinal) and chromatic contrast (in multiples of threshold), and observer was included as a random effect. Prior to this, outlying data points were removed using a threshold of 4 x Cook's distance. Visual inspection of the residuals of the model fit after removal of outliers showed a normal distribution.

Behavioural data were modelled using a generalised linear mixed effect model, including a binomial distribution and a logistic link function, including axis (cardinal and intercardinal) and contrast (multiples of threshold) as fixed effects, and again observer as a random effect. This process has the advantage of not assuming underlying distribution, and not excluding observers whose data do not follow a sigmoid.

The correlation coefficient is reported as a simple (unstandardised) effect size estimate. According to Baguley (2009) there are good reasons for preferring the simple compared to standardised effect size, firstly, the correlation coefficient is in the original units of measurement and is arguably more meaningful and easier to interpret than a standardised measure. Secondly, the simple effect size removes some of the pitfalls of standardising the measure - for example, correction for differences measurement design can be problematic, in particular for mixed effects models. Thirdly, it is unclear whether two studies using different measurement methods and designs would be able to be

compared using standardised effect sizes. Therefore, in the current study the regression coefficients are reported as simple (unstandardised) effect sizes.

3 Results

3.1 Behavioural Responses

Results showed a significant effect of axis ($F(1,2594) = 81.14$, $p < 0.01$), the cardinal axis was less likely to be chosen as uncomfortable compared to the intercardinal axis (by a coefficient of -1.08 ± 0.12 standard error, 95% confidence intervals [-1.31 -0.84]) (Figure 2). There was also a significant effect of contrast ($F(4,2594) = 4.23$, $p < 0.05$), compared to the lowest level of contrast (threshold), 2 x threshold was more likely to be chosen as uncomfortable (coefficient 0.38, ± 0.17 SE, 95% CIs [0.036, 0.71]), as were 3 x threshold (coefficient 0.43, ± 0.18 SE, 95% CIs [0.08, 0.77]), 4 x threshold (0.48 ± 0.18 SE, 95% CIs [0.13, 0.82]) and 5 x threshold (0.72 ± 0.18 SE, 95% CIs [0.36, 1.07]).

**********figure 2 here **********

3.2 Event-Related Potentials

Figure 3 shows the ERP waveforms for chromatic axis and chromatic contrast.

**********figure 3 here **********

3.2.1 P1

Chromatic axis did not statistically significantly predict P1 amplitude ($F(1,2445) = 3.62$, $p = 0.057$), and contrast did not predict P1 amplitude ($F(4,2445) = 0.35$, $p = 0.84$) (Figure 4). Compared to cardinal, the response to intercardinal axis colours was reduced by -0.66 (±0.51 standard error (SE), 95% confidence intervals of [-1.66, 0.32]). Compared to the lowest contrast level (threshold), responses to 2 x threshold were increased by -0.32, (±0.51 SE, 95%CIs [-1.32, 0.68]), 3 x threshold were increased by 0.38 (±0.51 SE, 95% CIs [-0.62, 1.37], 4 x threshold was reduced by -0.42, (±0.51 SE, 95% CIs [-0.98, 1.01]), and 5 x threshold was increased by 0.1 (±0.51 SE, 95% CIs [-0.98, 1.01].

**********figure 4 here **********

3.2.2 N2

Chromatic axis predicted the N2 component amplitude ($F(1,2461) = 4.88$, $p = 0.027$), but contrast did not ($F(4,2461) = 0.87$, $p = 0.48$), see Figure 5. The N2 response for the intercardinal axis decreased compared to the cardinal axis with a coefficient of -0.53, (±0.27 standard error, 95% confidence interval [CI]= [-1.00 -0.06]). Compared to threshold contrast levels, 2 x threshold was reduced by -0.71 (±0.38 SE, 95% CI = [1.45 0.04]) as was 3 x threshold by -0.35, (±0.38 SE, 95% CI = [-1.09 0.39]), 4 x threshold by -0.37 (±0.38 SE, CI = [-1.12 0.37]), and 5 x threshold by -0.33, (±0.38 SE, 95% CI = [-1.08 0.41]).

**********figure 5 here **********

3.2.3 P3

There was no statistically significant effect of chromatic axis ($F(1,2476) = 0.81$, $p = 0.37$), or contrast ($F(4,2476) = 0.14$, $p = 0.97$) (Figure 6). Compared to cardinal axis, responses to the intercardinal axis was reduced by -0.23 (±0.25 SE, 95% CIs [-0.72, 0.27]). Compared to threshold contrast levels, 2x threshold was increased by 0.14 (±0.40 SE, 95% CIs [-0.65, 0.92], 3 x threshold was reduced by -0.06 (±0.40 SE, 95% CIs [-0.85, 0.72]), 4 x threshold was reduced by -0.13, (±0.40 SE, 95% CIs [-0.91 0.65]), and 5x threshold was reduced by -0.09 (±0.40 SE, 95% CIs [-0.87 0.69]).

**********figure 6 here **********

3.3 Event-Related Spectral Perturbation (ERSP)

As a complementary measure, time-frequency analysis was conducted in addition to the ERP analysis. ERSP involves calculating the event-related dynamics of the data on a trial-by-trial basis. The time-series for the channels O1, O2, and Oz were averaged into one time series. The spectral power was estimated using FFT and Hanning-tapered sliding time windows of 250ms, estimated for 25 linearly spaced frequencies from 2 to 50Hz. The spectrum for each trial was normalised based on the average pre-stimulus baseline power for that individual. This normalisation shows the event-related change in spectral power after stimulus onset compared to before. Spectral analysis for each trial was taken, and the average over trials was estimated for each colour condition for each observer. The average time-frequency plot for all observers for the cardinal and intercardinal axes can be seen in Figure 7.

**********figure 7 here **********

Exploratory cluster-based permutation tests were conducted using the EEGLAB add-on of the toolbox “Fieldtrip” (Oostenveld et al., 2011) to compare each frequency-time pair in the ERSP estimate. Independent samples t-tests were used to detect clusters - a cluster was defined as two or more continuous time-frequency points exceeding a threshold of $p < 0.05$. The sum of the t-values within each cluster determines the cluster mass. The cluster mass values were compared to a null distribution created using the Monte-Carlo bootstrapping technique using 2000 random permutations. Clusters were deemed statistically significant if they had a cluster-mass value that exceeded the FDR adjusted critical value. This was performed for the comparison of cardinal vs intercardinal axis, and then subsequently for the five levels of contrast. Figure 8 shows the FDR-corrected p-values for the cluster-based permutation analysis for the comparisons of axis and also of contrast.

**********figure 8 here **********

The comparison of Axis revealed a statistically significant time period in the alpha band (8-12Hz), approximately 30 to 290ms post stimulus onset. The power in this time-frequency window was averaged, and then entered into a generalised linear mixed model, with Axis, and Contrast as fixed effects, and observer as a random effect. There was a significant effect of axis ($F(1,242) = 4.81$, $p = 0.029$), with intercardinal axis showing lower power compared to the cardinal axis by -0.33 (± 0.15 SE, 95% CIs [-0.62 -0.03]). Figure 9 shows the effect of axis and the tuning function shown by contrast. There was no obvious statistically significant time-frequency window in the alpha band for the Contrast comparison. Using the same band determined for axis, there was no significant effect of contrast, compared to threshold, 2 x threshold decreased by -0.11 (±0.23 SE, 95% CIs [-0.58, 0.35]), 3 x threshold increased by 0.07, (± 0.23 SE, 95% CIs [-0.39, 0.53]), 4 x threshold increased by 0.17 (±0.23 SE, 95% CIs [-0.30, 0.64]), and 5 x threshold decreased by -0.05, (±0.23 SE, 95% CIs [-0.51, 0.41]). However, there does appear to be two significant clusters, the first spanning from approximately 11-16Hz in the time-window 90-140ms. The second appears to be approximately in the beta band around 18-22Hz from 120 to 165ms. These would be considered to be in the beta, rather than the alpha band.

**********figure 9 here **********

3.5 Control Measures

In the current study, the stimuli were expressed in DKL colour space. However, as a control measure, and to facilitate comparison with previous research (Haigh et al., 2013; Haigh et al., 2018) the stripes making up each hue were expressed in terms of chromaticity separation in CIE u'v' colour space. There was greater chromatic separation for the intercardinal compared to cardinal axes when expressed in CIE u'v' colour space ($t(18) = -2.58$ $p < 0.05$). The strength of the relationship between chromaticity separation in CIE u'v' colour space and visual discomfort was not statistically significant ($p = 0.212$). There was also no statistically significant correlation between chromaticity separation and the P1 component ($p = 0.193$) or the P3 component ($p = 0.123$). There was a correlation between the chromaticity separation and the N2 component ($r(18) = -0.458$, $p = 0.043$).

There was no relationship between the P1 component and discomfort judgements ($p = 0.202$), nor was there a relationship between the P3 component and discomfort judgements ($p = 0.649$). However, there was a negative correlation between discomfort judgements and the N2 component ($r(18) = -0.558$, $p = 0.011$), the more negative the N2 component, the more discomfort for the stimuli.

In the current study, the four individual hues were combined into cardinal and intercardinal directions. In the Supplementary Material 2 the results on the ERPs for each hue individually can be seen. To summarise, there is an effect of hue when all four colours are considered separately on the P1 response, but not on N2 or P3. Salmon-pink showed the greatest P1 response compared to the three other hues.

4. Discussion

Observers experience less discomfort when viewing colours along the cardinal compared intercardinal axes, as predicted by the inefficient coding hypothesis (Hibbard and O'Hare, 2015; Penacchio and Wilkins, 2015). There was greater chromatic separation when stimuli were expressed in CIE u'v' colour space for the intercardinal compared to the cardinal directions, it might be argued that this could be due to increased visibility. However, one of the important goals of this study in comparison to previous work was to match stimuli for visibility by finding the isoluminant point for each individual observer. Additionally, there was no relationship between chromaticity separation in CIE u'v' colour space and visual discomfort judgements.

The EEG results show a more pronounced negative N2 response, and increased cortical excitability, for the intercardinal axes compared to the cardinal axes. Similarly, time-frequency analysis showed the intercardinal axes had decreased alpha-band oscillations compared to the cardinal axes. Time-frequency analysis is complementary measure to the ERP components. It is important as the amplitude and phase of ongoing oscillations affect not only the ERSP, but also ERP components (Barry et al., 2003). In short, oscillatory brain activity (ERSP) and transient ERP components (P1, N2, P3) are related, but different measures of brain activity.

4.1 ERP components

Chromatic stimuli elicit a negative response ~120ms after stimulus onset, known as N2 (Tobimatsu et al., 1996). We found a significant effect of chromatic axis for the N2 component, indicating increased negative amplitude for the intercardinal compared to the cardinal axes. This suggests increased neural activity for colours which are processed by more than one mechanism, supports the inefficient coding hypothesis.

The two other ERP components of interest are P1 and P3. P1 responds strongly to luminance contrast (e.g. Sousza et al., 2007), and P3 is associated with stimulus mismatch (Mehaffey et al., 1993). P1 has shown more pronounced transient ERP responses to more uncomfortable stimuli, achromatic stripes (O'Hare et al., 2015). In the current study, there were no differences for either the P1 or P3 components. One possible explanation is that P1and P3 are unaffected by chromatic variation, and only respond to luminance modulation. Alternatively, it may be due to the temporal properties of the stimuli. Lindquist and colleagues (2021) demonstrated increased VEP responses with increased chromaticity separation when flickered at 5Hz, but no comparable relationship at 3Hz. This suggests the relationship between transient VEP amplitude, colour and discomfort may depend on temporal characteristics. Stimuli in the current study were not flickered but displayed constantly for around 500ms. Future work is needed to investigate the effect of combining not only different colour and luminance properties, but also temporal information.

There was no effect of chromatic contrast expressed in DKL colour space for any of the ERP components, which contradicts the predictions we would make based on the behavioural judgements, and the inefficient coding hypothesis. As outlined above, we may not necessarily expect P1 and P3 to be modulated by colour contrast in the same way as N2 which is directly related to chromatic content (Tobimatsu et al., 1996). However, that does not explain why we did not find an effect of chromatic contrast in the N2 component. However, there was a relationship between chromaticity separation in CIE u'v' colour space and the N2 component only. Speculatively, this could be because the cortical areas may respond more to CIE colour space, which is based on perceptual similarity, rather than DKL space, which is more relevant for earlier areas of colour processing (Brouwer and Heeger, 2009).

ERP components can vary depending on *contrast* level of isoluminant stimuli (e.g. Jennings and Martinovic, 2015). For example, P1, N2, and P3 are lower in amplitude and also delayed in latency for isoluminant compared to luminance modulated stimuli (Wijers et al., 1997). As the stimuli in the current experiment are isoluminant and vary according to contrast, it is possible that extraction of the ERPs may add noise to the estimate, as the latency of the peak may vary slightly according to stimulus contrast. To address this, subsequent analyses using peak estimations (the local maximum/minimum, rather than the mean, over the time window) were conducted, and these showed comparable results to the original analyses (see Supplementary Material 1). Therefore, it is unlikely that this can account for the lack of relationship between contrast and ERP amplitude.

4.2 Alpha band oscillations

Increased visual discomfort in chromatic stimuli has been attributed to event-related desynchronisation (ERD) and increased cortical excitability (Haigh et al., 2018). ERD is used as a proxy for increased activation, and increased information processing capabilities, which can be interpreted as cortical excitability (e.g. Pfurtscheller, 2001). Time-frequency analysis in the current study showed lower alpha power, a measure of ERD, for intercardinal axes compared to cardinal axes in the time period 30-140ms after stimulus onset. Greater ERD in the intercardinal axes is consistent with increased cortical excitability, and so more neural activity. Furthermore, individual differences in alpha power (e.g. Smit et al., 2006) may relate to susceptibility to discomfort. This is beyond the scope of the current study, but could be established in populations with more extreme responses to visual discomfort, such as those with migraine, who also show differences in colour vision specifically with cone-opponent stimuli (Shepherd, 2005; Shepherd, 2006).

4.3 Beta band oscillations

In the current study, beta band activity was modulated by chromatic contrast around 90-165ms after stimulus onset. Beta band activity is related to perception of isoluminant stimuli. Time-frequency analysis of MEG data shows there to be reduced beta band power (15-20Hz; 12-20Hz) in response to isoluminant- compared to luminance-modulated gratings (Adjamian et al., 2008). Beta band synchronisation is related to the size of the neural network involved in the percept (Piantoni et al., 2010), and this relationship could underpin the modulation of beta band activity by chromatic contrast.

4.4 Conclusion

The inefficient coding hypothesis predicts that colours along the intercardinal axes would be more visually uncomfortable, due to an increase in recruitment of neural resources. As predicted, intercardinal axes were judged to be more uncomfortable than cardinal axes in a behavioural task. Similarly, N2 responses, which are related to chromatic stimulus processing, showed greater amplitude for the intercardinal compared to the cardinal axes. Furthermore, ERSP showed that alpha power was lower for intercardinal compared to cardinal axes, indicating increased cortical excitability. Taken together, these findings support the idea that inefficient coding may be responsible for visual discomfort when viewing certain chromatic stimuli.

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Data Statement

Anonymised data can be found at the Open Science Framework: https://osf.io/xsge9/?view_only=99db7c7c6a2a42038121630af39c7034

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Figure captions

Figure 1: Left: Azimuth of DKL Space showing the cardinal colour directions (horizontal and vertical) and colour naming conventions. Right: Examples of the four stimulus types, cardinal directions on the top row – lime/violet, turquoise/salmon, and intercardinal directions below blue/orange, pink/green. Figure for illustrative purposes only.

Figure 2. Plot showing behavioural responses (probability stimulus was chosen as more uncomfortable) against axis (left) and contrast (right). Contrast levels are multiples of threshold for each observer. Error bars show 95% confidence intervals.

Figure 3. ERP waveform showing axis (top) and contrast (bottom). Contrast levels are multiples of threshold. Lines indicate the time period for the definition of the ERPs. Solid lines mark the boundary for the P1 response (70-100ms); dashed lines indicate the boundary for the N2 component (150-230ms); dotted lines the P3 component (250-400ms).

Figure 4. Plot showing the effect of axis (left) and the effect of contrast (right) on P1 amplitude. Contrast levels are multiples of threshold for each observer. Error bars show 95% confidence intervals.

Figure 5. Plot showing the effect of axis (left) and the effect of contrast (right) on N2 amplitude. Contrast levels are multiples of threshold for each observer. Error bars show 95% confidence intervals.

Figure 6. Plot showing the effect of axis (left) and the effect of contrast (right) on P3 amplitude. Contrast levels are multiples of threshold for each observer. Error bars show 95% confidence intervals.

Figure 7. Grand average (mean) time-frequency plots of spectral power for the (top) Cardinal Axis, and the (middle) Intercardinal Axis. Lower plot shows the FDR-corrected p-values for the cluster-based permutation analysis for the comparison of Axis. Statistically significant p-values after FDR correction are in blue, non-significant values are in yellow.

Figure 8. Grand average (mean) time-frequency plots of spectral power for the five levels of contrast. The final plot (bottom-right) shows FDR-corrected p-values for the cluster-based permutation tests for the comparison of Contrast. Statistically significant p-values after FDR correction are in blue, non-significant values are in yellow.

Figure 9. Mean alpha power over the time-frequency window of interest identified by cluster-based permutation analysis. ERSP is reduced in the intercardinal compared to the cardinal axis (left), no effect of contrast on the ERSP in the alpha band. Error bars show 95% confidence intervals.

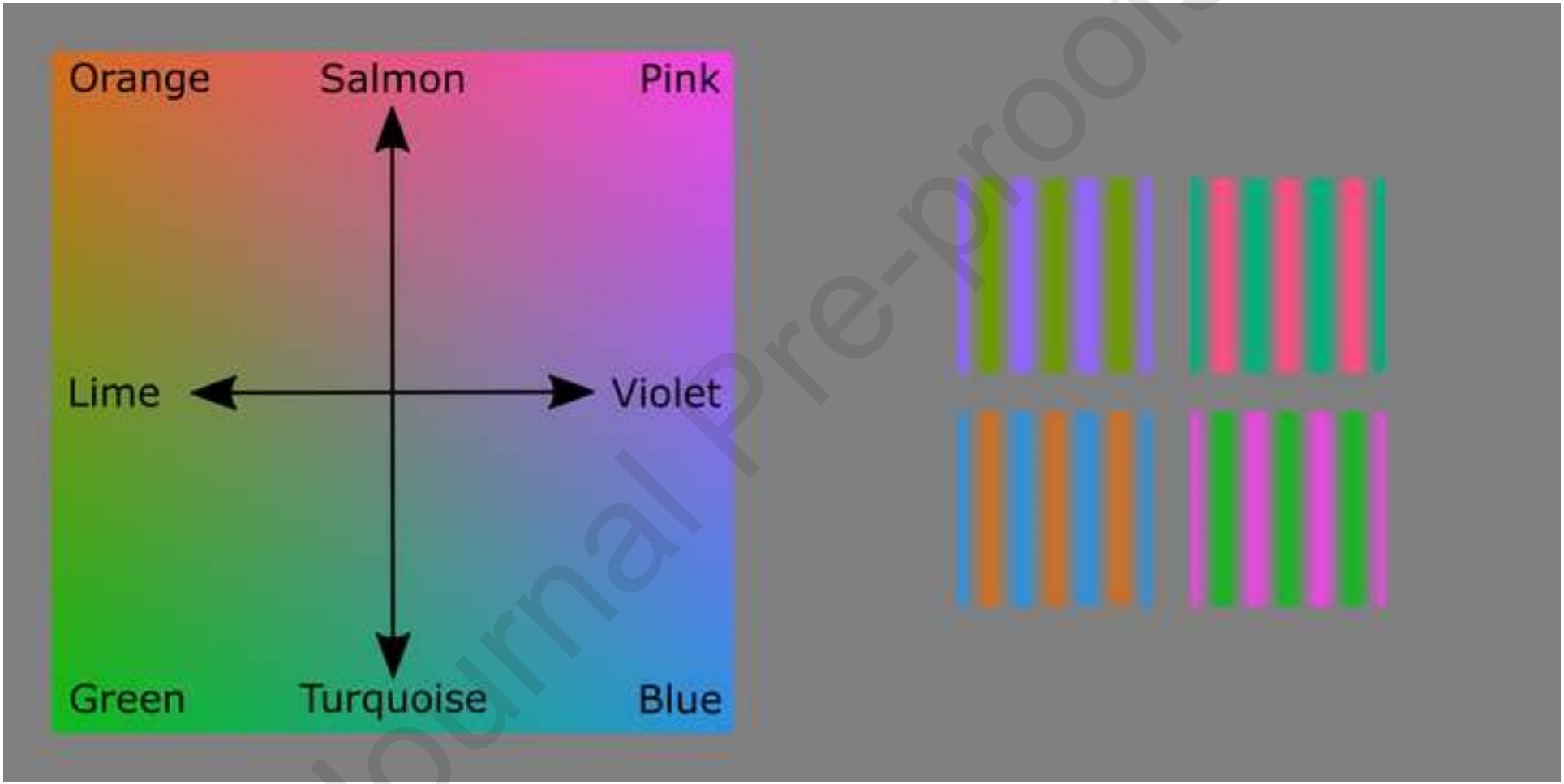


Figure 2

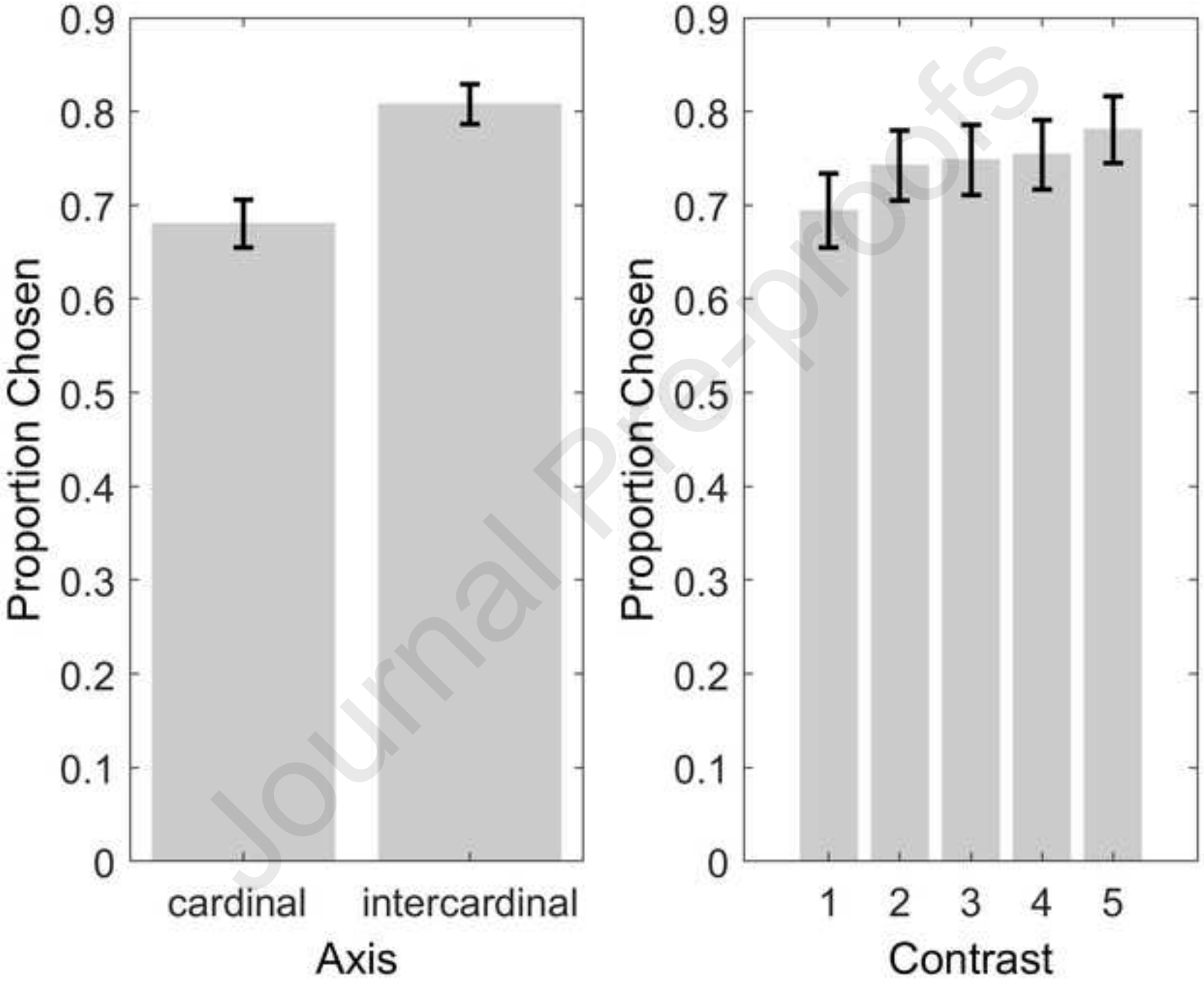


Figure 3

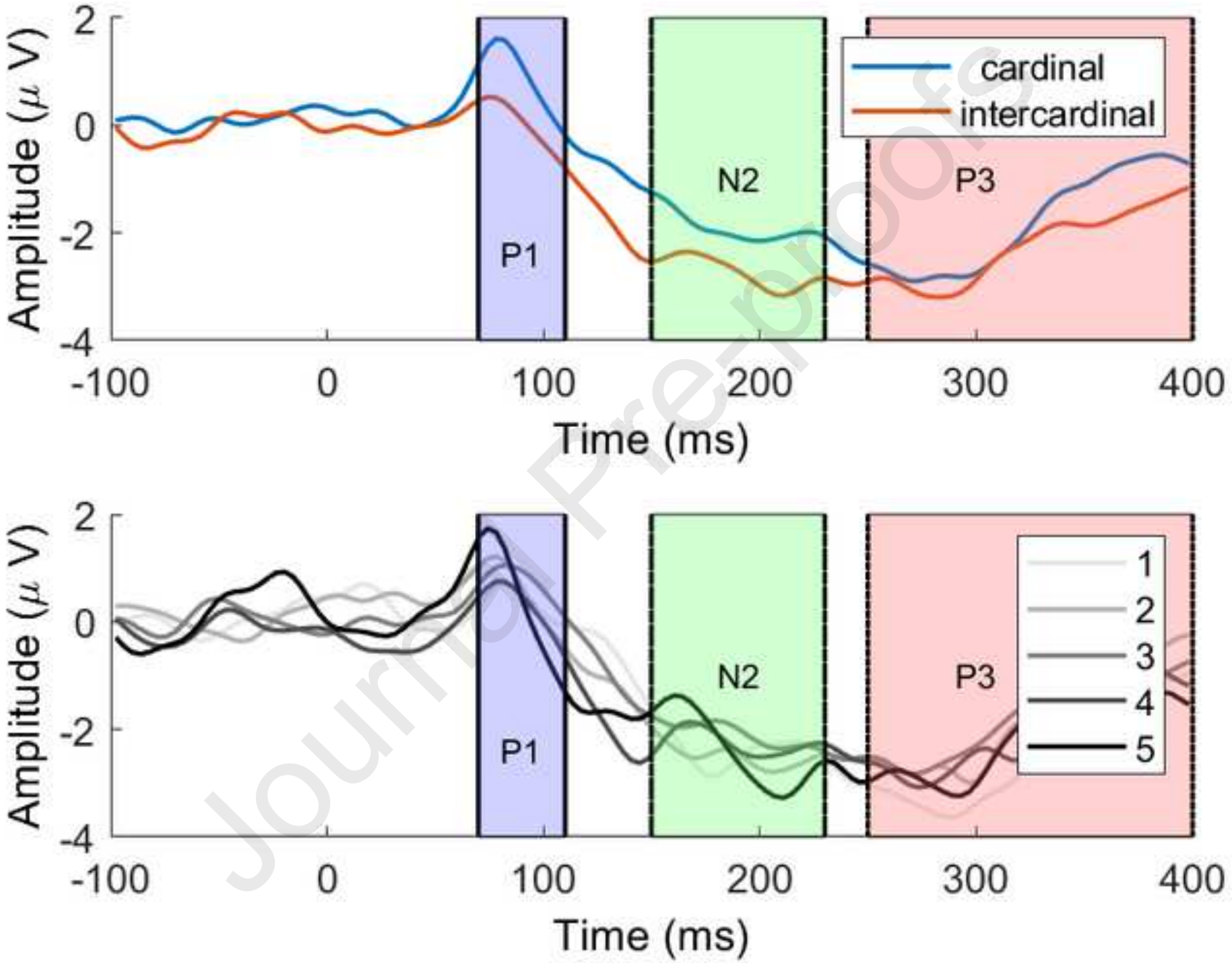


Figure 4

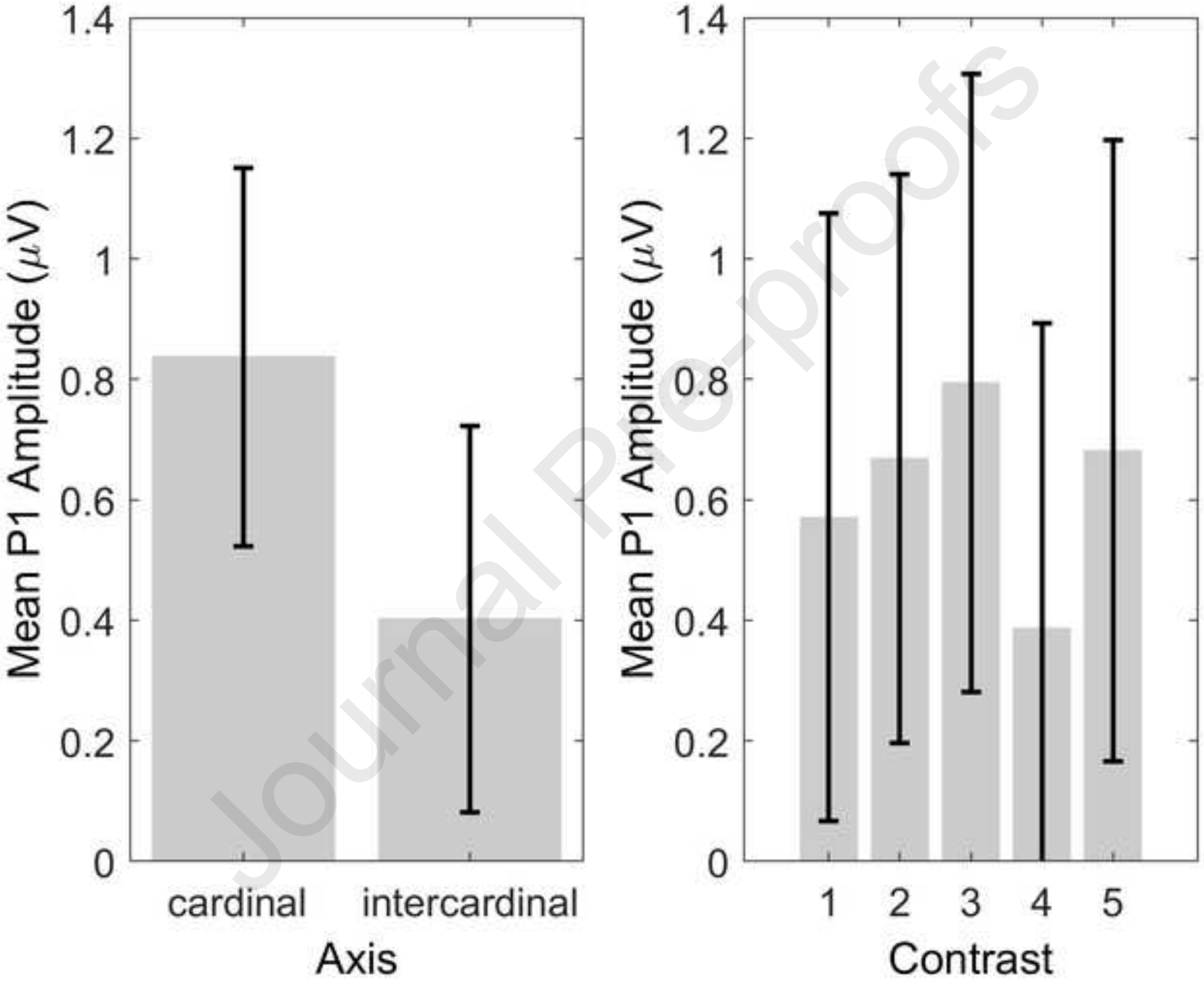


Figure 5

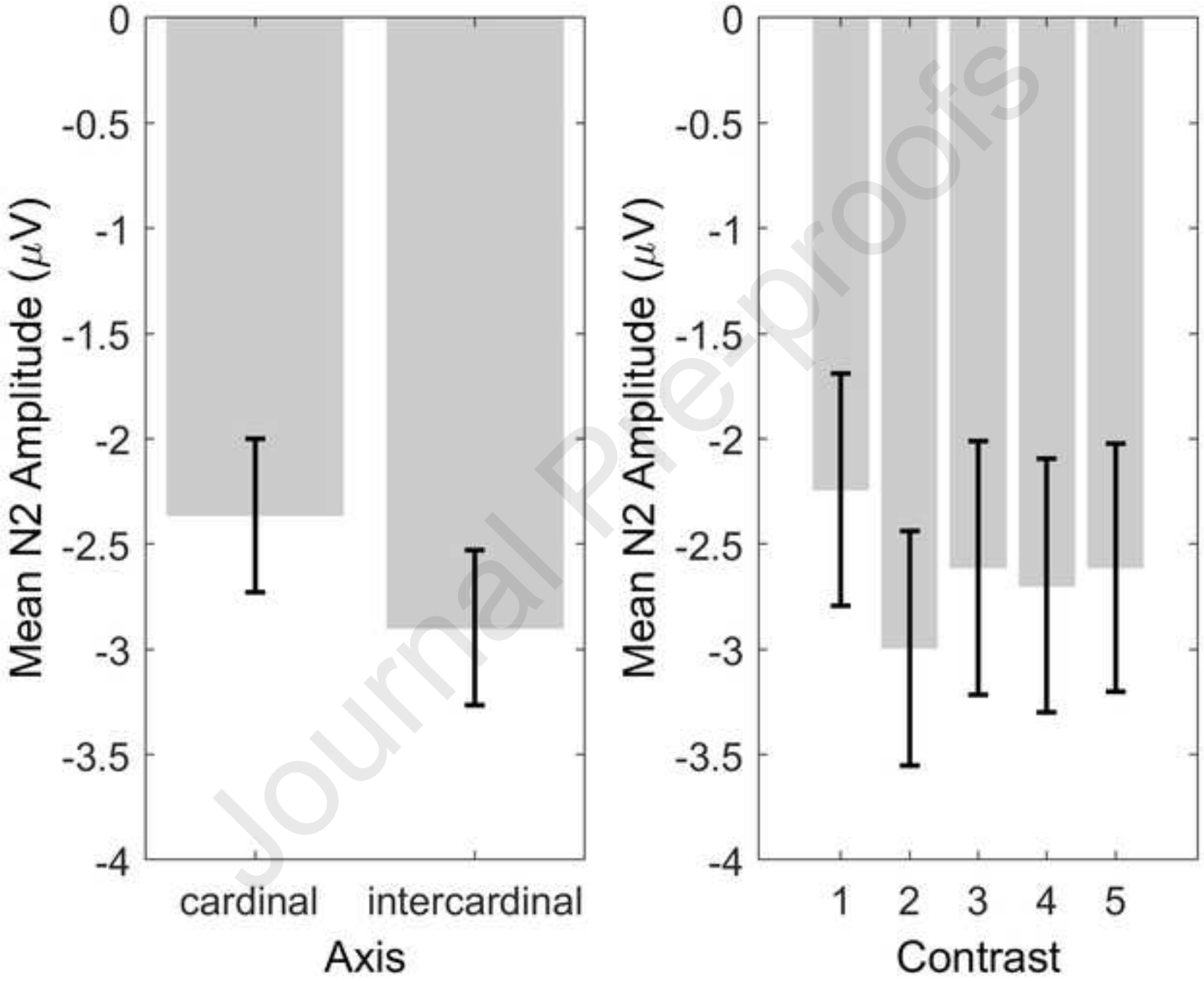


Figure 6

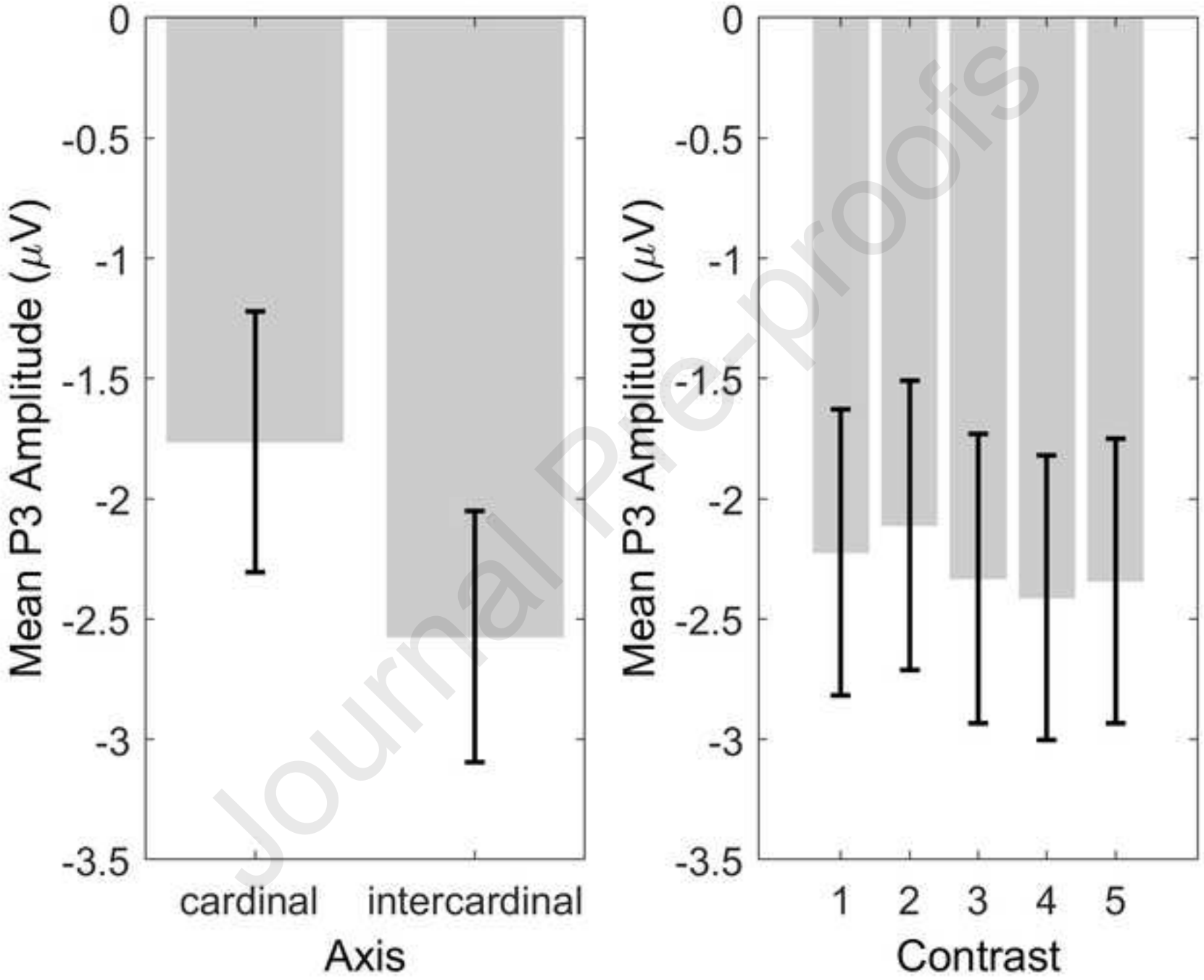


Figure 7

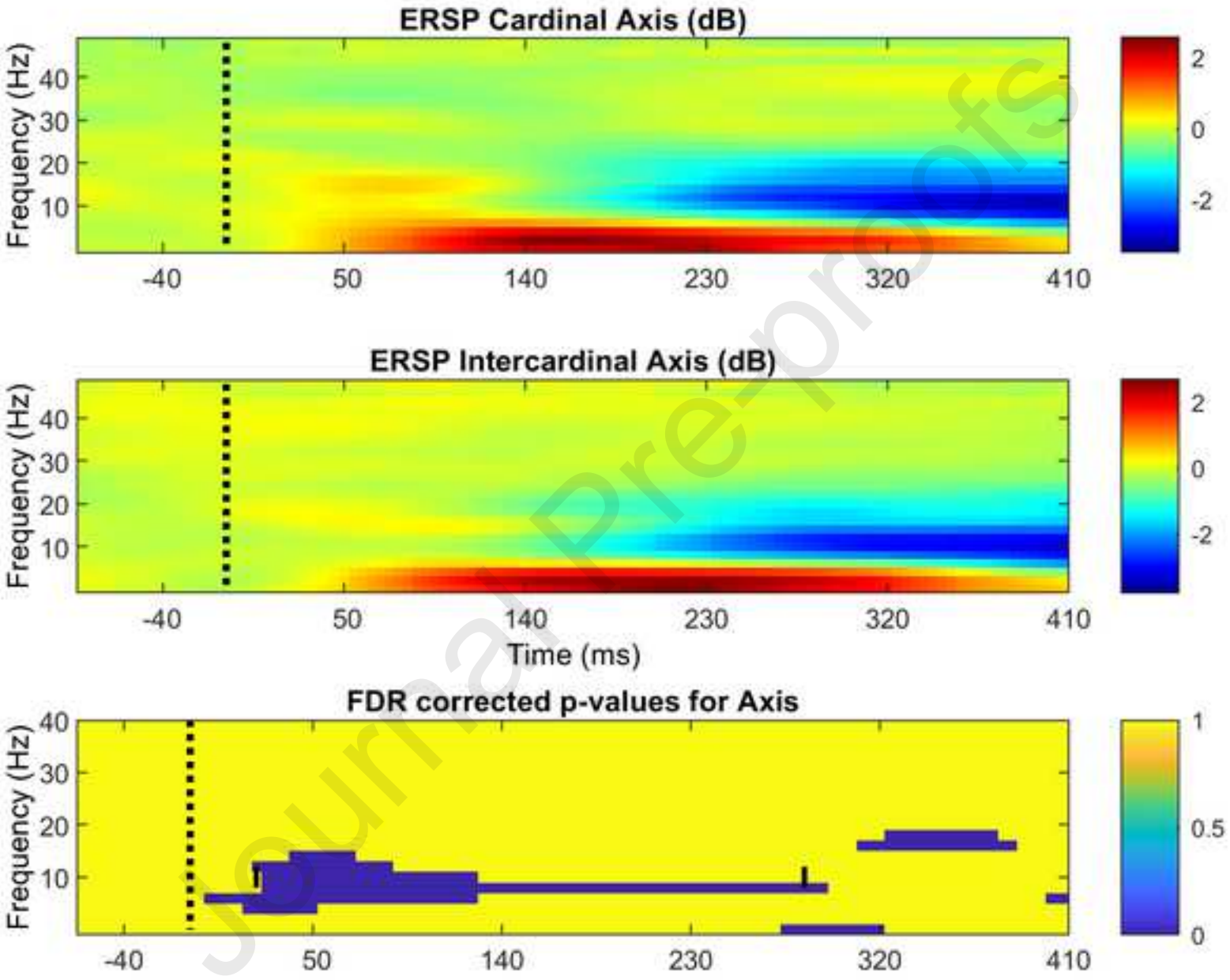


Figure 8

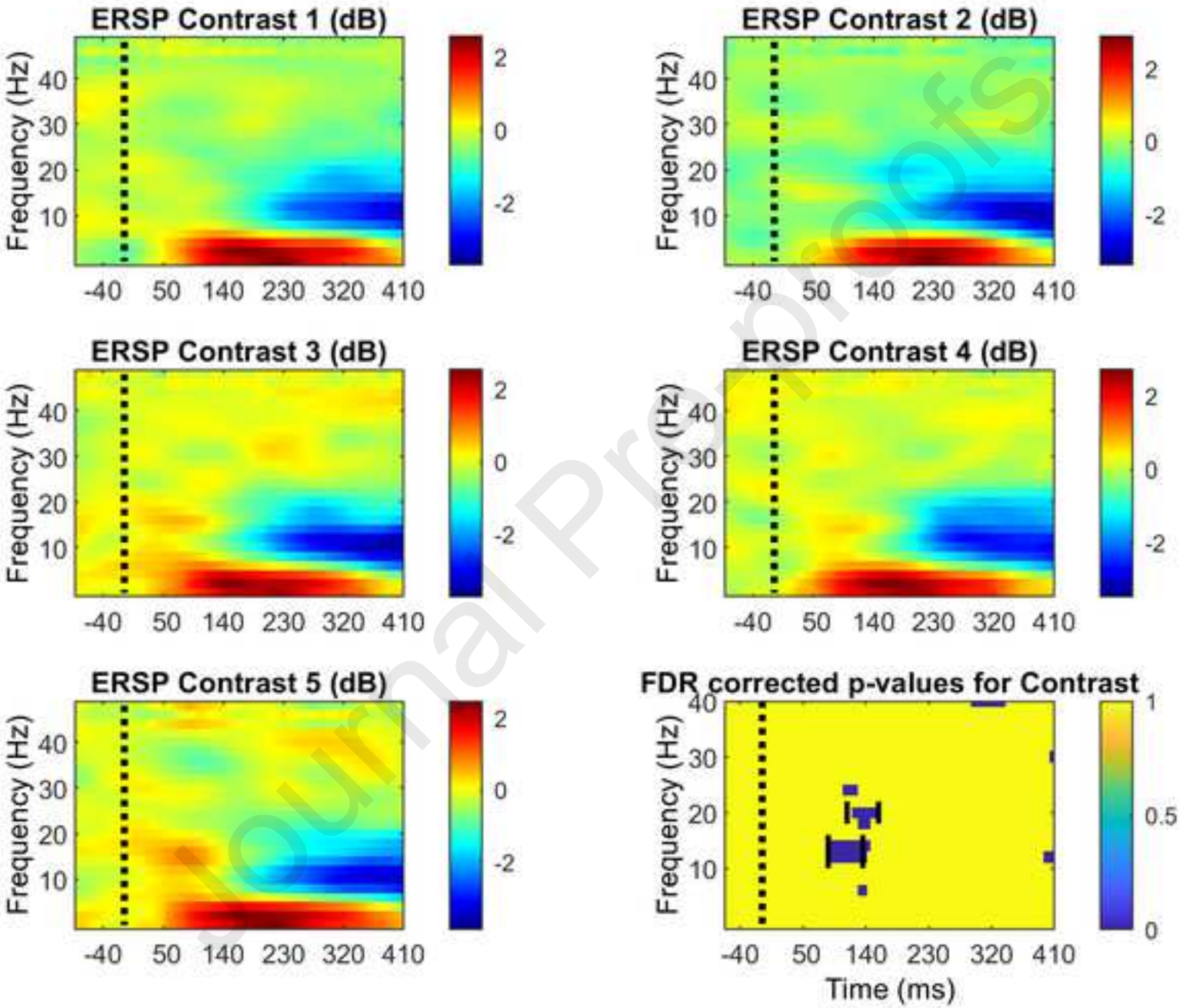
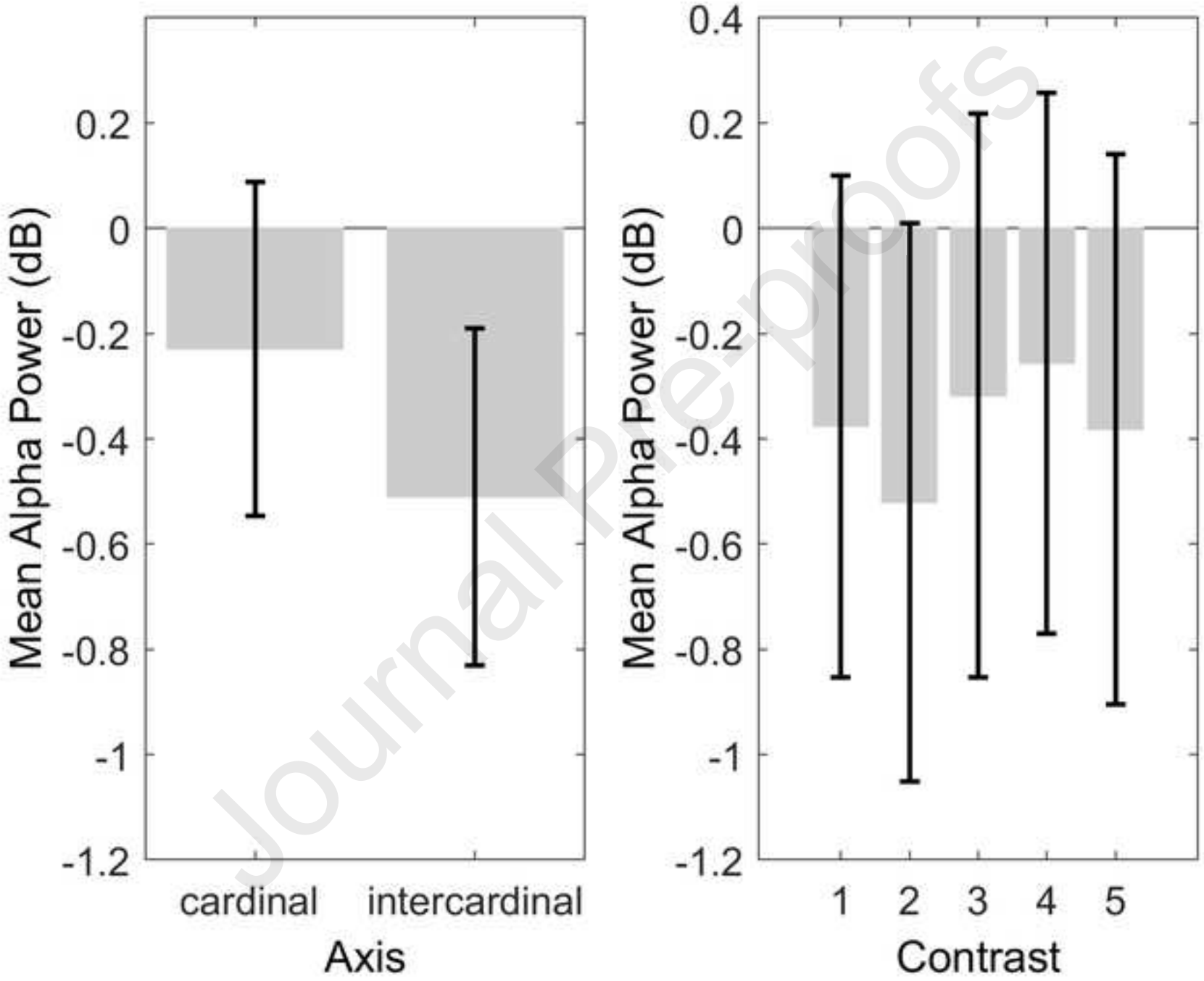


Figure 9



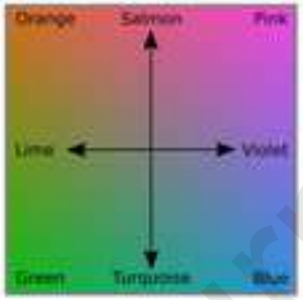
Graphical Abstract

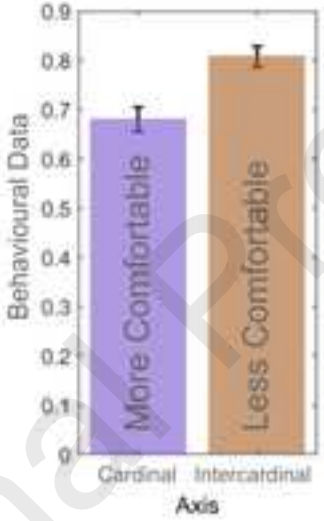
The relationship between visual discomfort and cortical excitability

Some colour combinations are more uncomfortable than others

Is this because they require more metabolic resources?

Cardinal = fewer resources
Intercardinal = more resources





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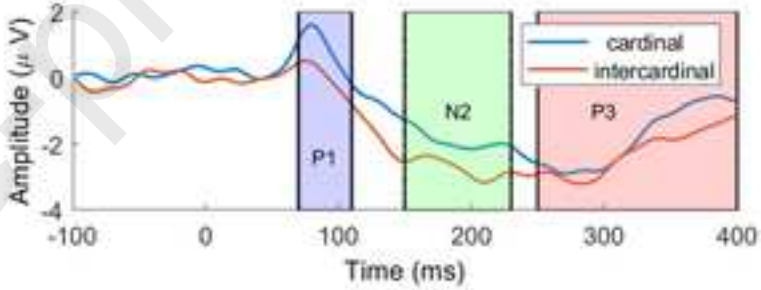

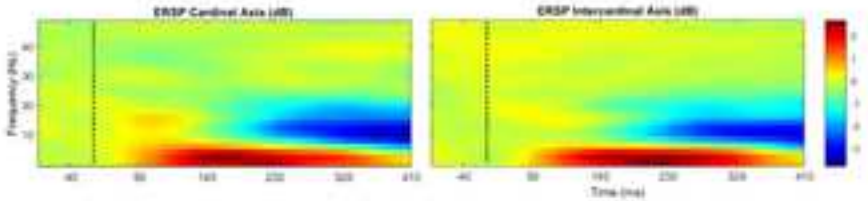

Uncomfortable stimuli increase N2 amplitude and reduce alpha band power (increase excitability)

Credit Author Statement

LOH: conceptualisation, methodology, software, formal analysis, writing – original draft, writing – review and editing, supervision

PG: conceptualisation, methodology, investigation, data curation, writing – original draft, writing – review and editing, supervision

RJS: conceptualisation, methodology, writing – original draft, writing – review and editing, supervision