

A dichoptic color fusion EEG paradigm for isolating neural correlates of
conscious perception

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Table of Contents

Introduction	1
Consciousness.....	1
Neuroimaging	2
Methods for Studying Consciousness.....	3
Previous Dichoptic Color Fusion Studies.....	5
The Present Study	7
Methods	11
Participants	11
Equipment.....	11
Stimuli.....	12
Procedure	13
Results	19
Behavioral Results.....	19
Electrophysiological Results.....	23
Discussion	31
Overall	31
Electrophysiological Results.....	32
Limitations	34
Future Directions	35
Conclusion	36
Appendices.....	37
A. Electrode cap layout.....	37
B. Color-contrast curves	38
C. Behavioral report control results for all subjects	41
D. ERPs for blank stimuli across color conditions.	42

E. ERPs for face stimuli across color conditions.....	43
F. ERPs for house stimuli across color conditions.....	44
G. ERPs for same-color condition of all stimuli.....	45
H. ERPs for opposite-color condition of all stimuli.	46
Bibliography	47

List of Figures

Figure 1. Dichoptic color fusion visual manipulation using a stereoscope.	5
Figure 2. Typical occipital site ERPs in response to visual stimuli.	8
Figure 3. Schematic of the stimuli used.....	12
Figure 4. Stimuli used to check fusion.....	14
Figure 5. Color contrast training scheme.	15
Figure 6. Ideal color contrast curve.....	16
Figure 7. Stimuli for behavioral report control.....	18
Figure 8. Color contrast curve examples from participants.	20
Figure 9. Behavioral report control performance.....	22
Figure 10. Mass univariate analysis results.	24
Figure 11. ERPs and difference maps visualizing the VAN.....	26
Figure 12. ERPs and difference maps visualizing the LP.	28
Figure 13. ERPs comparing stimuli within each visibility condition.....	30

Abstract

To investigate the neurophysiological basis of consciousness, brain activity can be compared when viewing images that are consciously seen versus unconsciously processed in order to identify potential neural correlates of conscious perception (NCCs). Dichoptic color fusion is a uniquely promising technique for manipulating visual awareness. In altering the color arrangements of images presented independently to the left eye and the right eye through a stereoscope, the result is that images with opposite colors are fused and perceived as a blank image ("invisible" condition), while images with the same colors are fused and perceived as normal ("visible" condition). The only physical difference between the visible and invisible conditions – the color assignments in each eye – can be controlled for by using blank stimuli viewed in a same-color and opposite-color condition. In the current study, electroencephalography (EEG) data were recorded during a no-report dichoptic color fusion task. Subjects viewed faces, houses, or blank control stimuli, presented for 100 ms durations, that were either visible or invisible due to dichoptic color fusion. The stimuli were task-irrelevant, while spatial and temporal attention to these stimuli were ensured by the design of an infrequent target detection task. A post-experiment report-based task confirmed that the color-inverted stimuli were mostly invisible while the color-matched stimuli were visible. Early visual-evoked potentials (P1/N1) were identical for visible and invisible stimuli due to minimal differences in the physical stimuli. Differential brain activity associated with stimulus visibility was evident later in time (starting at ~ 200 ms). These differences matched the spatiotemporal characteristics of the previously reported visual awareness negativity (VAN), followed by a smaller late positivity (LP). This pattern of results informs competing theories of consciousness such as recurrent processing theory and global neuronal workspace theory.

Introduction

Consciousness

In references to consciousness, there is a distinction made between phenomenal consciousness, which describes the subjective experience, and access consciousness, which refers to the state of cognitive accessibility of information, e.g., from perceptual or affective systems (Block, 1995). Here, the term consciousness is used to refer to the former type. The neurophysiological basis of phenomenal consciousness is a long-standing topic of inquiry that has given rise to many diverging theories but is still not fully understood (Doerig et al., 2021). Some prominent examples are global neuronal workspace theory, recurrent processing theory, attention schema theory, and integrated information theory. Each attempts to explain the nature of the process through which consciousness arises from neural activity. According to global neuronal workspace theory, there are cerebral networks processing information unconsciously, and through top-down attentional amplification this information can become conscious by virtue of becoming accessible to other processes, such as memory, language, decision-making, etc. (Prakash et al., 2008). Recurrent processing theory proposes that a feedforward sweep of activation throughout the brain mediates unconscious feature extraction, while conscious functions related to perceptual organization occur only through recurrent feedback activity spreading back to lower brain regions by cortico-cortical connections (Lamme, 2010). Attention schema theory suggests that the brain constructs a schematic model of the process of attention as a mechanism to achieve better control over attention, which leads the brain to conclude that it has a subjective experience (Graziano & Webb, 2015). According to integrated information theory, the physical substrate of consciousness maximizes intrinsic cause-effect power and

allows for assessment of the quantity and quality of experience (Tononi et al., 2016).

A major strategy used to investigate these theories has been to identify neural correlates of consciousness (NCCs), which are the minimally sufficient neural mechanisms for a given conscious perceptual experience (Koch et al., 2016). A typical study investigating NCCs compares neural activity associated with consciously perceived stimuli to neural activity from unconsciously perceived stimuli and identifies the time course and neuroanatomical locations of any differences. This information can help to support or refute proposed theories on consciousness, and contribute to the pursuit of understanding its neural origins.

Neuroimaging

The neural mechanisms of consciousness have been investigated through a variety of techniques. Functional magnetic resonance imaging (fMRI), which allows for depiction of changes in brain metabolism in response to neural activity, has been used to associate network dynamics with consciousness, and offers excellent spatial resolution but poor time resolution (Glover, 2011; Crone et al., 2020). Another tool is magnetoencephalography (MEG), which records the neuromagnetic fields produced by chemical transmission across synapses, non-invasively outside of the head, allowing for analysis of the approximate spatial distribution of underlying brain activity with excellent time resolution (Ahlfors & Mody, 2019). MEG has been used to understand visual consciousness through the temporal dynamics of information processing (Mai et al., 2019). Similar to MEG, electroencephalography (EEG) allows for temporally precise measurements of brain activity, and measures the same synaptic potentials, but has slightly lower spatial resolution due to the blurring of electrical signals by the meninges, skull, and scalp between the brain and the recording electrodes

(Tivadar & Murray, 2019). Due to the excellent time resolution, EEG and MEG can be used to extract event-related potentials (ERPs) or event-related magnetic fields (ERMFs), which are changes in EEG/MEG signal strength time-locked to a stimulus or event (Sur & Sinha, 2009). This allows for the study of the different stages of neural processing at each specific time point between a stimulus and a response, i.e., tracking sensory, cognitive, and motor systems.

Methods for Studying Consciousness

In pursuit of understanding the relationship between neural processing and consciousness, electrophysiological techniques can be employed to monitor brain activity in response to different manipulations. Common paradigms used to distinguish conscious and unconscious perception of stimuli include masking, inattention blindness, and binocular rivalry, all of which work to hide a stimulus from conscious perception (Dehaene & Changeux, 2011). Masking involves weakened perception of a briefly flashed target due to the timing and placement of a masking stimulus, allowing for manipulation of the degree of conscious registration (Ansorge et al., 2008). Inattention blindness describes the failure to notice a clearly visible stimulus due to attention being engaged in an unrelated demanding task (Jensen et al., 2011). A review of implicit processing in inattention blindness concluded that unconscious and unattended visual stimuli can still be processed, and that the degree of processing depends on the load of the task (Nobre et al., 2020). Binocular rivalry occurs when different images presented independently and simultaneously to each eye cause an incongruence, and perception alternates between them, with the eyes able to settle on perceiving only one of the two competing images at a time (Blake et al., 2014).

Relative to these approaches, dichoptic color fusion has been less utilized. However, this technique shows promise as a powerful tool for manipulating

visual awareness, and has been successfully employed in a few studies so far as a method for altering consciousness of visual stimuli (Moutoussis & Zeki, 2002). In particular, dichoptic color fusion allows for stimuli presented to both eyes to be viewed and attended, while still remaining perceptually invisible. With use of a mirror stereoscope, images with certain opposite colors at a low contrast are presented independently and simultaneously to each eye, and the counterbalance of colors causes a fusion effect resulting in the perception of a blank image (Figure 1). Unlike masking, which relies on extremely brief stimulus presentation times followed by stronger pattern masks that are always seen, and unlike inattention blindness, which relies on attentional distraction, dichoptic color fusion presents longer-lasting unmasked images in the center of view while participants fully attend to them. And unlike binocular rivalry, in which one of the two presented images is always consciously seen, dichoptic color fusion allows for a clean baseline of an unseen condition. This ability to manipulate the awareness of image perception is highly useful in the investigation of conscious versus unconscious processing.

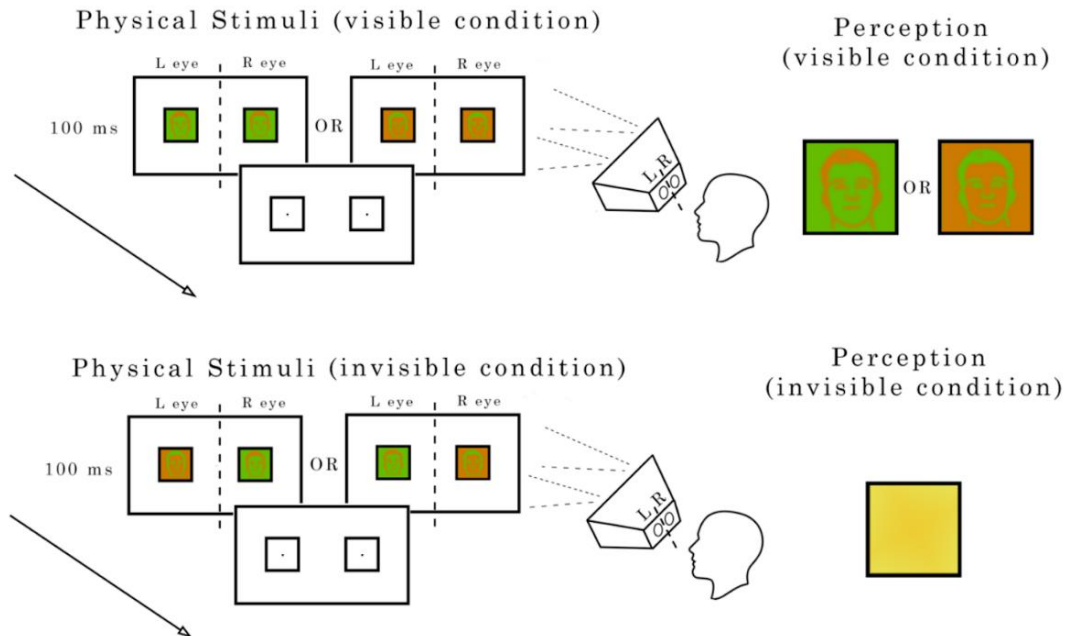


Figure 1. Dichoptic color fusion visual manipulation using a stereoscope.

The coloring of images presented independently to the left and right eye can establish a visible or an invisible state of perception.

Previous Dichoptic Color Fusion Studies

The technique of dichoptic color fusion has been useful for investigating the relationship between cortical activation and visual perception. It was originally used with fMRI to compare brain activity from perception of faces and houses that were perceptually visible or invisible (Moutoussis & Zeki, 2002). The main finding was that some brain regions involved in perception of faces and houses (e.g., the fusiform face area) were activated regardless of whether the stimuli were consciously perceived. Dichoptic color fusion has been used in additional studies to investigate the neural mechanisms of consciousness. Using MEG, cortical activity was shown to be more stable when stimuli were consciously perceived (as opposed to unconsciously processed), implying that conscious perception may involve a transient state of cortical network

stabilization (Schurger et al., 2015). Dichoptic color fusion has also been used to conclude that, while the perceptually invisible face condition does not alter the face-specific response, it is distinguishable by the absence of processes related to neural information integration, e.g., between face-specific areas and primary visual cortex (Fahrenfort et al., 2012).

Importantly, all previous studies using dichoptic color fusion were designed such that subjects were required to report, after each stimulus presentation, whether they perceived the stimulus or not. In several studies over the past 10 years, it has been found that the neural activity related to accessing and reporting what one perceives can be easily confused with the neural activity associated with conscious perception itself (Pitts et al., 2014; Tsuchiya et al., 2015; Cohen et al., 2020). For example, if faces and houses in visible and invisible conditions are presented, and the task is to report on each trial whether you see a face or a house, there will be additional brain activity on consciously seen trials (related to categorization, judgment, decision-making, working memory, preparation of motor responses, etc.) as compared to unseen trials (in which you simply see nothing, and have to either guess “face” or “house” or just report “no, I didn’t see anything”). Based on this concern, more recent studies have started utilizing “no-report” designs in order to avoid this potential report-based confound when searching for NCCs. As long as researchers can validate their designs with report-based conditions, and reasonably ensure that the visibility manipulation still works under no-report conditions, such designs should provide a cleaner measure of NCCs. While there are other considerations of possible confounds when comparing responses to seen stimuli and unseen stimuli, eliminating reporting is a major shift toward fully isolating NCCs (Block, 2019).

The Present Study

This study seeks to investigate NCCs by using EEG to look at the difference between consciously and unconsciously perceived images. Specifically, the images used are faces and houses, which elicit distinct electrophysiological responses that can be characterized in ERP analysis (Allison et al., 1999; Itier & Taylor, 2004; Desjardins & Segalowitz, 2013). Manipulation of visual perception through dichoptic color fusion will allow for establishing conditions of perceptually invisible faces and houses. Additionally, this study employs a no-report design in order to distinguish NCCs from neural activity related to accessing and reporting perceptual information.

Previous research has identified characteristic ERP components, which are distinct negative or positive changes in voltage at specific time points (relative to stimulus onset) that correlate with different neural processes (Luck, 2014). Particularly relevant to this study are the visual awareness negativity (VAN), the late positivity (LP), a subcomponent of which is the P3b, and the N170 (Figure 2). The VAN is a negative wave at posterior occipital electrodes at around 200 ms after stimulus presentation that is correlated with visual awareness (Ojanen et al., 2003; Eklund & Wiens, 2018; Förster et al., 2020). The P3b occurs as a positive-going wave at parietal electrodes around 300 ms or more after the stimulus and is hypothesized to reflect context updating and access of memory storage (Polich, 2007; Verleger, 2020). The N170 is a negative-going ERP deflection between ~150 and 250 ms, usually peaking around 170 ms, that has been specifically linked to the processing of faces compared to non-face stimuli (Bentin et al., 1996; Gao et al., 2019).

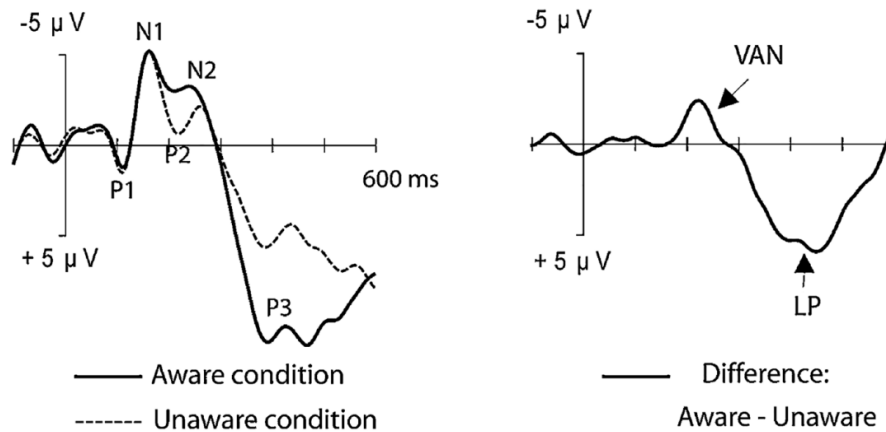


Figure 2. Typical occipital site ERPs in response to visual stimuli.

Koivisto & Revonsuo 2010 figure showing the resulting difference waveforms.

The P1 and N1 components, characterized respectively by a positive and negative peak over the occipital scalp following stimulus presentation (at roughly 100 ms and 150 ms, respectively), are known to be associated with early stages of visual sensory processing (Luck, 1995). The presence of both the P1 and N1 is expected in any experiment in which a flashed image is salient enough to evoke sensory processing, and most theories of consciousness predict comparable P1/N1 amplitudes for seen versus unseen stimuli. The subsequent VAN, on the other hand, is expected to manifest as a differential amplitude from ~200 ms to 300 ms for stimuli that are consciously seen versus unseen. All blank control conditions, regardless of stereoscopic color fusion, are not expected to show a VAN. The N170, which may peak during time periods overlapping the N1 and VAN, can be used to isolate brain activity specific to processing faces. If perceptually invisible faces do not show a VAN but show evidence of an N170, this could indicate that faces are being unconsciously processed and categorized. Because the P3b has been found to result from the accessing and reporting of perceptual information, the no-report design is expected to eliminate its presence (Pitts et al., 2014). If some indication of a P3b is found in the results, it could

indicate participants are still actively accessing and updating stimuli information even though they are not being asked to give any report on what they are seeing. This could add additional effects of visibility to the ERPs that are difficult to distinguish from correlates of consciousness. Importantly, any effect of color fusion can be accounted for through a blank condition control, which can be taken into consideration when comparing ERPs from the seen and unseen conditions.

Findings from this experiment are relevant to the "early vs. late" debate of visual consciousness, concerned with understanding how long after an event a conscious percept is formed. For example, the global neuronal workspace theory and recurrent processing theory predict that late versus early stages of neural processing, respectively, are most closely associated with visual awareness (Förster et al., 2020). More broadly, identified NCCs may eventually be useful as clinical tools for diagnosing and treating disorders of consciousness and certain neuropsychiatric conditions related to abnormal conscious processing (Estraneo et al., 2016; Sass & Parnas, 2003).

Methods

Participants

A total of 25 participants (12 female, ages 18 to 22) were recruited via flyers and online postings at Reed College in Portland, OR. All participants had no history of recent brain injury or neurological disorder, and reported no problems with stereopsis (e.g., strabismus or amblyopia). Participants were paid \$40 for their time after completing the experiment with funding from the Reed College Neuroscience Program. Experiments were conducted in accordance with Covid-19 guidelines, and the Reed Institutional Review Board approved all procedures.

Equipment

To establish fusion, a stereoscope was placed 57 cm from the screen of a computer. For EEG recording, participants were fitted with a 64-channel custom equidistant electrode cap (see Appendix A), and the skin was gently abraded with the wooden end of a swab stick to establish a good scalp connection with the saline-based gel. Electrodes were placed behind each ear to serve as a mastoid reference, on each temple even with the eyes as the HEOG channel for eye movements, and one below the left eye for the VEOG channel to detect blinks. Data was recorded with BrainVision Recorder and analyzed using BrainVision Analyzer.

Stimuli

The stimuli consisted of simplistic two-tone images of faces and houses, 10 for each category, colored to have a green image on a red background or a red image on a green background (Schurger et al., 2010). Colors were manipulated to be equiluminant so that the images were defined only by change in color value. By presenting identical images to each eye or inverting the color assignments in one of the two eyes, six conditions were established: same-color faces or houses (visible), opposite-color faces or houses (invisible), and same- or opposite-color blanks (Figure 3). Within each condition, left and right eye presentation of opposite-color conditions were counterbalanced to be equal for both eyes (when averaged across trials). Computerized stimuli presentations and tasks were created using Psych Toolbox in MATLAB.

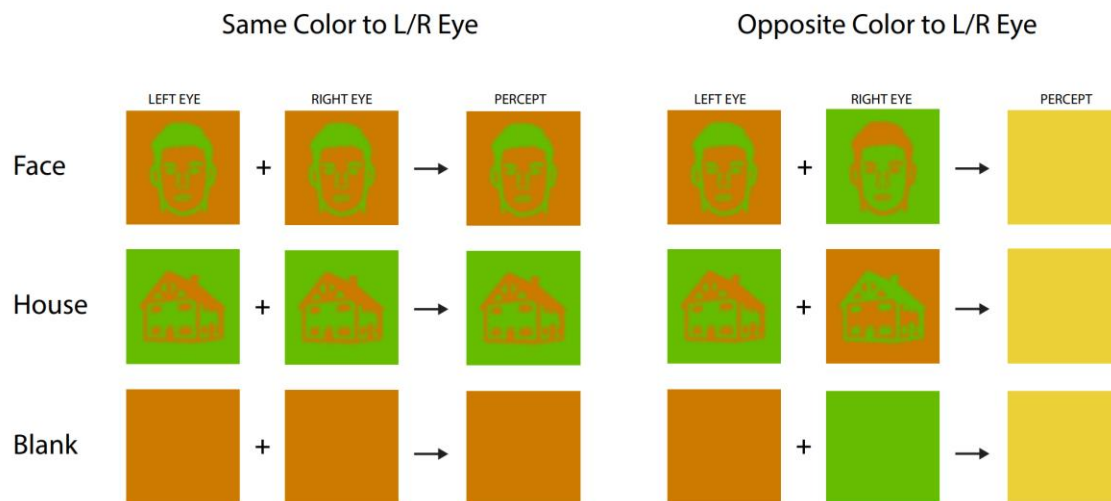


Figure 3. Schematic of the stimuli used.

By changing stimuli and color presentation, 6 conditions were established (face, house, or blank) x (same or opposite color to L/R eye). Color presentations to the left and right eye were counterbalanced.

Procedure

In order to determine the equiluminance settings specific to each person, participants were shown a grid of flickering color blocks at a range of contrasts and instructed to use the up and down arrow keys to adjust the settings until the flickering appeared to cease (heterochromatic flicker photometry). At that point, the space bar was pressed to record the favorable luminance value. This baseline setting was then used to set the luminance for the rest of the stimuli.

To achieve proper fusion of vision through the stereoscope, the height of the setup was moved to eye level, then participants were asked to adjust the lateral position of the image seen independently in each eye using knobs until the images were centered. Then, to confirm that fusion was working properly, images of the letter E that are revealed only through fusion (random dot stereograms) were shown in the four possible orientations facing up, down, left, or right (Figure 4). Participants were asked to press arrow keys that corresponded with the orientation of the E, and could continue if the response was correct three times in a row.

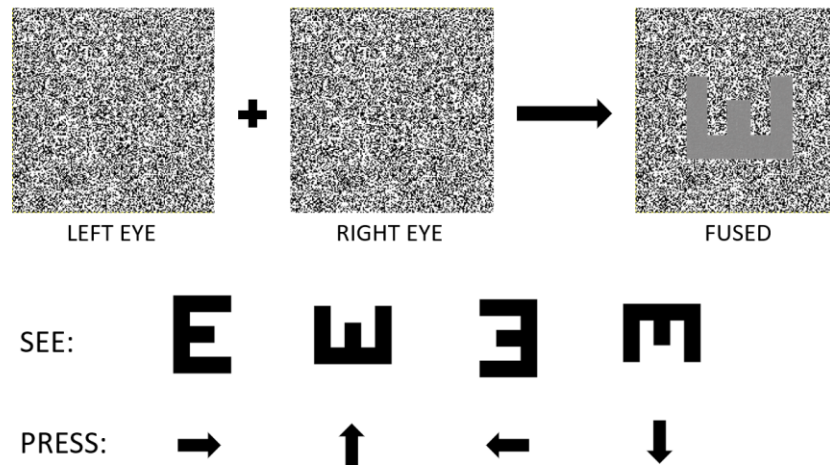


Figure 4. Stimuli used to check fusion.

The letter E that appears when images are fused using a stereoscope can face any direction, and participants press the corresponding arrow keys. Some readers should be able to “free fuse” the left eye and right eye images shown above (by crossing or uncrossing their eyes) to see the upward pointing E in stereoscopic depth.

After the fusion check, participants underwent color-contrast training to get accustomed to seeing images defined by color and not luminance. There were three rounds in the training, and each round showed images of faces and houses in which the same orientation of colors was presented to each eye (red/green or green/red) with 25 trials total. Participants were instructed to press the key F if a face was seen and H if a house was seen. The image presentation time and contrast were lowered for each round, and each round was repeated until the participant achieved > 95% accuracy (Figure 5).

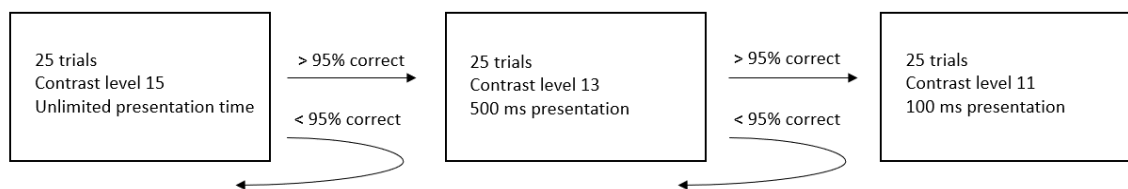


Figure 5. Color contrast training scheme.

Each block has 25 presentations of face and house stimuli and the task is repeated if identification accuracy is below 95% correct. Color contrast and duration of stimuli presentation decrease with each block.

Following the training, a color-contrast tuning experiment was run to determine the optimal color contrast level to use for the participant. Images of same- and opposite-colored faces and houses spanning 12 color-contrast levels were shown at 100 ms durations with an intertrial interval between 1000 ms and 1500 ms. Participants were instructed to make a two-alternative forced choice (2AFC) judgment of either pressing F for face or H for house, even in trials when they could not see either. There were three blocks to this section; the first block was for practice and the second and third blocks collected psychophysics data to use for determining the ideal contrast level. The goal of this section was to find a contrast level at which the percentage of images correctly identified by the participant was near chance level for the images with inverse coloring, while the images with the same coloring were seen well above chance at the same contrast (Figure 6). At this point in the session, if there was not a usable contrast level based on the response data that met these conditions, the participant was paid for their time and did not continue the full experiment.

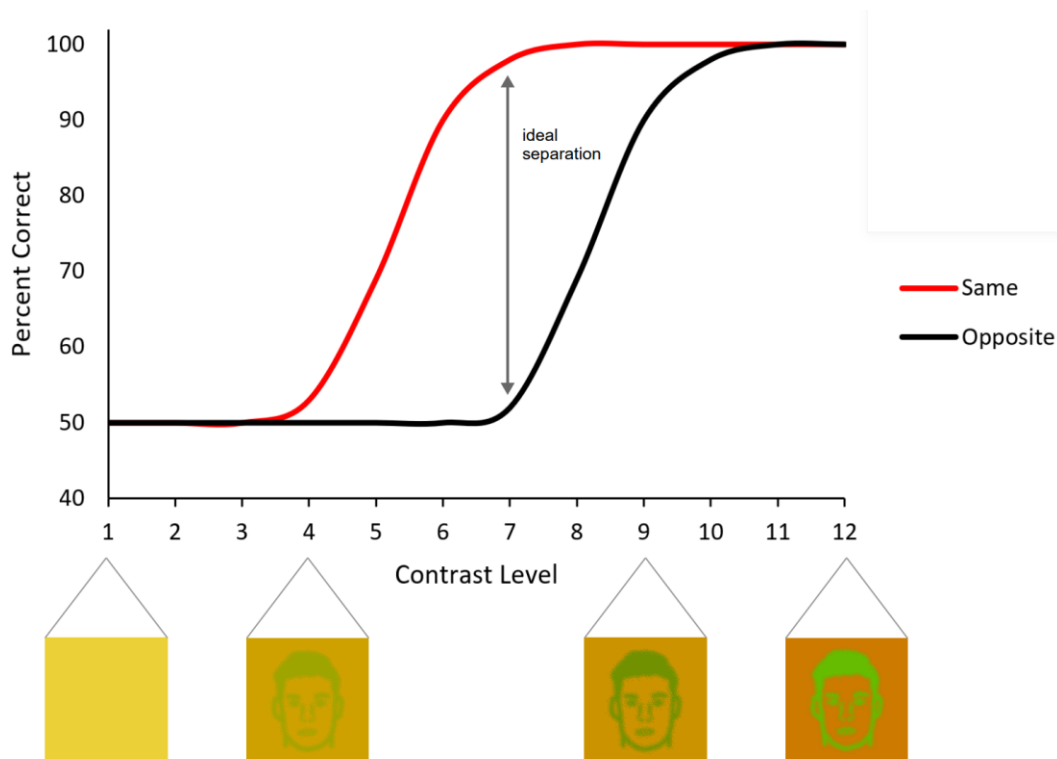


Figure 6. Ideal color contrast curve.

Illustration of an ideal contrast curve for the color contrast tuning with example stimuli. Curves are a measure of the percent correct when giving 2AFC responses to faces and houses, shown over a range of contrast levels. The point of "ideal separation," illustrated by an arrow on the graph using level 7 as an example, shows chance percent correct when stimuli have opposite colors causing images to be perceptually invisible, and ceiling level percent correct when stimuli have the same colors.

After the ideal color contrast level to use for stimuli in the EEG portion of the study was determined, participants were fitted with an electrode cap for recording EEG data. For the no-report EEG experiment, stimuli were perceptually visible or invisible faces, houses, and blanks, set to the determined contrast and presented for 100 ms with a 1000 ms to 1500 ms intertrial interval. In total, there were 1,200 trials split into 10 blocks of 120 trials each, between which participants were given self-regulated breaks. A red dot appeared anywhere on the stimuli in 15% of the trials. While participants were instructed to observe all

the images shown, the only task was to press the spacebar when a red dot appeared on the image. The location of the red dot was randomized to appear anywhere within the space of the stimuli at the time of presentation in order to ensure participants were attending the entire image and in effect perceiving any visible content. All trials in which the red dot appeared were later excluded from analysis. Following this portion of the study, the EEG cap was removed.

To confirm that participants were generally seeing the faces and houses with the same colors and not able to see the versions with opposite coloring, and additionally were not perceiving any images when shown blanks (in effect, hallucinating), a behavioral control experiment was run at the end of each session. The stimuli were exactly the same as in the EEG experiment but with no red dot trials, and there were 192 trials total. Participants were given unlimited time to respond after each image presentation, pressing F for face and H for house as 2AFC judgments, and then rating their awareness of each image on a four-point perceptual awareness scale (PAS) using number keys (1 = saw nothing, 2 = brief glimpse, 3 = almost clear perception, 4 = clear perception) (Sandberg & Overgaard, 2015). A brief prompt with the selection options was shown on the screen while subjects made their 2AFC judgments and PAS ratings (Figure 7). These trial-by-trial reports were then used to validate the visibility manipulation. For the 2AFC face/house responses, chance performance was expected for the opposite-color condition (invisible), and significantly above-chance performance for the same-color condition (visible). For the four-point awareness ratings, the invisible and blank trials should be rated similarly low on the scale, and the visible trials rated significantly higher.

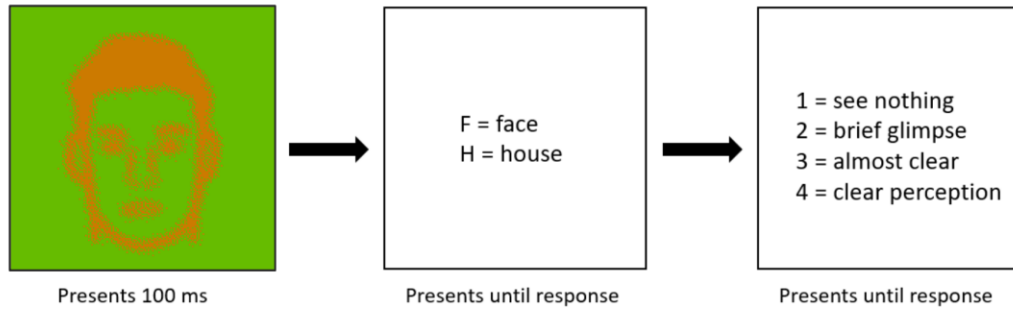


Figure 7. Stimuli for behavioral report control.

Participants are shown a brief presentation of the image, then are prompted to choose between face and house and give a visibility rating. No time pressure is imposed and key selection options appear on the screen.

Results

Behavioral Results

In total, 25 participants were recruited for the study, of which 21 met all conditions for the dichoptic color fusion paradigm and completed the main no-report EEG experiment followed by the report-based control task (one participant did not pass the stereoscopic fusion check; three participants did not have a color-contrast level that could reliably render the stimuli visible vs. invisible). Data from the color-contrast pre-test for a few example subjects is shown in Figure 8 (data from every individual subject's color contrast test is provided in Appendix B).

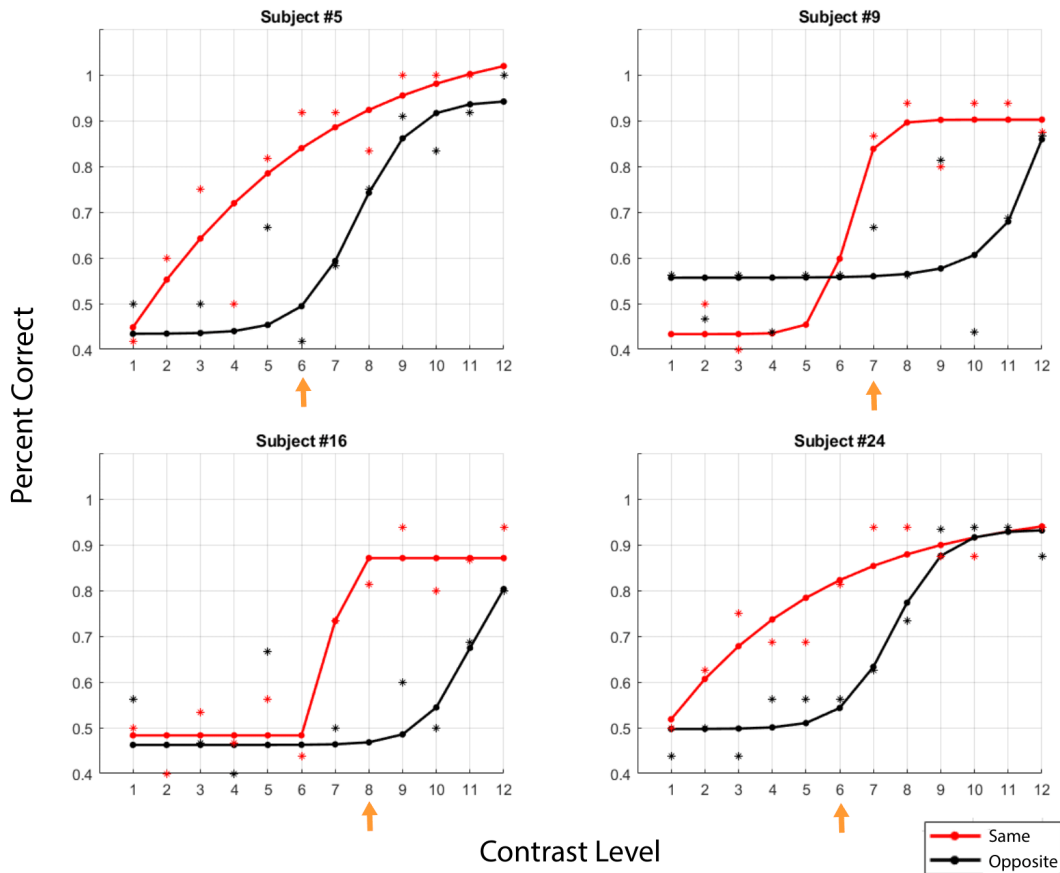


Figure 8. Color contrast curve examples from a subset of participants.

Examples visualizing percent correct in 2AFC discrimination between faces and houses shown at a range of contrast levels. Data pictured 4 subjects which show a clear choice for color contrast level marked by the orange arrow.

In the main no-report EEG experiment, participants performed well in the infrequent dot-detection task, confirming that they maintained attention to the location on the screen in which the key stimuli appeared. On average, participants detected 99.6% of the red dot targets.

To confirm that participants consciously perceived the visible (same colors to L/R eye) stimuli and did not perceive the invisible (opposite colors to L/R eye) stimuli, performance on the 2AFC discrimination test in the trial-by-trial report post-test was assessed, along with subjective visibility ratings for the same stimuli. A binomial test was used to determine that the significance threshold for

above-chance performance in the 2AFC (face/house) identification task was 61% correct (given the small number of trials, 64, and the probability of guessing correctly by chance, 50%). Participants who performed well above chance levels for face and house identification in the opposite-color (invisible) condition were excluded from further analysis (six participants total), leaving 15 participants for analysis of the no-report EEG data. Due to the small sample size, three participants who slightly exceeded chance-level performance in the invisible condition (66%, 67%, 68%) were included for analysis, particularly because their subjective visibility reports indicated that the invisible stimuli were almost never seen. In a longer study with the benefit of larger participant numbers, these individuals would be excluded, or analyzed separately to check for differential brain responses compared to those of participants who performed the task at statistical-chance levels.

Results of the report-based behavioral control task from the 15 included participants show that the desired visibility conditions were achieved (Figure 9). A one-sample Bayesian t-test was conducted for accuracy on the 2AFC face and house discrimination task in the invisible condition (not including the previously identified above-chance participants) to assess whether performance was at chance. The Bayes factor provided compelling support for above-chance performance ($BF_{10} = 51.43$), suggesting participants may have been conscious of some stimuli during the opposite-color condition and future studies may benefit from stricter exclusion criteria. Using a two-way ANOVA to analyze the average visibility rating results, with the factors color-to-L/R-eyes (same/opposite) and stimuli (face, house, blank), statistically significant main effects were found for color-to-L/R-eyes, $F(13) = 76.50$, $p < .001$, as well as for stimuli, $F(13) = 61.72$, $p < .001$, along with a significant interaction between color and stimuli, $F(13) = 56.03$, $p < .001$. Tukey post-hoc tests revealed significant pairwise differences between the same and opposite color presentations for house, $t(14) = 9.40$, $p < .001$, and face $t(14) = 10.78$, $p < .001$ stimuli, but not for blanks, $t(14) = 0.04$, $p = 1.0$.

Additionally, all stimuli had visibility ratings significantly different from each other in the same-color condition, where visibility was highest rated for faces, followed by houses, and lowest rated for blanks. Perfect achievement of visibility manipulation would show comparable visibility ratings for all stimuli in the opposite-color condition. While house and blank conditions did not show a difference ($t(14) = 0.97$, $p = 0.92$), the visibility ratings for the opposite-color face stimuli were slightly higher than for opposite-color blanks ($t(14) = 3.10$, $p = 0.04$). This suggests face stimuli were easier to see than houses and occasionally may have been seen in the opposite-color condition, although whether the particular image content was perceived is inconclusive given the lack of difference between face and house visibility ratings in the opposite-color condition.

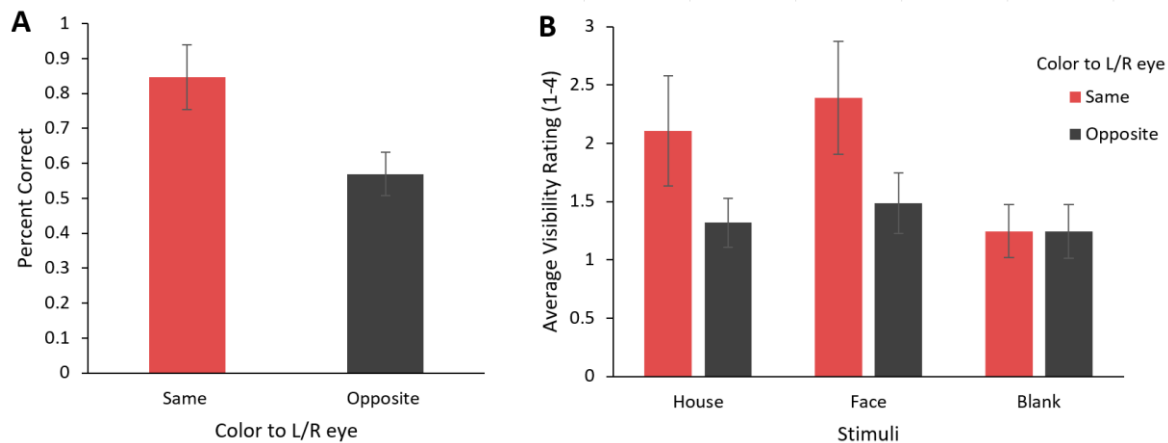


Figure 9. Behavioral report control performance.

Data is averaged across all subjects ($n = 15$). **A** Mean percent correct in 2AFC judgments between face and house for the same (visible) and opposite (invisible) conditions. **B** Mean visibility ratings on a 4-point perceptual awareness scale (1 = see nothing, 2 = brief glimpse, 3 = almost clear perception, 4 = clear perception) compared between same (visible) and opposite (invisible) conditions for the face, house, and blank stimuli. Error bars reflect standard deviation. See Appendix C for data from all subjects.

Electrophysiological Results

The ERP responses for all conditions showed comparable P1 and N1 waveforms. Mass univariate analysis of the EEG data was used to analyze the differences in recorded brain activity between the opposite-color and same-color conditions (i.e., the main visible vs. invisible contrast). These comparisons were made for each stimulus separately, and statistically significant effects were found only for face stimuli. As visualized in the mass univariate heat map, significant differences appear mostly between 260 ms and 640 ms after stimulus presentation (Figure 10). The posterior negativity around 260 ms to 320 ms, accompanied with a frontal positivity, is consistent with the previously reported visual awareness negativity (VAN).

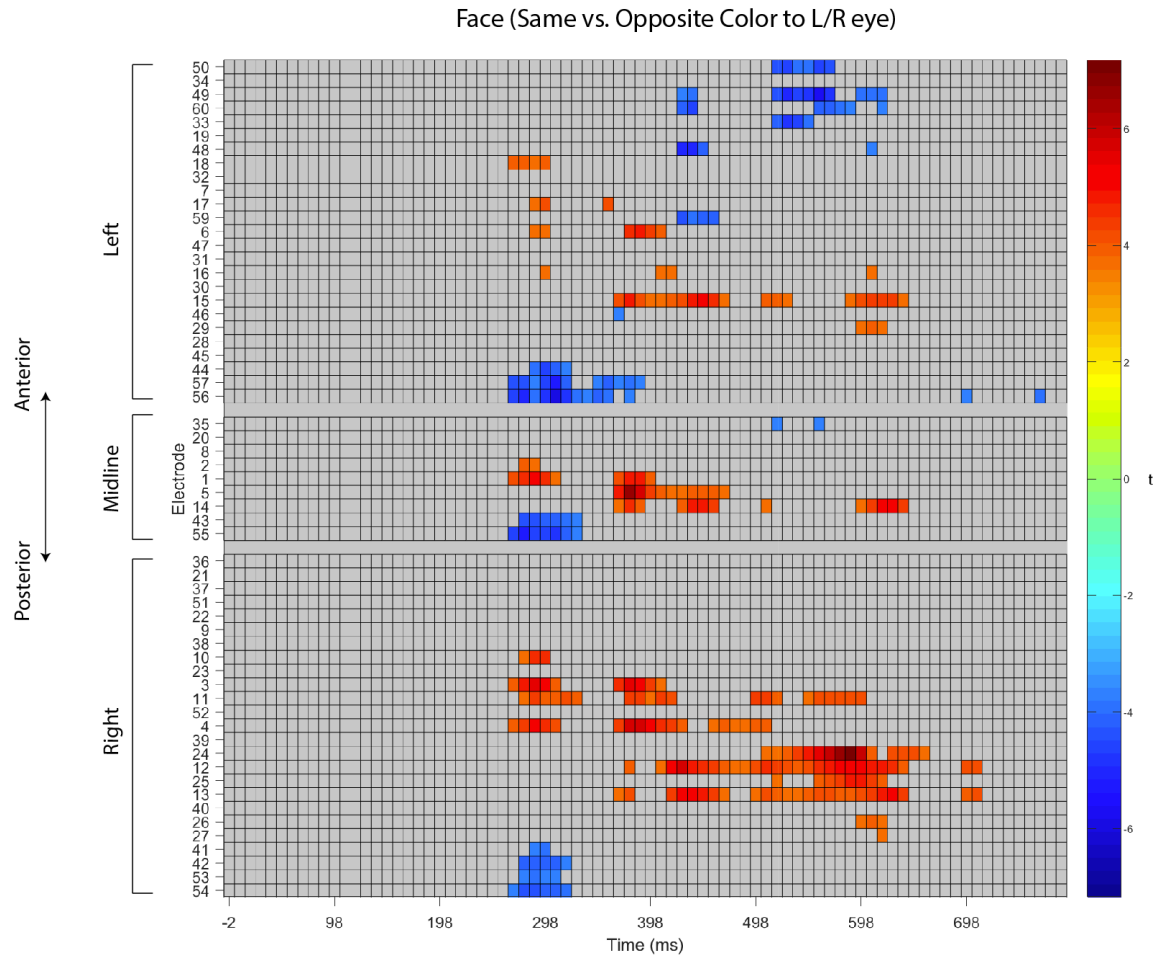


Figure 10. Mass univariate analysis results.

Analysis comparing the same (visible) and opposite (invisible) color conditions for face stimuli. False discovery rate was calculated using the difference in ERP amplitudes between conditions for each subject ($n = 15$). The grid illustrates all electrodes over all time points and color indicates statistical significance of the difference by t-value scale.

While only the face condition was found to have a statistically significant VAN, when visualizing the ERPs, the house condition did show clear signs of a less pronounced VAN (Figure 11). These preliminary results suggest that there is likely still a VAN for the house stimuli, but due to the small sample size these statistical analyses were too conservative to detect this smaller difference. When considering that visibility ratings in the report-based control task were lower for

houses than for faces, a more subtle distinction is expected which was consistent with the observed brain data. Importantly, according to the data, the blank condition did not show any significant differences in the mass univariate statistics, nor any hints of a negative difference during the VAN time frame, indicating that the effects in the face and house conditions were likely related to conscious perception rather than stereoscopic color fusion. The topographical distribution of the VAN appears to have slight differences between face and house stimuli, where the face VAN appears with a far posterior negativity and corresponding positivity toward the top of the head, while the house VAN shows a more parietal-shifted negativity reflected by the far frontal positivity. The ERPs comparing the same- and opposite-color conditions for all channels in each stimulus can be found in Appendices D through F.

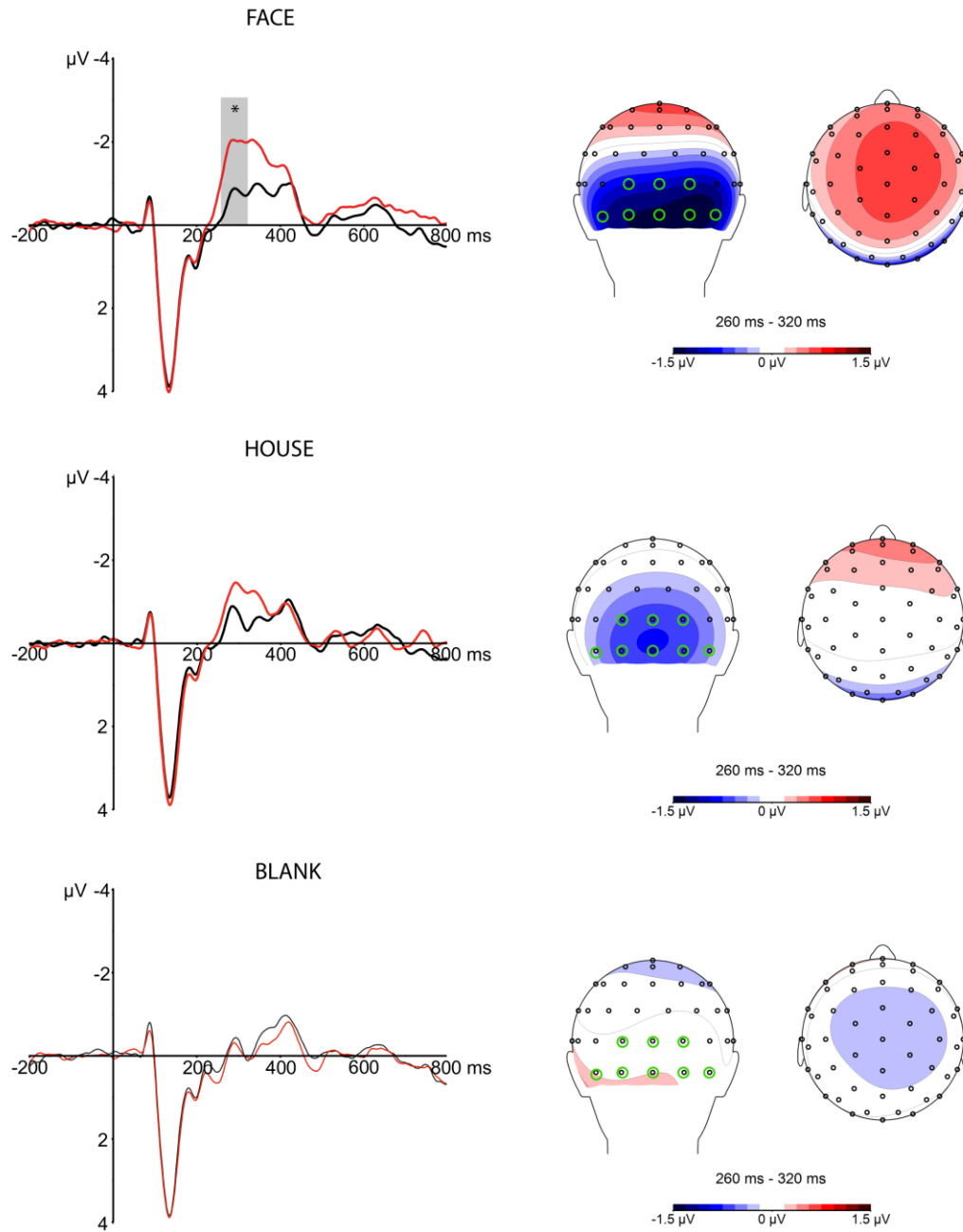


Figure 11. ERPs and difference maps visualizing the VAN.

Data is averaged across subjects and compared between same (visible) and opposite (invisible) conditions for face, house, and blank stimuli. Data for ERPs is from pooled channels (54, 53, 42, 55, 43, 56, 57, 44, circled in green) that showed a significant difference between color conditions for faces around 260 to 320 ms during mass univariate analysis. Effects for same minus opposite conditions in the same time window are represented topographically on difference maps.

In the face condition, differences subsequent to the VAN were detected in the mass univariate analysis, indicating a parietal positivity starting around 360 ms (Figure 12). This timing and location is consistent with a late positivity, possibly including a P3b, which has often been linked with reporting one's conscious visual perception and was expected to be eliminated in the current study by the no-report design.

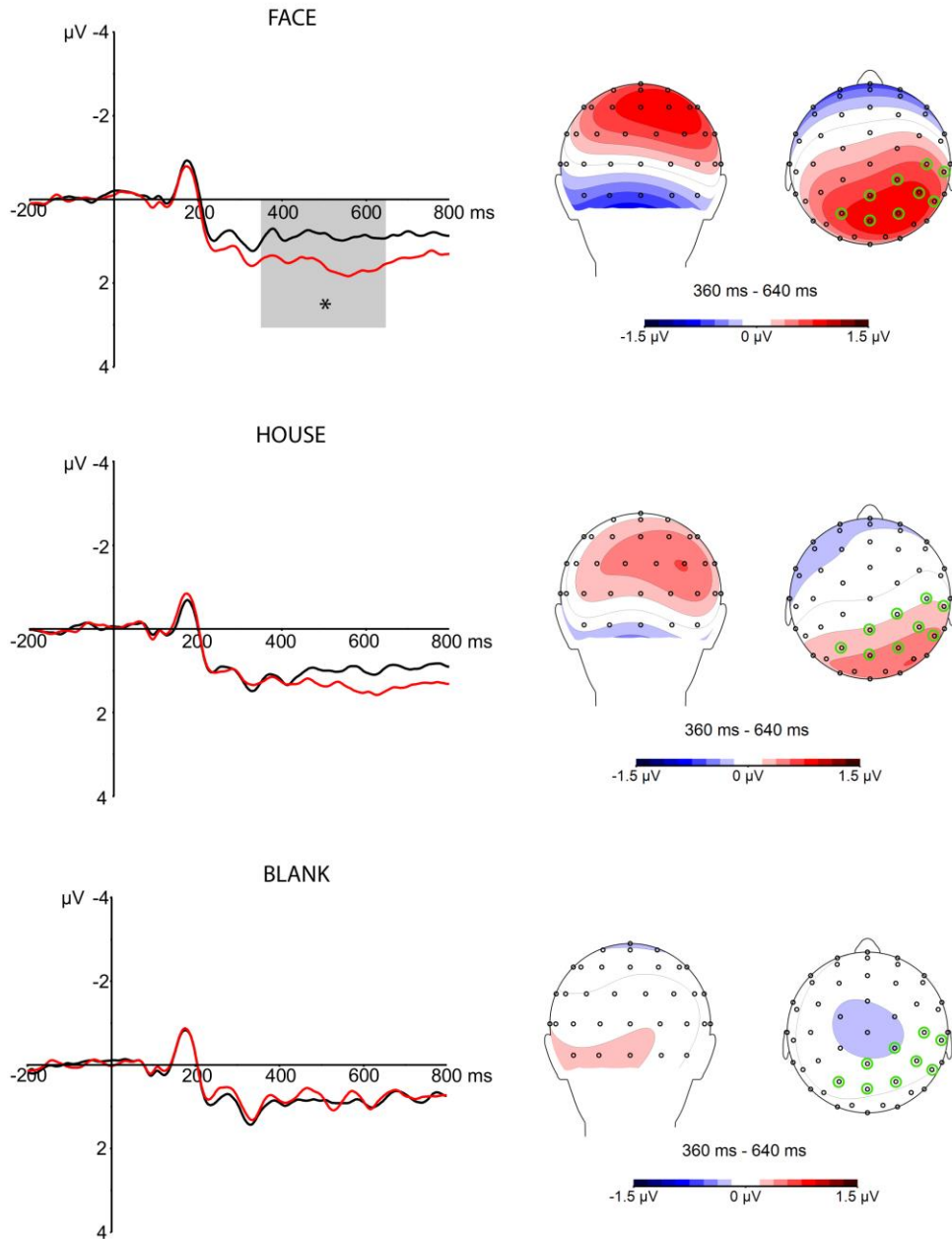


Figure 12. ERPs and difference maps visualizing the LP.

ERPs visualizing the LP averaged across subjects and compared between same (visible) and opposite (invisible) conditions for face, house, and blank stimuli. Data for ERPs is from pooled channels (4, 5, 11, 12, 13, 14, 15, 24, 25, circled in green) that showed a significant difference between color conditions for faces around 360 to 640 ms during mass univariate analysis. Effects for same minus opposite conditions in the same time window are represented topographically on difference maps.

Additionally, exploratory analyses assessed whether differences in ERP amplitudes might be observed between stimuli (versus blanks) in the same-color (visible) condition or the opposite-color (invisible) condition separately (Figure 13). Within the same-color (visible) condition, a clear gradation of posterior negative-going amplitudes was apparent, with the most visible stimuli, faces, showing the greatest negativity, followed by houses, and then the blanks. A face-specific N170 was expected in the visible face condition (compared to the house and blank conditions), where images presented to each eye had the same colors allowing the face to be perceived. While there was no distinct negativity around 170 ms, it should be taken into consideration that the stimuli were of very low contrast and hard to see, so as a result ERPs may be delayed (Ojanen et al., 2003). Potentially, the difference in negativity between face and house conditions starting around 210 ms can be attributed to a delayed N170, causing the face ERP to show earlier increased negativity. In comparing the stimuli while opposite colors were presented to each eye, in which all of the images were perceived as a blank yellow square, ERPs were much more similar, at all time points and electrode locations. However, in the same electrode location and time window in which the VAN was observed, a small negative difference was apparent for the face and house images as compared with the blank images (even when excluding the three subjects who had above-chance identification of images in the opposite-color condition). More subjects will be needed to confirm this subtle difference in brain activity that might indicate unconscious perceptual processing. The ERPs comparing stimuli across all channels for the same- and opposite-color conditions can be found in Appendices G and H.

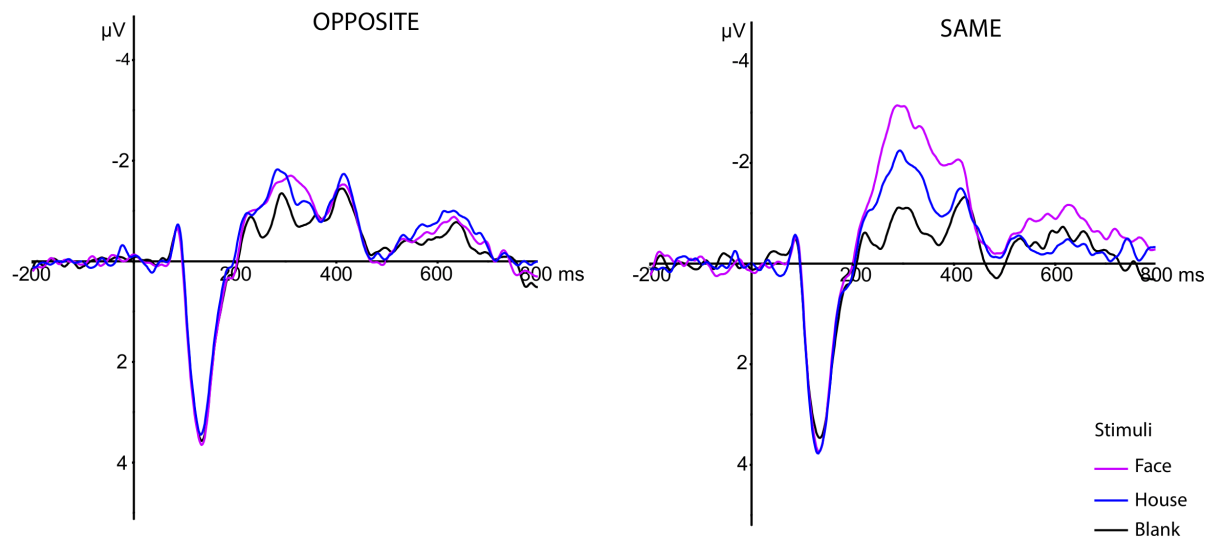


Figure 13. ERPs comparing stimuli within each visibility condition.

Data is from channel 54 averaged across subjects comparing face, house, and blank stimuli for same (visible) and opposite (invisible) conditions. Results are from 12 subjects, three subjects that had above chance stimuli detection in the behavioral report control were excluded on stricter criteria for this visualization so that the invisible condition could be properly analyzed.

Discussion

Overall

The present study used a dichoptic color fusion no-report paradigm to examine NCCs related to visual perception. Comparisons were made between brain-activity responses to stimuli consisting of images of faces, houses, and blanks presented in the same colors to each eye (visible) or opposite colors to each eye (invisible). The results showed that in comparing the visibility conditions, ERPs to visible faces exhibited a greater negativity starting around 260 ms consistent with the VAN, and a later positivity identified as a potential P3b which was expected to be eliminated by the no-report paradigm. House stimuli showed similar effects but were attenuated due to lower visibility and remained nonsignificant, while the blank condition showed no related differences that could indicate stereoscopic color fusion playing a role.

The behavioral report control post-test confirmed that dichoptic color fusion visibility manipulations established a same-color visible condition and opposite-color invisible condition to distinguish conscious and unconscious visual perception. Percentage accuracy in 2AFC face/house discrimination found near-chance-level performance in the opposite-color condition but high accuracy in the same-color condition, and this was reflected in the PAS visibility ratings. These results show dichoptic color fusion to be a highly promising technique for comparisons of conscious and unconscious processing, as images that are the same in every aspect except for color can be seen but either perceived as visible or invisible. Color arrangements between each eye were controlled for by the blank stimuli condition, which was presented with the same- or opposite-color blank to each eye. The opposite-color presentation offers a baseline for perception of a blank image but seen through stereoscopic fusion of different

colors, while the same-color condition is a control for standard perception of a blank image.

Electrophysiological Results

Importantly, blank stimuli in the same- and opposite-color manipulations generated near identical ERPs, and all small differences were not relevant to effects found in other stimuli conditions. This suggests electrophysiological differences between the visibility conditions are likely not due to any effects of stereoscopic color fusion. Mass univariate analysis found significant effects of visibility in the face condition. Visual inspection of ERPs found additional differences in the house condition that may correspond to effects that will appear as significant with an increased number of participants, so such instances are discussed as well.

The first correlate of visibility identified by mass univariate analysis for face stimuli was a posterior relative negativity of the same-color visible condition from 260 ms to 320 ms consistent with a VAN. A negativity at the same time points, but less differentiated from the opposite-color condition, similarly appeared for house stimuli. In visualizing the ERPs using difference maps, the face VAN appeared to have a more posterior negativity. Studies have shown that perceptual awareness negativities across visual, auditory, and somatosensory stimuli locate above their associated sensory cortices (Dembski et al., 2021), but little research has been done into whether alterations to the stimuli within these modalities have an effect on the spatial distribution of this negativity. Images of faces and houses have been found to distinctly activate the fusiform face area (FFA) and parahippocampal place area (PPA), respectively, so one explanation for distinct distributions is the differential projection of brain activity (Epstein & Kanwisher, 1998; Kanwisher et al., 1997). Blank stimuli showed a slight relative

positivity of the same-color conditions, suggesting that effects of stereoscopic fusion do not contribute to this difference and may even attenuate it.

The second correlate of visibility for face stimuli was a parietal area late positivity starting around 360 ms and continuing to around 650 ms, appearing strongest in the right hemisphere. This effect is consistent with an LP, potentially containing a P3b, which was expected to be eliminated by the no-report design, as studies have shown the P3b disappears when participants are not asked to perform task-relevant reporting (Cohen et al., 2020). The sessions immediately preceding the main no-report trials were the color-contrast training and contrast-tuning experiments, both of which tasked participants with discriminating between face and house images by pressing buttons accordingly. One explanation for the LP viewed in the current study then could be that subjects may have been internally reporting whether the stimuli being viewed is a face or house, even though they were tasked only with viewing the image. Another possible explanation would be that the LP is a neural correlate of consciousness and studies that achieved its elimination with a no-report design used visual manipulations that were so low-visibility that any effect was reduced. However, with the amount of evidence and replicable results supporting the LP as a correlate of task-relevant reporting, this seems a less likely explanation (Pitts et al., 2014; Cohen et al., 2020).

The results of this study best support the recurrent processing theory, which predicts an earlier onset of consciousness (Förster et al., 2020). The VAN occurs early in time after stimulus presentation and has been proposed to reflect consciousness related to recurrent processing (Koivisto et al., 2006). Additionally, a general localization of the VAN to the occipital region indicates visual sensory areas as key generators of the ERP. Global neuronal workspace theory, on the other hand, predicts a later onset of consciousness, ~300 ms to 500 ms post-stimulus, and less localization of brain activity (Förster et al., 2020). Under this mechanism for visual consciousness, the late positivity is viewed as the primary

correlate of consciousness (Sergent et al., 2005). While a small LP was potentially present in the current study, because it was preceded by the VAN, and because of the possible task-carryover effects from the training and pre-test, the results overall disagree with this prediction of the global neuronal workspace model. While the VAN is currently considered one of the most promising candidates for an NCC, it has been questioned as a correlate of attention rather than awareness, which is a topic that will need further investigation (Bola & Doradzińska, 2021). If this is the case, then the small negative difference when comparing blanks to face or house stimuli seen in the opposite-color condition may be an effect of unconscious attention.

Limitations

Due to the small sample size, more lenient inclusion criteria were used and three subjects with above-chance performance for the invisible condition of the behavioral report control were included in the analysis. Because the visibility ratings of these subjects indicated the invisibility manipulation was achieved, including their data allowed for more powerful investigation of correlates of consciousness, but it must also be considered that these subjects could have occasionally consciously perceived the stimuli in the invisible condition. This could allow correlates of conscious processing to appear at a very low level in the opposite-color condition ERPs. Additionally, even when including subjects on more lenient criteria, a total of 15 subjects is low for the confidence needed to identify statistically significant effects. In modern-day EEG experiments like this, researchers more commonly aim for 25 to 40 subjects total. This likely explains the absence of effects of visibility in the mass univariate analysis for the house condition.

Future Directions

Data collection for the study will continue into the future, hopefully resolving the need to use lenient inclusion criteria and also increasing the power for analysis in order to identify more effects of visibility on electrophysiological data. Additionally, this dataset is a great opportunity for exploring other avenues of analysis. This could include time-frequency analysis, decoding, temporal generalization, and investigations into correlations with alpha, beta, and theta powers. The same EEG data collected here can be analyzed in a variety of different ways to investigate additional neural signals that may be relevant for conscious visual perception.

Future studies may also want to investigate unresolved questions in the results of this paradigm, such as the absence of a clear N170 and the unexpected late positivity. It has been found that inverted (upside down) face stimuli evoke an enhanced N170 at a delayed latency, making it distinguishable from the response to upright faces (Allen-Davidian et al., 2021). Using the dichoptic color fusion setup for comparing responses to upright faces and inverted faces may help to disambiguate the N170 from the VAN and answer whether it is appearing as a delayed effect or absent altogether. If the absence of the N170 was confirmed, this would raise questions as to whether the stimuli were visible enough for participants to be able to discriminate particular perceptual content, or whether the behavioral data reflects a more basic detection of an image versus a blank. Another area of the results to investigate is the late positivity that was expected to be eliminated by the no-report design. If one possible explanation is the subject's internal reporting of faces and houses facilitated by preceding the main trials with face or house discrimination tasks, then running the color-contrast trials on a separate day from the main EEG trials would distance the tasks more, and a future study could see if the positivity is in turn attenuated. Additionally, the current data could be used to compare EEG responses from the

first half of the main trials versus the second half, and if there is a carry-over effect of face house discrimination from previous tasks, and larger P3b would be expected towards the first half of the trials. Another option would be running the same study with subject reporting, which would allow for comparison of the LP to gain more information on its cause. This would additionally be useful for checking that the VAN is still observed in a reporting paradigm, as would be expected.

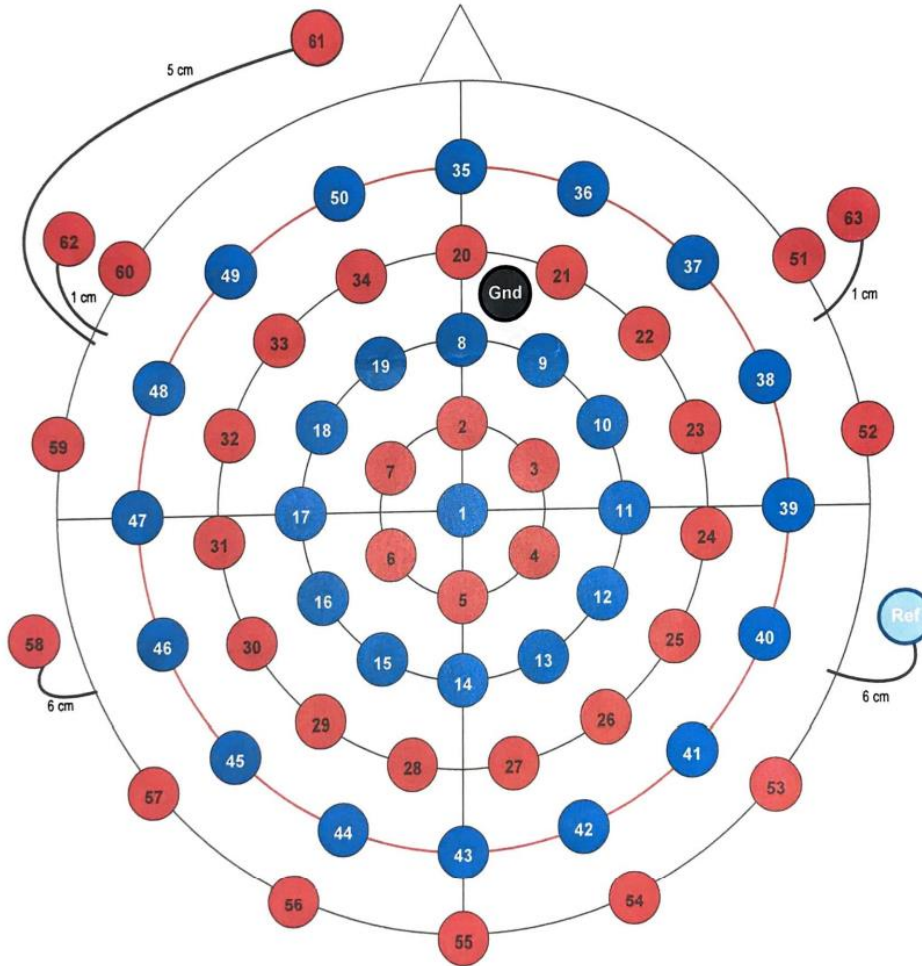
Conclusion

The brain activity of subjects who viewed stimuli consciously versus unconsciously in a dichoptic color fusion no-report paradigm was compared to investigate the neurophysiological basis of phenomenal consciousness. As both the VAN and LP were present as effects of visibility for face stimuli, the results support theories that predict an early onset of consciousness, while not ruling out a potential contribution from later-stage cognitive mechanisms predicted by competing theories. Continued collection of data using the same design may help to confirm the presence of a VAN and LP. Additional analysis using the same raw EEG data (event-related time-frequency spectra, multivariate pattern classification, etc.) can supplement and extend the basic ERP analysis supported here.

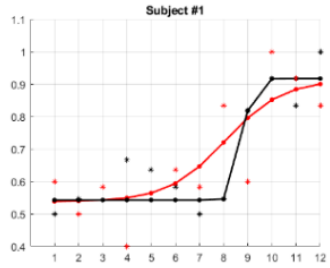
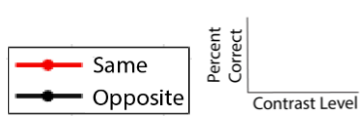
Appendices

A. Electrode cap layout

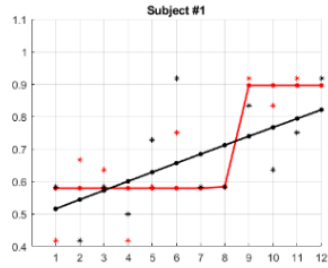
Electrode Layout and Channel Assignment:



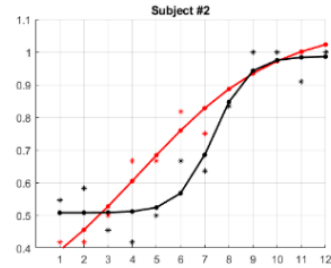
B. Color-contrast curves



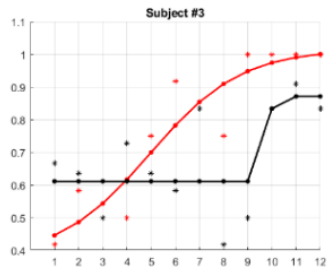
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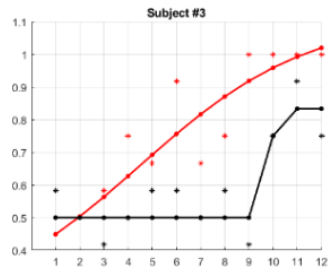
(2/2)



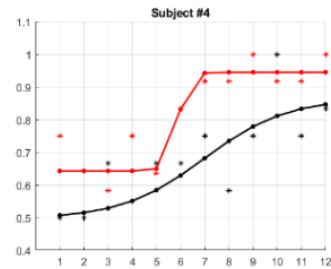
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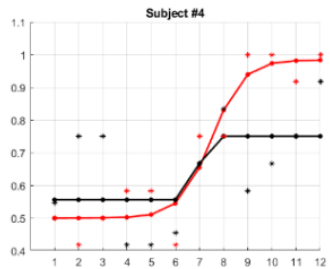
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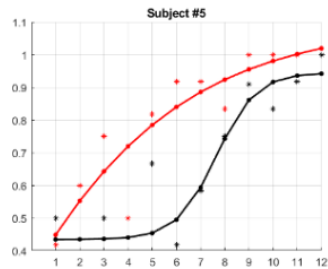
(2/2)



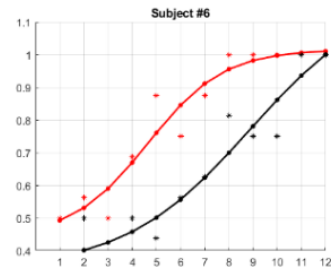
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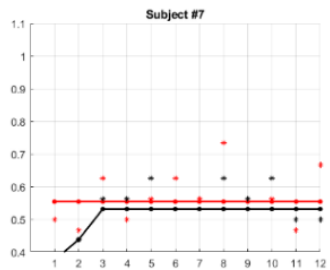
(2/2)



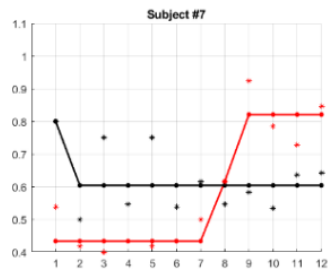
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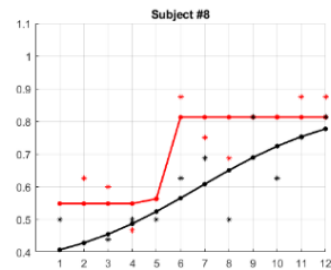
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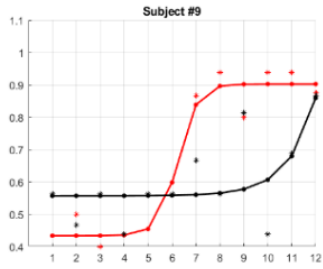
contrast level: 9 (1/2)



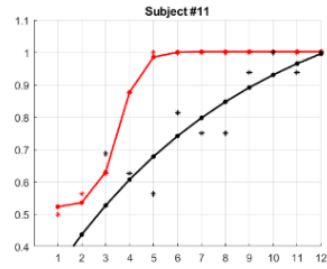
(2/2)



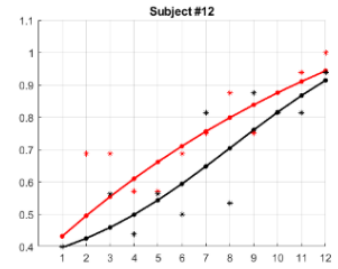
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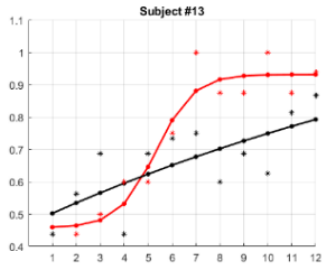
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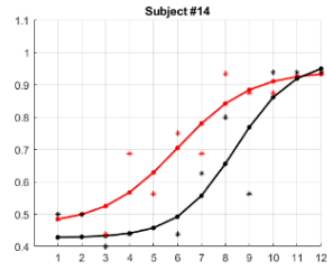
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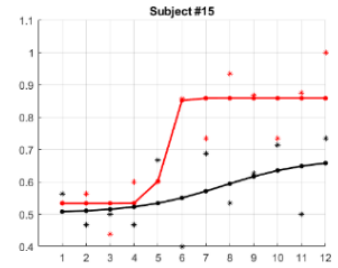
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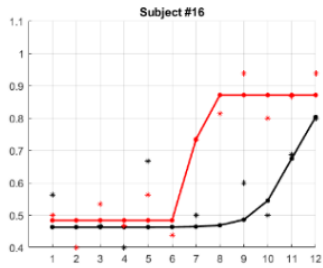
contrast level: 6



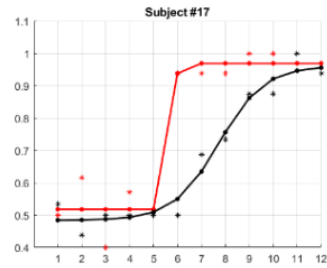
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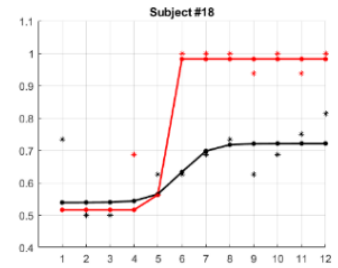
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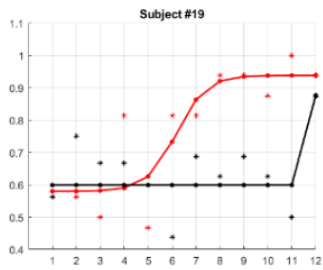
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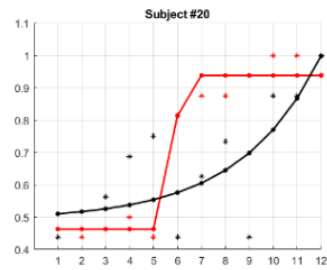
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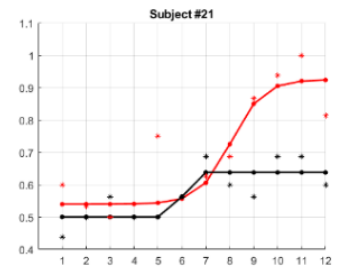
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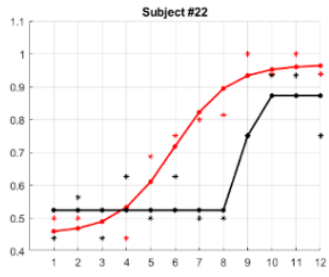
contrast level: 6



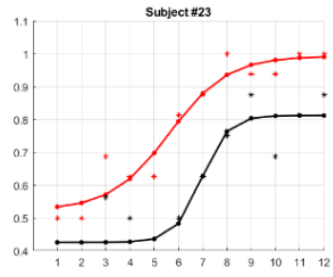
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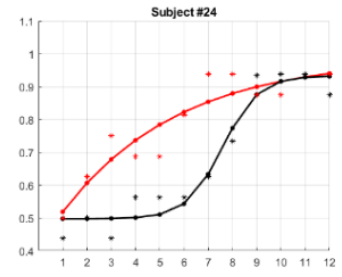
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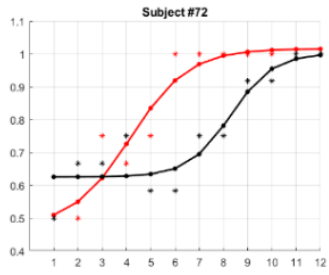
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contrast level: 6



contrast level: 6



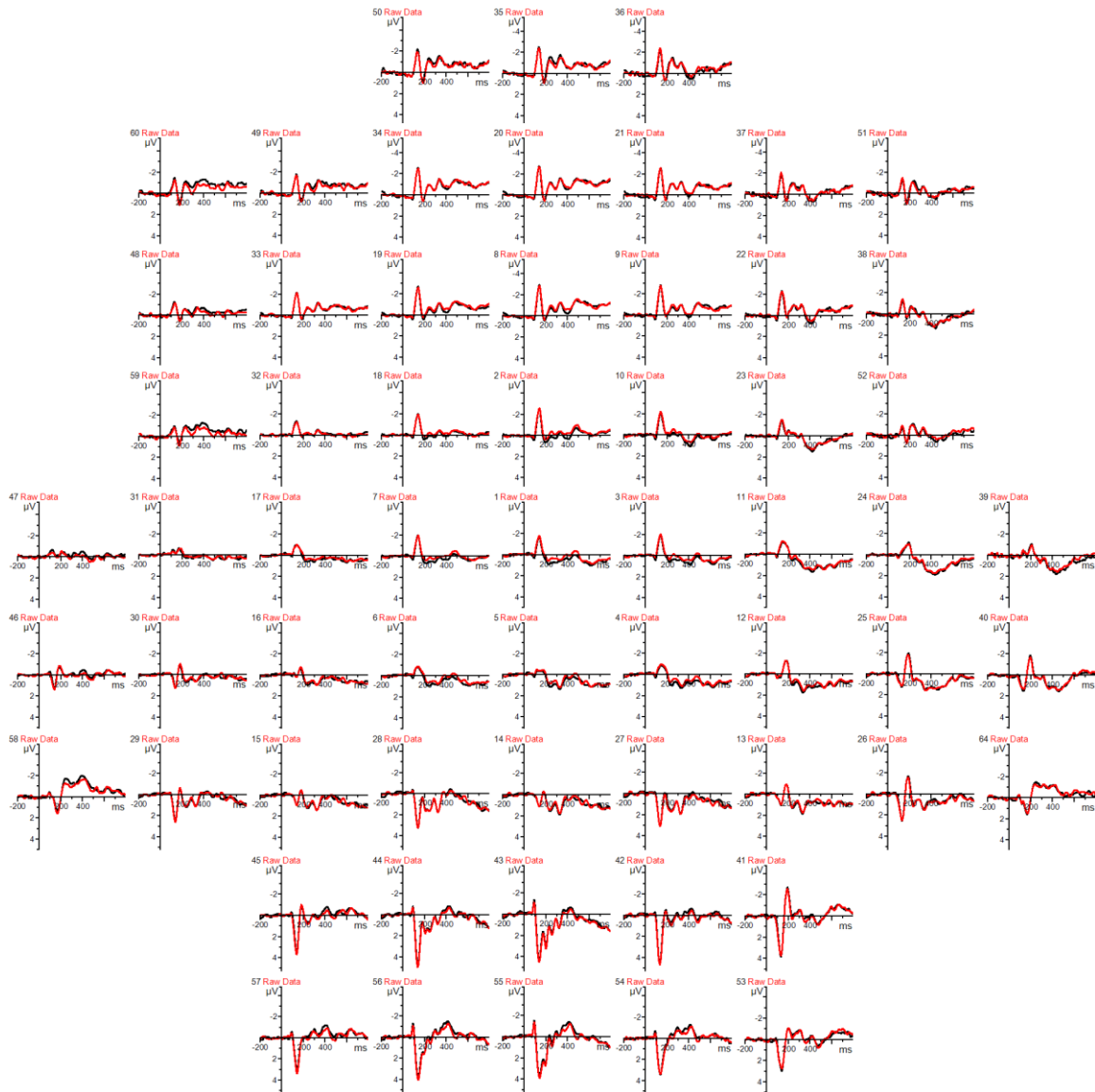
contrast level: 6

C. Behavioral report control results for all subjects.

Subject	Percent Correct (2AFC Face/House)		PAS Visibility Ratings (1-4)						Inclusion Status
	Same Color	Opposite Color	Same Color House	Opposite Color House	Same Color Face	Opposite Color Face	Same Color Blank	Opposite Color Blank	
1	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	excluded
2	0.73	0.58	1.97	1.47	2.13	1.81	1.5	1.28	included
3	0.81	0.5	2.22	1.44	2.69	1.59	1.59	1.56	included
4	0.84	0.7	2.44	1.47	2.41	1.72	1.34	1.19	excluded
5	0.79	0.48	1.75	1.13	1.88	1.28	1.09	1.06	included
6	0.83	0.69	1.09	1.09	1.47	1.25	1	1	excluded
7	0.91	0.77	2.03	1.56	2	1.59	1.06	1.06	excluded
8	0.57	0.52	1.03	1.03	1.19	1	1	1	excluded
9	0.72	0.53	1.63	1.19	1.65	1.28	1.25	1.25	included
10	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	excluded
11	1.0	0.81	2.47	1.53	2.34	1.97	1.25	1.31	excluded
12	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	excluded
13	0.83	0.52	2.13	1.59	2.59	1.72	1.22	1.5	included
14	0.75	0.57	2.03	1.34	2.32	1.44	1.44	1.28	included
15	0.98	0.59	2.53	1.66	2.55	1.81	1.47	1.44	included
16	0.98	0.5	1.91	1	2.28	1.16	1	1	included
17	0.98	0.66	1.78	1.13	2.13	1.25	1.09	1.16	included *
18	0.98	0.67	3.13	1.31	3.03	1.44	1	1	included *
19	0.66	0.68	1.16	1.03	1.41	1.07	1.03	1	excluded
20	0.83	0.56	1.38	1.06	1.75	1.06	1.03	1	included
21	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A	excluded
22	0.83	0.58	2.97	1.44	3.39	1.78	1.26	1.23	included
23	0.81	0.55	2.28	1.63	2.88	1.81	1.66	1.75	included
24	0.84	0.68	1.91	1.23	2.03	1.55	1.06	1.13	included *
25	0.83	0.56	2.03	1.19	2.5	1.31	1.03	1	included

* subjects with above chance performance in the opposite condition determined by binomial test (above 61% correct) but were still included for analysis on more lenient criteria for the purposes of this study.

D. ERPs for blank stimuli across color conditions.

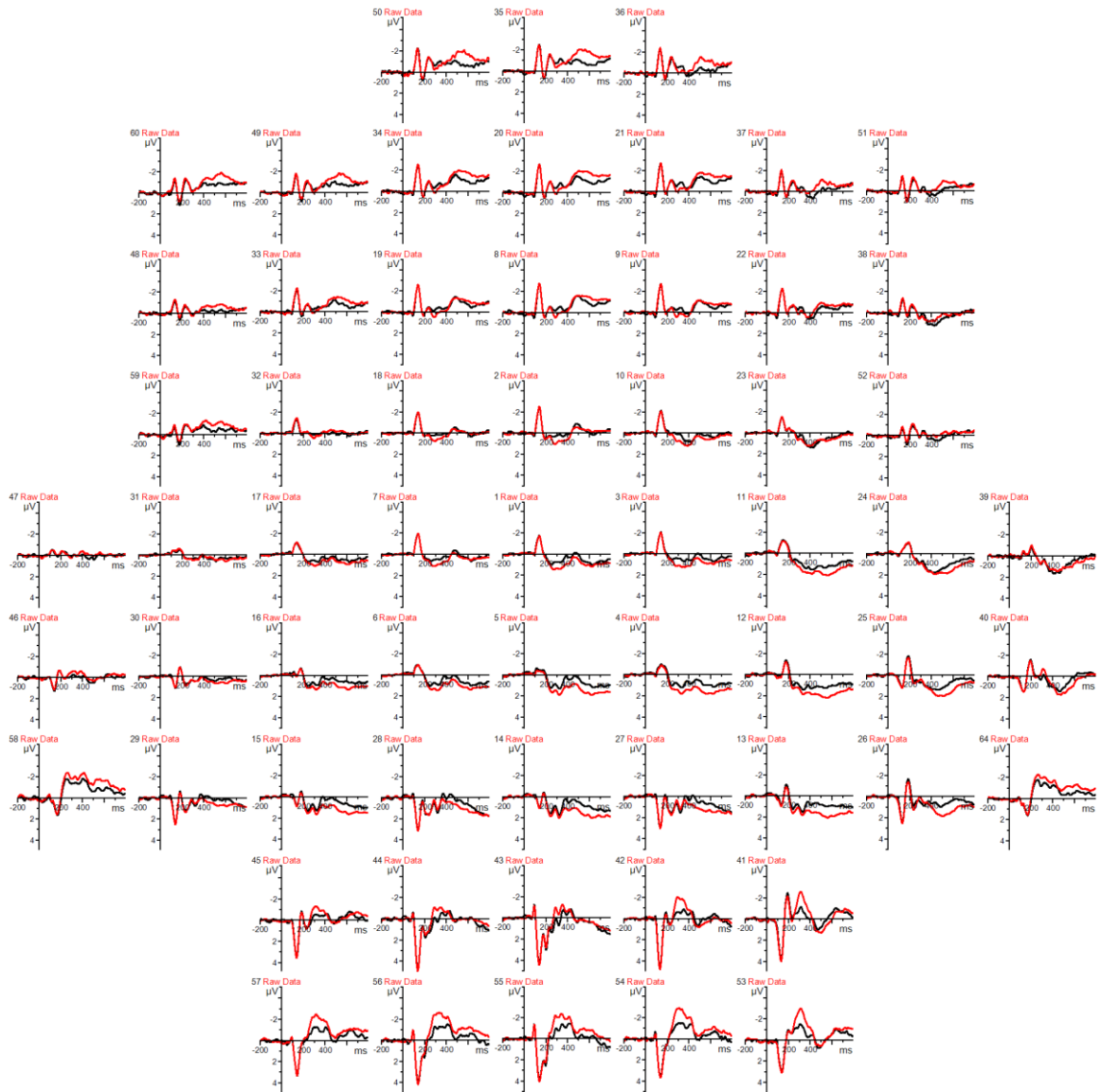


Color to L/R eye

— Same (visible)

— Opposite (invisible)

E. ERPs for face stimuli across color conditions.

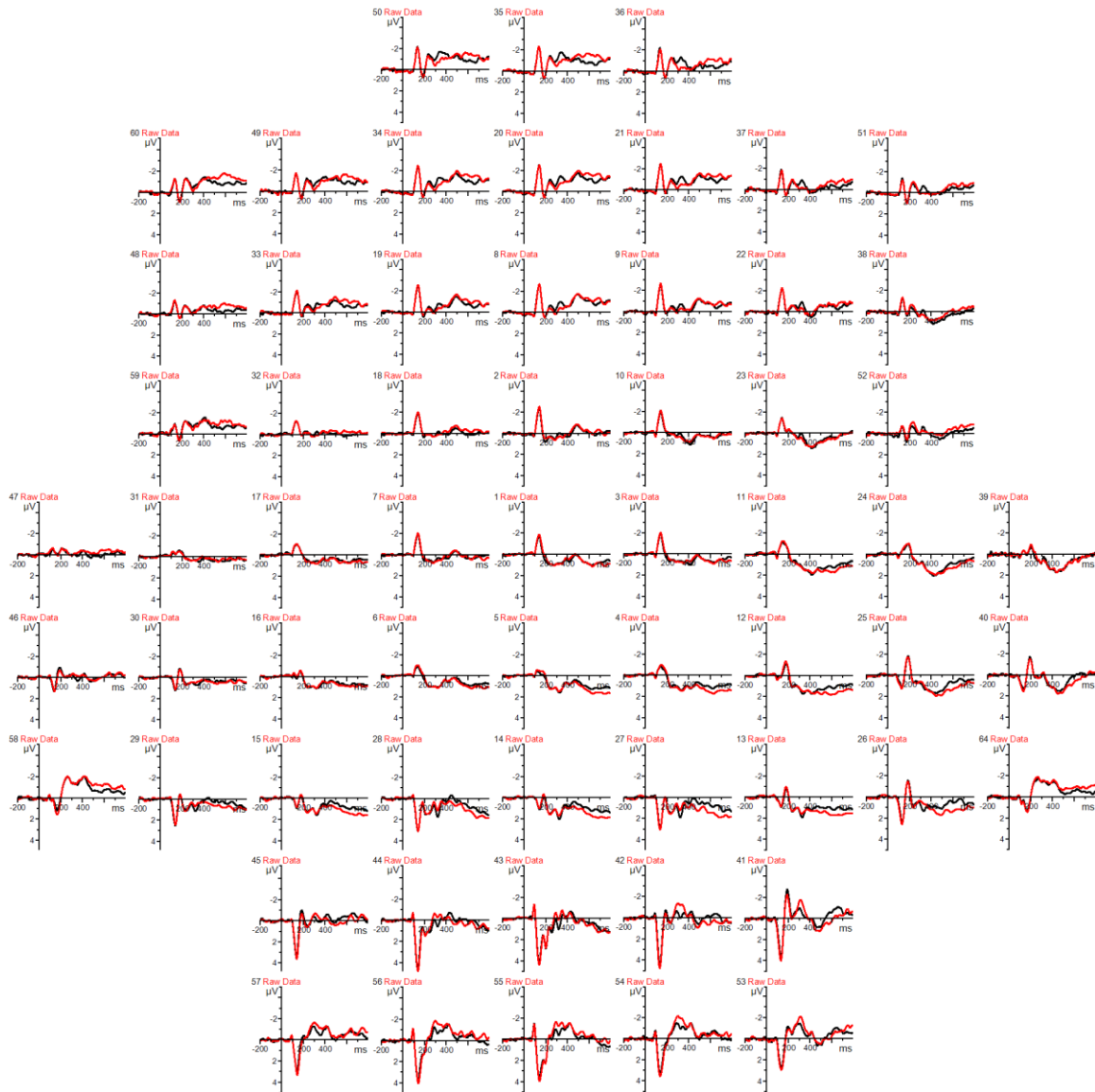


Color to L/R eye

— Same (visible)

— Opposite (invisible)

F. ERPs for house stimuli across color conditions.

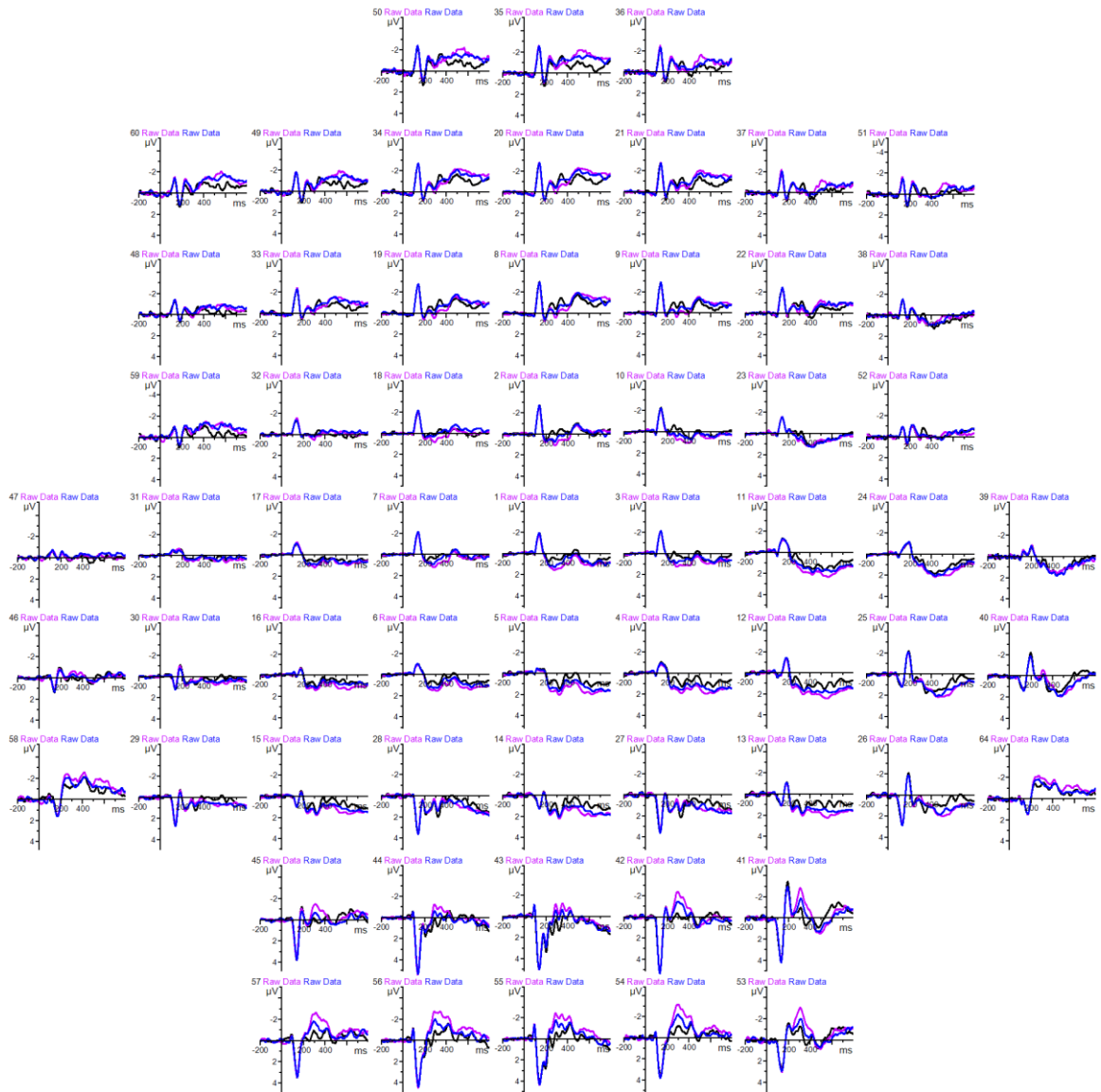


Color to L/R eye

— Same (visible)

— Opposite (invisible)

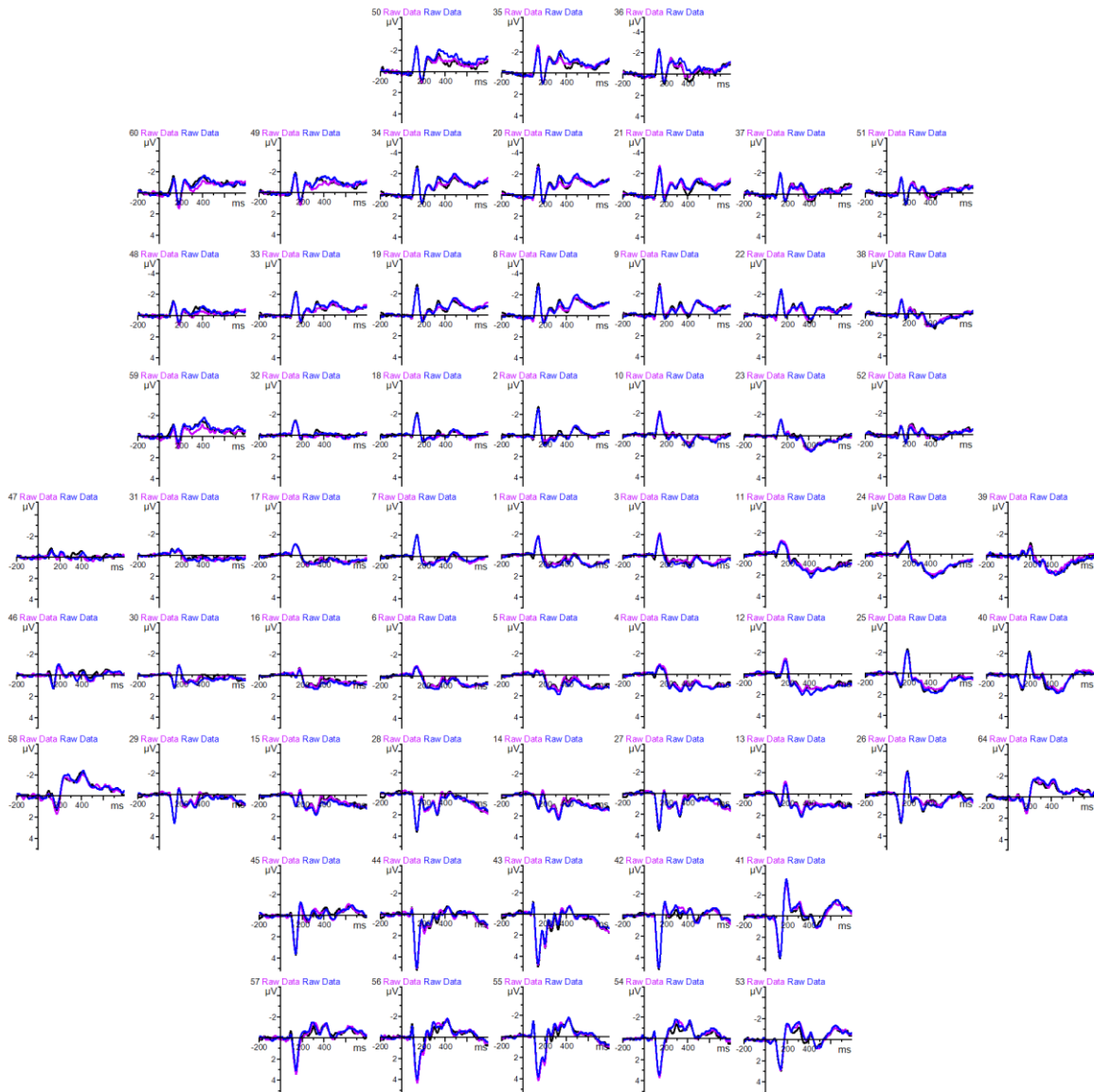
G. ERPs for same-color condition of all stimuli.



Stimuli

- Face
- House
- Blank

H. ERPs for opposite-color condition of all stimuli.



Stimuli

- Face
- House
- Blank

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