Title
Neural timing and patterns of color vision

Author
Lee, Hannah

Publication Date
2011

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA, SAN DEIGO

Neural Timing and Patterns of Color Vision

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

In

Biology

By

Hannah Lee

Committee in charge:

Professor Vilayanur S. Ramachandran, Chair
Professor Christopher Wills, Co-Chair
Professor Andrew Huberman
Professor Takaki Komiyama

2011

The Thesis of Your Full Legal Name is approved and it is acceptable in quality and form for publication on microfilm and electronically:

Co-Chair

Chair

University of California, San Diego

2011

DEDICATION

This thesis is whole-heartedly dedicated to my family:

To my father, Byung-Eun,

and

my mother, Mikyoung, for teaching me the way to live life to its fullest and happiest.

To my brother, Joshua, for being the best brother a sister can ask for.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKNOWLEDGMENTS

Those of us fortunate enough to know Prof. Vilayanur S. Ramachandran knows him for his passion and joy in finding logic in the tangled surface of nature. As an undergraduate, it was one of my ambitions to meet and converse with him—to personally experience the presence of one of the greatest scientific mind the 21st century. Then it is predictable how thrilled I was when I joined his lab, and, furthermore, became his graduate student to join his exploration to unravel mysteries of nature itself. I would like to thank Prof. Ramachandran for his mentorship that taught me beyond just facts and theories, but also the romance behind the pursuit for science driven purely by curiosity.

I would like to thank Prof. Christopher Wills, my co-chair, for supporting me with great advices, not only in research but also in life. Prof. Wills has influenced my way to live, as he expresses and integrates his passion for science in his frequent travels around the world.

I would like to thank Prof. Seana Coulson for guiding me through the process of ERP. Her support made it possible for me to utilize the amazing method of ERP in order to develop my thesis. I am also in debt of her insightful advices on the direction and analysis of my thesis.

I would like to thank Prof. Komiyama and Prof. Huberman for being members of my committee.

I would like to express my gratitude toward David Brang who has been my biggest support in guiding me in every step in my master's. David has inspired me to find joy in productivity and efficiency as well as fueling my passion in the field of vision.

Of course, my MS thesis would not have been possible without the help of

outstanding research assistants: Andrew Bryant, Ethan Soutar-Rau, and Kun Chhai Meas. They have shown continuous dedication and excellent work ethics, which have kept me motivated.

I would also like to thank the rest of the members of the Ramachandran Lab for all their guidance and moral support that made my experience in the lab to be exceptionally delightful.

Abstract of the Thesis

Neural Timing and Patterns of Color Vision

By

Hannah Lee

Master of Science in Biology

University of California, San Diego, 2011

Professor Vilayanur S. Ramachandran, Chair

Professor Christopher Wills, Co-Chair

Visual perception helps us navigate through the world full of sensory information. The method by which the neural system organizes and modulates information has been studied but still remains elusive. To investigate how our brain encodes sensory information, we targeted color since it is one of the rudimentary features of vision. Using event-related potential (ERP), we tested healthy participants with normal color vision and instructed them with tasks of viewing isoluminant

colored squares while focusing on a certain color to press a button. Also, another task of viewing colored squares and graphemes was given while participants were focusing on a certain grapheme to focus. Results show that the brain has a distinct pattern for each color in regards to amplitude of potential after 60 ms of onset. Our results give a glimpse of V4 activation time as well as the existence of the brain's mechanism to encode colors. The encoding of color may be orchestrated by the activation of different V4 neurons, the frequencies of V4 neurons, or location of the V4 neurons. Also, our studies introduce a decoding difference between different compartments of the visual cortex; the color effect on potential amplitude and activation timing differs on different activation time windows. Between the external stimulus of light and the perception of color, distinct decoding mechanisms of color seem to occur in different compartments of the brain.

INTRODUCTION

1.1 Physiological Track of Color Vision

Color vision is an essential characteristic of human perception. Evolutionary evidence shows the presence of trichromacy, which occurs only in humans and closely related primates (Jacobs et al 1993); this prevalence of trichromacy and the remnant presence of dichromacy in 8% of males and 0.5% of females (DeebSS 2005) suggest that trichromatic vision has been a rather recent evolutionary adaptation and its benefit could have been the reason for its maintenance.

Color perception, as with other types of visual perception, starts with a photon of wavelength from 400 – 700 nm, the range visible to the naked eye. The photon, depending on its wavelength, reaches the retina of the eye and is picked up by one of the three types of cone, a photoreceptor sensitive for color. The stimulus from the photon is relayed from the cone to the bipolar cells, followed by amacrine cells and ganglion cells. This cascade of neuronal signaling carries on to the optic nerve, which is crossed at the optic chiasm, then continues the transmission towards the contralateral brain. Whether the signal ends at the right or left hemisphere depends on the side—either right or left—of the visual field and not of the eye. The signal is next passed to the lateral geniculate nucleus (LGN), the primary processor of visual information, and then to the visual cortex of the occipital lobe. Once in the visual cortex, the signal reaches the primary visual cortex (V1) first, then the secondary visual cortex (V2), and finally to the fourth visual area (V4)—the color center of the brain.

In addition to the neural mapping of perception, the field of neuroscience has attempted to understand how our neural system processes and categorize visual

information; perception of color derives from relative comparison of stimulated cones. There are three types of cone for humans: L cone, M cone, and S cone. The L cone is sensitive to long-waves around 560nm, M cones sensitive to middle-waves around 530nm, and S cones are sensitive to short-waves around 420nm. Signals from cones are later processed categorically by three paths of red-green, blue-yellow, and luminance opponencies. Each path crosses a different layer of the lateral geniculate nucleus (LGN): M cells of the magnocellular layer is responsible for the neural basis of luminance; S cells of the koniocellular layer is responsible for processing blue-yellow distinction; P cells of the parvocellular layer for red-green opponency.

The physiological pathway of visual processing, from the retina to the visual cortex, has been laid out extensively. However, the main question still remains: how does the brain process these signals to give rise to the unique perception of color? In order to approach this question, we attempted to collect electrophysical responses of the visual cortex in response to color stimuli of different saturations and luminance levels.

1.2 Background of Color Topography and Electroencephalography (EEG)

The visual cortex lies within the occipital lobe and processes visual information. Within the visual cortex, several regions have been compartmentalized, among which is the fourth visual area (V4) responsible for the conscious experience of color. Several studies (REFS) have shown that damage to V4 in humans produces achromatopsia, or a reduction/loss in the ability to consciously perceive hues. As with each visual area, V4 shows retinotopic mapping: stimuli in the upper visual field are represented medially, while stimuli in lower visual field are represented laterally in V4. Furthermore, Zeki (1980) demonstrated the existence of hue topography

(chromatopography) in V4 as well, such that in macaque monkeys, neurons responding to similar hues were proximally mapped. There has been lack of research on the chromatopography in human vision. Therefore, we have used ERP as a noninvasive method to detect topography of hues and their coding pattern.

Electroencephalography (EEG) incorporated with Event Related Potential (ERP) is a powerful tool used to measure the electrophysical signal of the brain by placing electrodes along the scalp. It has an advantage of fine temporal resolution for accurate measurement of brain response for each color stimulus. The activation timing of V4 is still not clear, although speculated to contribute to the P1 component of ERP around 90 – 150 ms of onset (Mangun, 1990; Brang, 2010; Buchner, 1994). Using ERP to accurately measure the timing of both the stimulus onset and the brain's response is critical to view temporal differential responses. Such temporal resolution is not adequately offered in other methods such as MRI of fine localization. ERP does not have a fine structural resolution; however, as the location of color processing—the V4—is already known, its spatial caveat was not crucial for our study.

By ERP, we investigate the possible factors attributing to color vision. In alignment of Zeki's study with macaque monkeys, our visual cortex may have a chromatopography in human V4, thus the location of the firing neurons are responsible for color perception. Another factor may be a specific pattern of firing rate for each color. Szatmary (2010) shows that within a group of neurons, the firing pattern and frequency rates differed for different stimuli. Lastly, but not at the least, neurons in the visual cortex may have been developed to be 'red' or 'blue' cells to process and respond to the corresponding color information.

1.3 Color Attention

As we are bombarded with visual information from our environment, our neural system has adapted to process and select certain information to attend. The stage at which selective visual attention modulates and influences vision has been studied yet is still elusive. The ability of our neural system to have an attentional modulation causes a top-down control in the process of perception.

Event-related potential (ERP) is a good method to identify such stage of modulation due to its advantage in temporal resolution. With ERP, previous studies have found that spatial attention plays a role in neural mechanism shown by increased amplitude for attended stimuli. Mangun et al shows P1 component to have larger amplitude for attended bars of the contralateral visual field. Discrimination tasks with grapheme viewings have also confirmed that the ventral stream of the visual track is affected by attention.

There are debates around whether V4 activation is modulated by chromatic attention. Attention has been known to have no effect on the striate cortex (V1). However, attention could be involved in modulating sensory gain mechanism, change in excitability of sensory neurons involved in early visual perceptual processes, in extrastriate cortex such as V2, V3, V4 (Wijers, 1997). Zhang (2009) suggested that color-based attention can be influential within 100 ms after stimulus onset, and is independent from spatial attention. Andersen (2009) has performed EEG experiments to show that attention causes a sensory gain modulation at early levels of the visual cortex. To control for attention effect, we devised two tasks of different attention modules: one task for color discrimination and another for grapheme discrimination with passive viewing of color. With evidence of amplitude difference in brain response from attention, we expect a difference only in amplitude for attended colors while maintaining the pattern or timing.

METHODS

2.1 Participants

Data were collected from 16 participants, 12 out of 16 of whom were native English speakers. All participants had normal or corrected-to-normal vision with normal color vision, confirmed by the Ishihara color test. 13 out of 16 participants were females. 15 participants were right-handed, which was assessed via Edinburgh Inventory (Oldfield, 1971) and their ages ranged from 18 to 26 (mean age = 21.4 years, SD = 3.29).

Recruitment of participants was executed by the distribution of fliers at the UC San Diego campus and advertisements on the UC San Diego websites. Participants were compensated either by an hourly pay or a fulfillment of course credit. All participants signed an informed consent prior to the experiment. Only one participant reported to have a history of depression and the rest of the participants did not report any past or current neurological or psychiatric disorders.

2.2 General Procedure

All participants were prepared with an electro-cap fit for their head size. Participants were seated in a sound-attenuated room, 54 in. from a 19 in. monitor.

Two main tasks were given: (1) button-pressing for a specific color; (2) button-pressing for a specific letter. Six types of color stimuli were presented (**Fig 1**): colors of red, green and blue in two types of luminance (e.g. light red, dark red). Within each luminance, the colors were controlled to be equiluminant, and within each color, the two shades of a color had the same saturation. Four types of grapheme stimuli were presented: an alphabet O or X on either the right or left side of the screen.

Each stimulus, a square of color (1.86° horizontal x 1.86° vertical degrees of visual angle), was presented one at a time for 200 ms against a gray background in a randomized order with equal probability.

2.3 Stimulus Setup

We used colors with coordinates of CIELAB space, the most complete color space describing colors visible to the human eye. The La*b* values were used to create the colors; the Yxy values, the two-dimensional representation of colors without lightness, are the values to report. Table 1 and 2 represents the color systems used to create and evaluate our stimuli set.

Table 1. La*b* and Yxy values for color stimuli. La*b* values are used to represent the CIE color space. L represents the lightness of color; a* represents the red-green chromaticity (negative value indicate green and positive value indicates red); b* represents the blue-yellow chromaticity (negative value indicates blue and positive value indicates yellow).

	L	a*	b*	Y	x	y
Light Red	96	127	115	19.5	0.607	0.345
Light Blue	35	-73	-120	19.2	0.164	0.114
Light Green	51	-73	127	19.6	0.297	0.593
Dark Red	31	110	127	12.5	0.603	0.317
Dark Blue	25	-100	-92	12.5	0.163	0.11
Dark Green	41	-73	127	12.7	0.297	0.593

The Munsell color system, a color system which values colors according to its hue, brightness, and saturation, was used for color evaluation. The following table is the approximate values for the Munsell chips that we used for each of 6 colors.

Table 2. Munsell values for color stimuli. H value represents hue; v value represents lightness; c value represents chroma (color purity).

	h	V	C		h	V	C
Light Red	7.5R	5	16	Dark Red	7.5R	4	16
Light Blue	7.5PB	5	20	Dark Blue	7.5PB	4	20
Light Green	7.5GY	5	12	Dark Green	7.5GY	4	12

The luminance of each set is calibrated equal, using a PR-650 photometer from PhotoResearch. As separate neuronal populations demonstrate preferential firing patterns for luminance or hue, through matching luminance between the hues, and comparing results at 2 different luminances, we can be confident that results will reflect general principles of hue neurons. Since the caveat of EEG is the spatial recording, equiluminance is important to ensure the firing of visual cortex to be the responsible by V4 instead of V1, which responds to light intensity. Keeping luminance level same will ensure that the V1 contribution to be constant for all colors.

Amplitude of potential may differ for each color stimuli due to the differing topographic location of neurons corresponding to different colors; the closer the red neurons are to the electrode, the higher the amplitude of potential picked up from the electrode. As individual topography may differ, we anticipate seeing at least a consistent amplitude difference within an individual for different colors. The consistency between individuals may be an implication of universal chromatopography within the V4. CIE perceptual space is a three-dimensional color opponency space, in which the axes represent opposing colors of red-green, yellow-blue, and black-white. The purpose of having two different sets of luminance of the same color is to confirm that at least within the same color in CIE perceptual space,

the firing frequency and amplitude is the same. This limitation allows to test for the influence of luminance and to safely generalize the results. The complete set of color stimuli is shown in **Figure 1.**

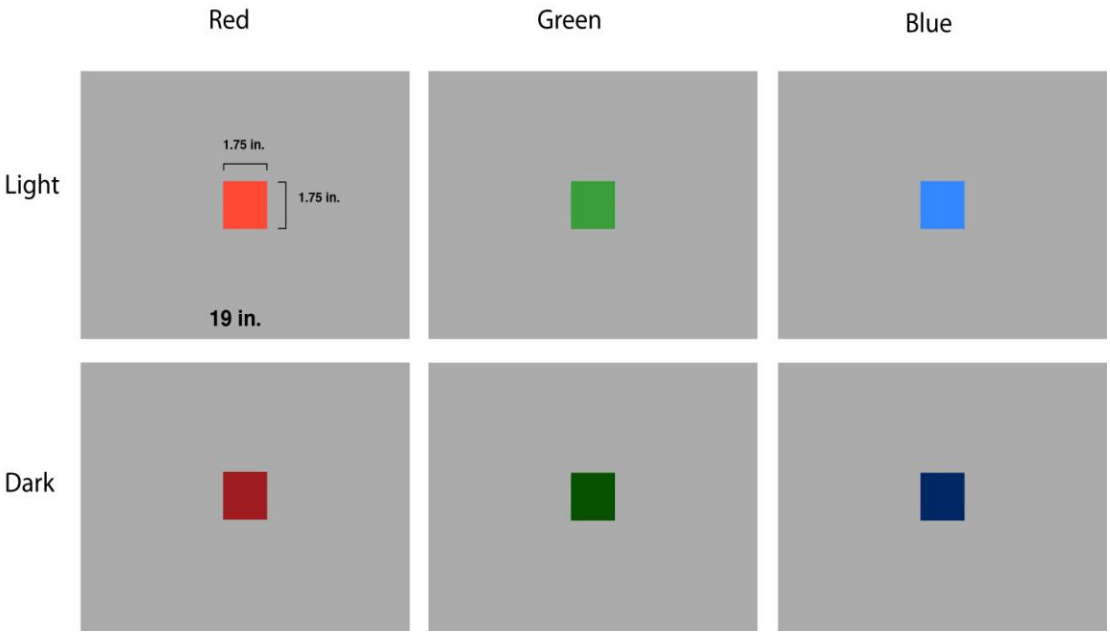

Figure 1: Color stimuli, calibrated on saturation and luminance. Colors were shown in a 1.75 in. x 1.75 in. (1.86 x 1.86 degrees of visual angle) square on a 19 in. monitor. Three colors of red, green, and blue were shown in two different shades of light or dark—total of six stimuli. Within each color, the saturation was same between the two luminance levels, and within each shade, the luminance levels were calibrated.

2.4 Task I: Color Task—attending a color

The first task was divided into 6 blocks, with a total of 1188 stimuli. Each type of stimulus was presented 198 times for 200ms in a random order. Between the blocks, participants were given breaks to stretch, eat, or drink. During each block of stimuli, participants were instructed to press the button for a color—red, green, or blue. A total of 2 blocks were instructed to be dedicated for each color; a third of the stimuli for each color, 66 stimuli, were attended, and two-thirds, 132 stimuli, were unattended. When presented with an unattended color for the block, participants were not to do anything.

To minimize artifacts resulting from eye-blinking and other facial muscle tensions, and to maximize participants' attention, participants were asked to blink after the button press and come back to focus on a fixation cross, which were presented for 200 ms before each stimulus (**Figure 2**).

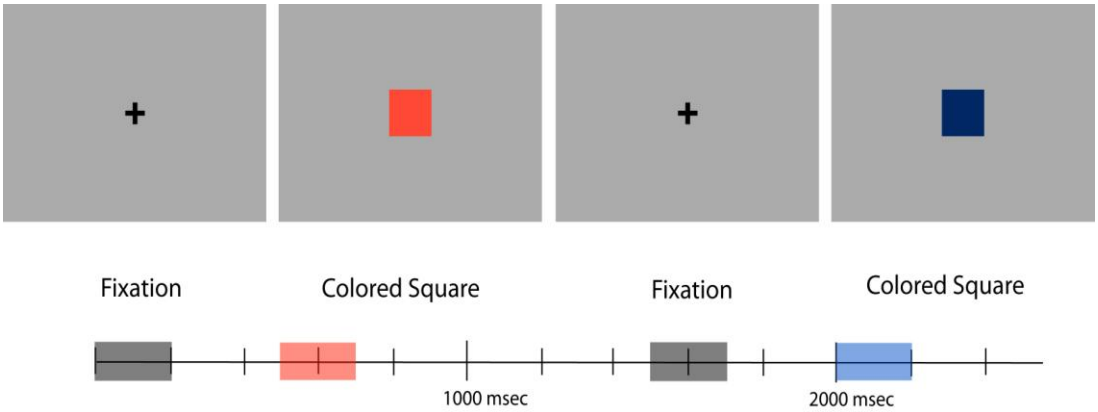

Figure 2: Example trial illustrating the display of sequence for Task I—color task. Each of the 6 stimuli (red, green or blue in two shades) were presented in a randomized order. The entire task was divided into 6 blocks in which participants were given different colors to focus and press a button

2.5 Task II: Grapheme Task—attending an alphabet

The second task had a total of 1296 stimuli; 216 stimuli per type of colored square. Participants were asked to press for an O amidst Os or Xs, which appeared in a randomized order with equal probability. As before, artifacts were attempted to be controlled by instructing participants to blink after the button-press, and to focus at the appearance of the fixation cross. Each trial started with a fixation cross for 200 ms, a colored square for 200 ms, followed by another a grapheme—either an O or X—for 200 ms (**Figure 3)**. Alphabets were presented in two different locations: either on the left or the right of the screen. Task II was divided into 9 blocks, in which stimuli were presented in a randomized order with equal probability.

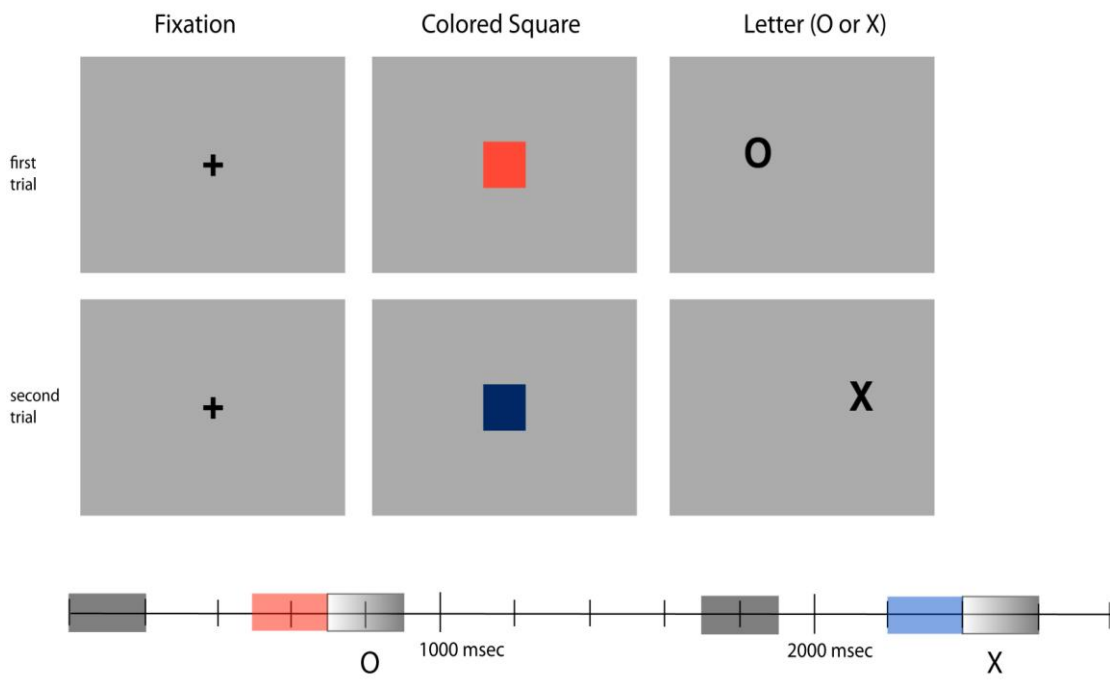

Figure 3: Example trial illustrating the display of sequence for Task II. Each trial had a presentation of color stimulus, followed by either an O or X on the right or left side of the screen. The whole task was divided into 9 blocks in which participants were asked to focus and press a button for either an O or X on any side of the screen.

2.6 Discrimination Study

To assure that each subject is correctly attending to the task, we evaluated their participation by their accuracy in pressing buttons for the instructed stimulus. Throughout the tasks, subjects were asked to press a button whenever they view a certain color or letter. Subjects, on average, scored 81.6 % on correctness, which confirms that subjects were adequately attending given tasks. Correctness of button presses was determined by whether the participant has pressed the correct button between 200 and 1000 ms after the stimulus.

2.7 ERP Study

Participants' EEG were recorded using a commercial electrode cap with 29

scalp sites arranged according to the International 10-20 system (Ebner, Sciarnetta, Epstein, & Nuwer, 1999). A total of five electrodes were placed on different facial areas: two horizontal to each eye to measure eye movements; one below the right eye to catch blinks and vertical eye movements; two on the mastoids, and of the two, the one on the left was used as reference. Electrodes were placed and set with impedances maintained below 5 kΩ. Sampling rate was kept at 250 Hz with SA Instruments 32-channel bioamplifiers. EEG data was recorded with a band pass of 0.01 and 100Hz. All data were stored on a password protected computer hard disk stored in a secured room on UC San Diego campus.

2.8 Analysis of ERPs

ERPs were time locked to the onset of color stimuli, and the time window of -100 to 400ms after onset was viewed for analysis. A time span of -100ms until the onset of stimuli was used as the baseline. Epochs containing artifact were manually rejected prior to the analysis. Rejection criteria were individualized yet the rejection values were uniformly applied within the individual. The average rejection threshold was 225 μV for blinks, 550 μV for eye movements, or 430 μV for amplifier drifts. Three main time windows were analyzed: 60 - 90 ms post onset to analyze C1, an index of V1 response; 90 - 150 ms post onset to P1 component that assumes major V4 attribution; 200-400 ms post-onset to analyze P300, an attention response. C1 component of ERP is considered to represent V1 response, which activates around 45 – 60 ms and peaks between 70 – 100 ms (Foxe 2008). **Figure** 4 illustrates expected C1 and P1 components of ERP (Proverbio, A.M. 2010)

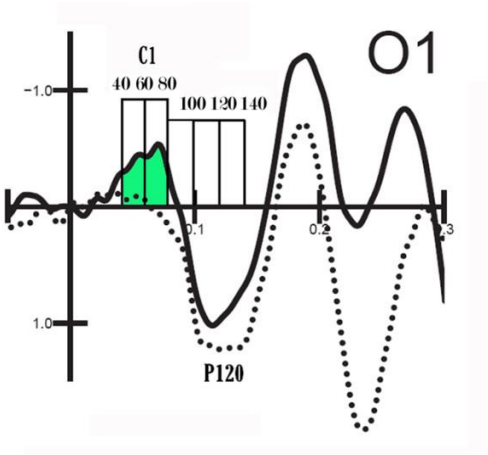

Figure 4: Sample ERP of C1 and P1 components.

Unless noted otherwise, mean amplitude measurements of each participant were used for analysis. Statistical analysis involved ANOVA with factors of attention (attended/unattended), grapheme (color/ alphabet), luminance (light/dark), and color (red/green/blue). Analyzed electrodes were those located by the occipital lobe: O1, Oz, and O2. Statistical analysis used p-values subjected to Greenhouse-Geisser correction (Greenhouse & Geisser, 1959).

RESULTS

3.1 Color Response

With the speculation of neural pattern contributed from V4 occurring around 90 - 150 ms for colors, we tested to see whether this pattern is valid despite differing levels of luminance. Each color was shown in two levels of luminance—light and dark. Comparison between the luminance was performed to ensure that the ERP pattern from previous was not due to influences of luminance levels, which may occur from former V1 activation.

In Task I, participants were instructed to attend a specific color without luminance discrimination and press a button at its sight. Within this module, ERPs were measured from -100 to 400 ms after the onset of color. Mean amplitude was measured to view and analyze the resulting power from potentials. Peak amplitudes were also analyzed to analyze the peak potential amplitude of either polar—positive or negative—ends. **Fig 5** and **Fig 6** is the grand-average ERP for 16 subjects' responses to the attended colors in all 32 electrode channels. (Note that the top of the Y-axis is negative and bottom is positive).

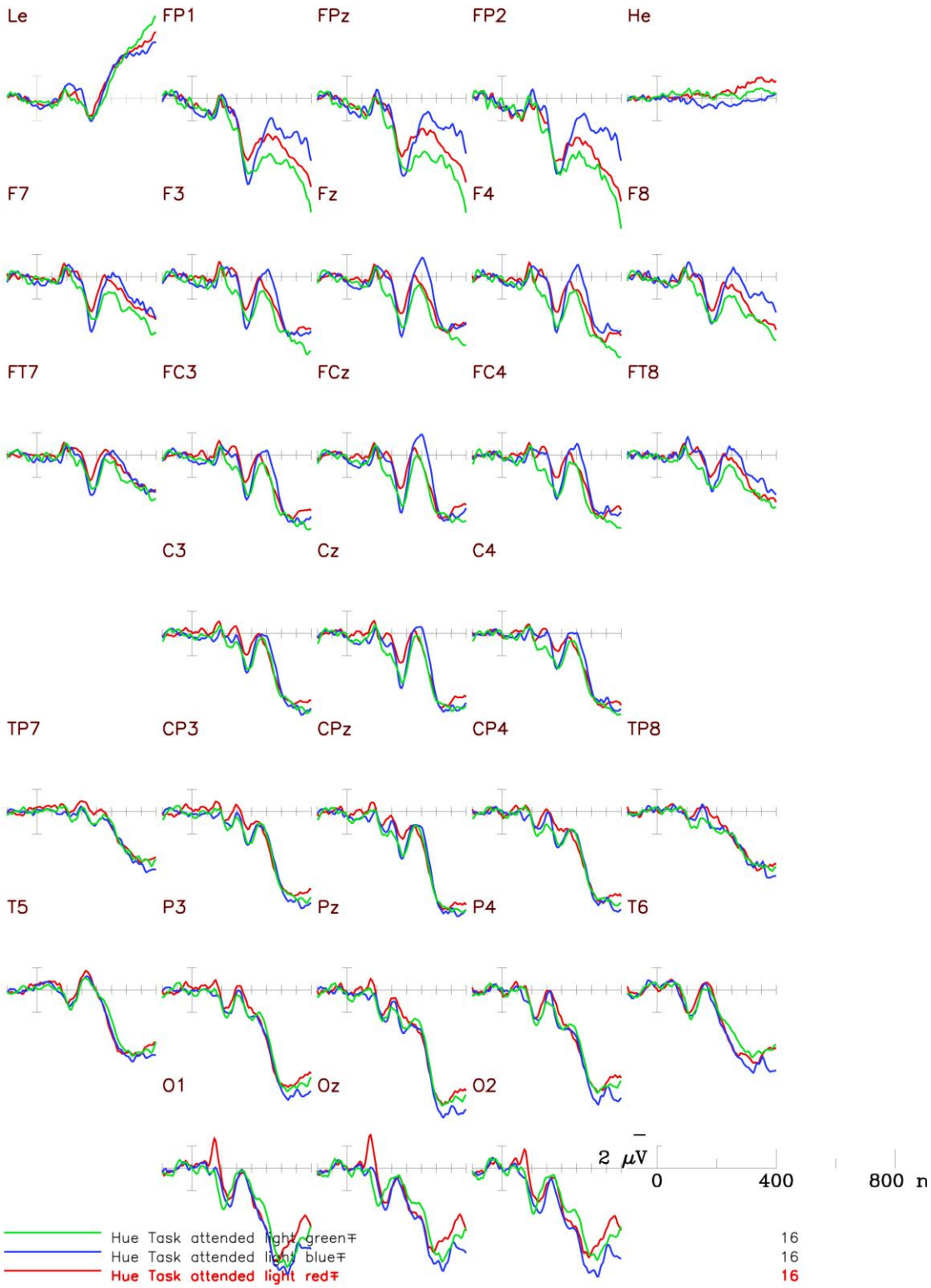

Figure 5: Grand-average ERP (N =16) of all 32 channels for attended light colors during Task I—color task.

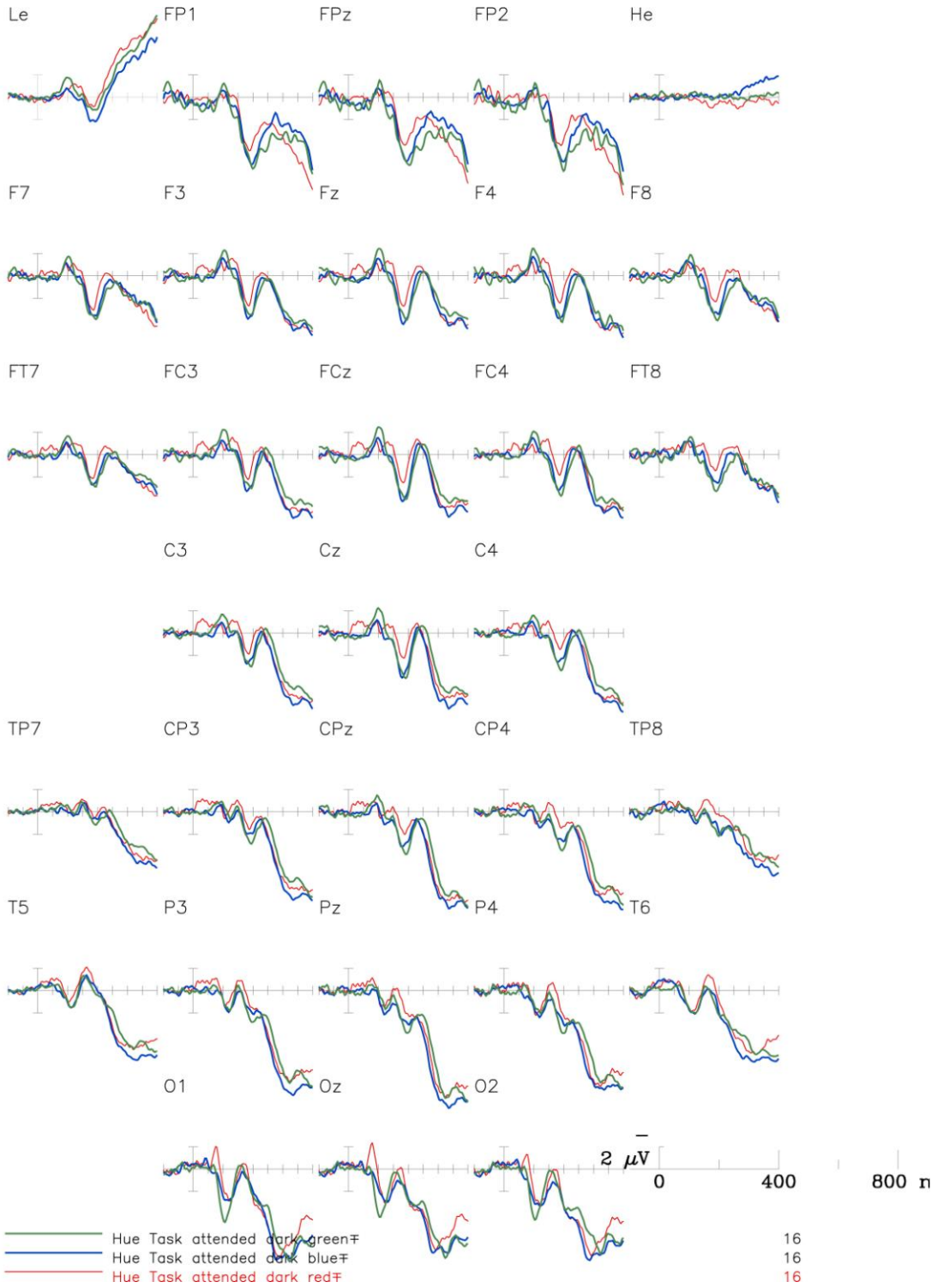

Figure 6: Grand-average ERP (N =16) of all 32 channels for attended dark colors during Task I—color task.

As it is already known that the occipital lobe processes visual information including color, we narrowed down to analyze only the occipital channels—O1, Oz, and O2. For luminance effects, we compared ERP from difference levels of luminance for each color. **Figure 7** is the resulting grand-average ERP for 16 subjects at the occipital electrodes during the events of colored squares at different luminance levels. ERP results for 60 – 90 ms and 90 – 150 ms are confirmed by a statistical test shown in the ANOVA table of **Table 3** and **Table 4,** respectively**.**

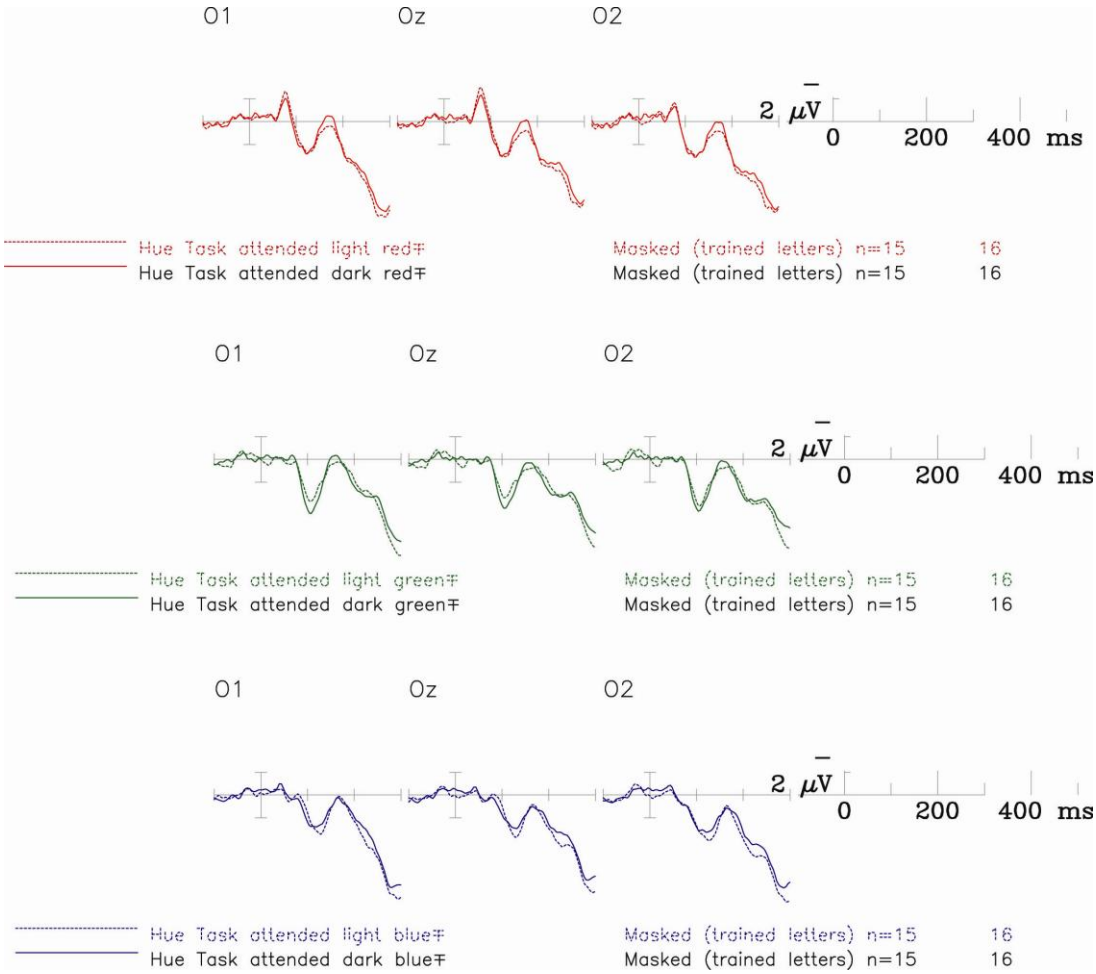

Figure 7: Grand-average ERP (N = 16) of occipital channels for attended colors during Task I—color task—comparing luminance. Solid lines represent the darker luminance of a color; dotted lines represent the lighter luminance of a color.

Table 3: ANOVA of mean amplitude (N = 16) during 60 – 90 ms (C1) for Task I with factors of attention, luminance, color, and electrodes. Asterisked numbers indicate that the result is statistically significant and different.

Source	SS	DF	MS	F	P	pGG	pHF
MEAN	38.95	1	38.95	0.31	0.5841		
S	1866.63	15	124.44				
AAttention	15.99	1	15.99	3.09	0.0990	0.0990	0.0990
AS	77.57	15	5.17				
BLuminance	13.81	1	13.81	5.31	0.0360*	0.0360*	0.0360*
BS	39.03	15	2.60				
AB	4.04	1	4.04	1.59	0.2264	0.2264	0.2264
ABS	28.06	15	2.54				
CColor	353.39	2	176.70	34.55	0.0000*	0.0000*	0.0000*
CS	153.41	30	5.11				
AC	10.10	2	5.05	1.34	0.2765	0.2770	0.2765
ACS	112.84	30	3.76				
BC	2.55	2	1.27	0.34	0.7164	0.7165	0.7164
BCS	113.35	30	3.78				
ABC	0.19	2	0.10	0.05#	0.9558	0.9558	0.9558
ABCS	62.59	30	2.10				
D	30.23	2	15.12	3.88	0.0316*	0.0635	0.0627
DS	116.75	30	0.15				
AD	0.06	2	0.23	0.19	0.8272	0.6676	0.6673
ADS	4.46	30	0.15				
BD	0.46	2	0.23	1.02	0.3715	0.3251	0.3251
BDS	6.69	30	0.22				
ABD	0.02	2	0.01	0.13	0.8749	0.7186	0.7184
ABDS	1.98	30	0.07				
CD	10.20	4	2.55	5.32	0.0010*	0.0118*	0.0112*
CDS	28.75	60	0.48				
ACD	0.88	4	0.22	2.87	0.0303*	0.0692	0.0466*
ACDS	4.62	60	0.08				
BCD	0.53	4	0.13	0.9323	0.9323	0.5799	0.5796
BCDS							
ABCD	0.09	4	0.02	0.21	0.9323	0.8122	0.8894
ABCDS	6.32	60	0.11				

Table 4: ANOVA of mean amplitude (N = 16) during 90 – 150 ms (P1) for Task I with factors of attention, luminance, color, and electrodes. Asterisked numbers indicate that the result is statistically significant and different.

Source	SS	DF	MS	F	P	pGG	pHF
Mean	2698.80	1	2698.80	7.96	0.0129*		
S	5088.66	15	339.24				
AAttention	12.94	1	12.94	3.40	0.0850	0.0850	0.0850
AS	57.06	15	3.80				
BLuminance	21.95	1	21.95	5.31	0.0359*	0.0359*	0.0359*
BS	61.98	15	4.13				
AB	4.99	1	4.99	3.23	0.0924	0.0924	0.0924
ABS	23.16	15	1.54				
CColor	33.19	2	16.59	5.67	0.0082*	0.0088*	0.0082*
CS	87.80	30	2.93				
AC	13.52	2	6.67	1.43	0.2556	0.2562	0.2556
ACS	142.03	30	4.73				
BC	3.85	2	1.93	0.98	.3878	.3900	0.3886
BCS	59.06	30	1.97				
ABC	3.97	2	1.99	0.96	0.3953	0.3961	0.3935
ABCS	62.28	30	8.29				
D	26.70	2	13.35	1.61	0.2165	2.183	0.2215
DS	248.59	30	8.29				
AD	0.23	2	0.11	1.66	0.2066	0.2127	0.2119
ADS	2.05	30	0.07				
BD	1.02	2	0.51	4.22	0.0242*	0.0547	0.0539
BDS	3.63	30	0.12				
ABD	0.14	2	0.07	1.29	0.2904	0.2720	0.2720
ABDS	1.61	30	0.05				
CD	5.84	4	1.46	7.96	0.0000*	0.0003*	0.0002*
CDS	11.00	60	0.18				
ACD	0.05	4	0.01	0.13#	0.9699	0.9402	0.9403
ACDS	6.08	60	0.10				
BCD	0.34	4	0.09	1.22	0.3111	0.3070	0.3137
BCDS	4.23	60	0.07				
ABCD	0.00	4	0.00	0.01#	0.9998	0.9987	0.9987
ABCDS	4.53	60	0.08				

Results show that luminance has an effect starting after the 60 – 90 ms of stimulus with amplitude difference ($F(1, 15) = 5.31$, $p = 0.036$), which is an expected

difference in response from C1 component as V1 is responsible for detecting luminance gradients; different shades were expected to give different V1 responses. Amplitudes of potentials for the interaction of color and luminance are not statistically different after 60 ms ($F(2,30) = 0.34$, $p = 0.7165$) indicating a consistent and independent pattern of response for each color ($F(2, 30 = 34.55$, $p < 0.0000$) regardless of luminance. Statistics regarding color factor was expected as well because V1 is also considered to have initial color processing, which is also confirmed by the differential ERP response to color.

For 90 – 150 ms response of P1 component expected from V4 influence, the three colors gave statistically significant different responses of p-value = 0.0088 ($F(2, 30) = 5.67$). Also, the two different luminance levels gave statistically significantly different responses of p-value < 0.0359 ($F(1, 15) = 5.31$). However, the interaction of both luminance and color results in a statistically similar response of p-value = 0.39 ($F(2,30) = 0.98$); therefore, the electrophysiological response of a dark red is statistically similar to that of a light red. As expected, the electrodes do not have difference in ERP responses ($F(2, 30) = 1.61$, $p = 0.2165$). However, for each color there seems to be a statistically significant ERP response difference in electrodes ($F (4, 60) = 7.96$, p-value < 0.0000); confirming a possibility for chromatopography within the V4 to be a main factor of color perception. To investigate further, we plan future studies with electro-caps consisting of more electrodes concentrated around the occipital lobe. Again, the interaction with luminance and color do not seem to present ($F (2, 30) = 0.98$, $p = 0.39$), suggesting that the V4 responses for colors obtained are not significantly affected by the luminance gradient, but rather responding to the perceptual space of color.

P300 component of ERP is known as the objective evaluation of

cerebral activity during discrimination of stimulus discrimination, in which around 200 ms after stimulus onset, the attended stimulus showed a positive amplitude while the unattended stimulus shows a negative amplitude. Ito et al., 2006, shows that around 200-400ms, subjects have shown significantly different response depending on whether they were focusing on the stimuli. The attended colors produce a more positive amplitude than unattended.

To verify that our ERP results were generally considered valid and reproducible, we also measured the attention component of the task. Our result also shows a statistically significant difference regarding attention component. In Task I, the P300 response for attended colors and unattended colors had a statistically significant difference with p-value < 0.0001 ($F(1, 15) = 30.77$). **Table 5** is the ANOVA for P300 response comparing the different attention conditions within Task I—between the attended and unattended colors. Grang-average ERP responses of both conditions are also shown in **Figure 7.** Figure 7 illustrates the more positive response for attended conditions (Note that the top of the Y-axis is negative and bottom is positive).

Table 5: ANOVA of mean amplitude (N = 16) during 200 – 400 ms (P300) for Task I with factors of attention, luminance, color, and electrodes.

```
Title Color meana 200 - 400 Color Frequency Study
Factors 5 2 2 3 3 16
Sample Size 1
Model Mixed (AxBxCxDxS)
Names AAttention BLuminance CColor DElectrodes SSubjects
Options Means A B
Options Epsilon
C A: Attention (attended/ unattended)
C B: Luminance (light/dark)
C C: Color (red/green/blue)
C S: Subjects
C
C D: Electrodes: Only Os
```

DESIGN SUMMARY

Factor A	2 Levels	Within Subjects
Factor B	2 Levels	Within Subjects
Factor C	3 Levels	Within Subjects
Factor D	3 Levels	Within Subjects

N = 16

TABLE OF MEANS

A	B	C	D	S	MEAN	SD	SEM	N
1	1	0	0	0	6.0937	4.2010	0.3501	144
1	2	0	0	0	5.6787	3.8309	0.3192	144
2	1	0	0	0	2.4772	2.2320	0.1860	144
2	2	0	0	0	2.6993	2.4526	0.2044	144
0	1	0	0	0	4.2854	3.8154	0.2248	288
0	2	0	0	0	4.1890	3.5407	0.2086	288
1	0	0	0	0	5.8862	4.0186	0.2368	288
2	0	0	0	0	2.5882	2.3434	0.1381	288
0	0	0	0	0	4.2372	3.6777	0.1532	576

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	10341.53	1	10341.53	33.96	0.0000*		
S	4567.45	15	304.50				
AAttention	1566.25	1	1566.25	30.77	0.0001*	0.0001*	0.0001*
AS	763.49	15	50.90				
BLuminance	1.34	1	1.34	0.21	0.6517	0.6517	0.6517
BS	94.60	15	6.31				
AB	14.61	1	14.61	5.57	0.0323*	0.0323*	0.0323*
ABS	39.37	15	2.62				
CColor	40.54	2	20.27	3.56	0.0409*	0.0413*	0.0409*
CS	170.61	30	5.69				

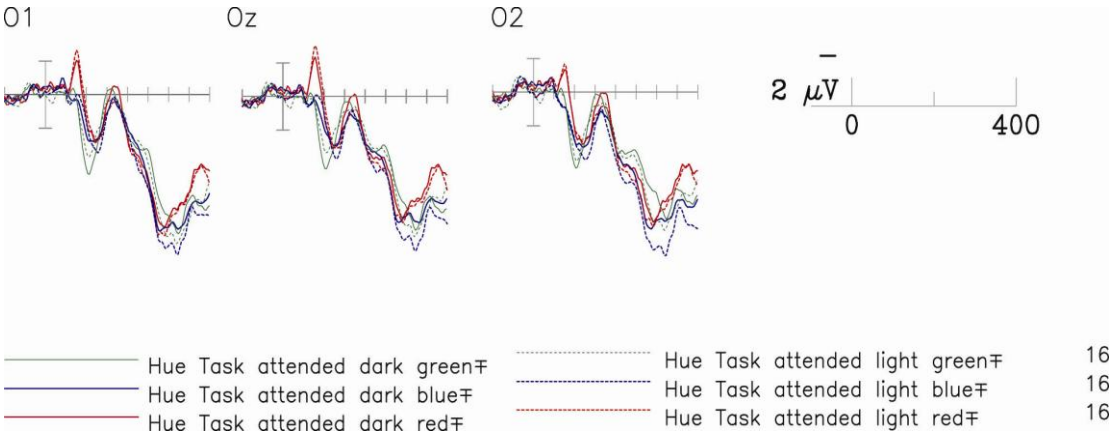

Figure 8: Compiled Grand-average ERP (N = 16) of occipital channels for attended colors of different luminance level during Task I. Each mark on the x-axis represents 50 ms after the stimuli onset. Each colored line represents the stimuli color. The solid lines are the dark luminance; the dotted lines represent the light luminance. Each color shows a distinct pattern despite the luminance difference.

Figure 8 shows the electrophysical power difference of C1 response for each color during Task I of color discrimination. Red, either light or dark, shows the strongest power with the most negative amplitude around 60-90ms. The next strongest negative amplitude comes from blue—light and dark—, with the weakest coming from both luminances of green. As the amplitudes of potential for blue and green seem similar by eye, we compared the two colors in ANOVA (**Table 6** and **Table 7**).

ANOVA for both time windows of C1 and P1

Table 6: ANOVA of mean amplitude (N = 16) during 60 – 90 ms (C1) for Task I with factors of attention, luminance, color, and electrodes

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	24.22	1	24.22	0.34	0.5696		
S	1074.76	15	71.65				
AAttention	22.36	1	22.36	5.39	0.0347*	0.0347*	0.0347*
AS	62.23	15	4.15				
BLuminance	7.82	1	7.82	3.73	0.0726	0.0726	0.0726
BS	31.45	15	2.10				
AB	1.65	1	1.65	0.73	0.4061	0.4061	0.4061
ABS	33.87	15	2.26				
CColor	10.59	1	10.59	2.85	0.1121	0.1121	0.1121
CS	55.76	15	3.72				

Continued...

AC	13.92	1	13.92	5.18	0.0379*	0.0379*	0.0379*
ACS	40.29	15	2.69				
BC	0.08	1	0.08	0.03	0.8715	0.8715	0.8715
BCS	44.74	15	2.98				
ABC	0.20	1	0.20	0.07	0.7951	0.7951	0.7951
ABCS	42.60	15	2.84				
D	9.01	2	4.50	2.63	0.0885	0.1204	0.1197
DS	51.34	30	1.71				
AD	0.00	2	0.00	0.00#	0.9975	0.9603	0.9603
ADS	4.21	30	0.14				
BD	0.07	2	0.03	0.24	0.7861	0.6286	0.6286
BDS	4.25	30	0.14				
ABD	0.18	2	0.09	0.74	0.4855	0.4016	0.4016
ABDS	3.67	30	0.12				
CD	3.38	2	1.69	6.22	0.0055*	0.0239*	0.0232*
CDS	8.15	30	0.27				
ACD	0.71	2	0.36	6.66	0.0040*	0.0052*	0.0046*
ACDS	1.60	30	0.05				
BCD	0.32	2	0.16	1.48	0.2447	0.2393	0.2385
BCDS	3.20	30	0.11				
ABCD	0.02	2	0.01	0.14	0.8740	0.8742	0.8741
ABCDS	2.21	30	0.07				

Table 7: ANOVA of mean amplitude (N = 16) during 90 – 150 ms (P1) for Task I with factors of attention, luminance, color, and electrodes.

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	2073.34	1	2073.34	9.46	0.0077*		
S	3287.53	15	219.17				
AAttention	24.51	1	24.51	5.17	0.0381*	0.0381*	0.0381*
AS	71.11	15	4.74				
BLuminance	21.36	1	21.36	5.80	0.0293*	0.0293*	0.0293*
BS	55.20	15	3.68				
AB	4.59	1	4.59	2.51	0.1342	0.1342	0.1342
ABS	27.46	15	1.83				
CColor	4.04	1	4.04	2.00	0.1777	0.1777	0.1777
CS	30.31	15	2.02				

Continued...

AC	1.35	1	1.35	0.28	0.6053	0.6053	0.6053
ACS	72.49	15	4.83				
BC	1.95	1	1.95	0.69	0.4191	0.4191	0.4191
BCS	42.35	15	2.82				
ABC	3.67	1	3.67	1.70	0.2123	0.2123	0.2123
ABCS	32.44	15	2.16				
D	15.28	2	7.64	1.46	0.2485	0.2405	0.2399
DS	157.05	30	5.23				
AD	0.13	2	0.07	1.15	0.3310	0.2975	0.2962
ADS	1.76	30	0.06				
BD	1.28	2	0.64	6.06	0.0062*	0.0249*	0.0249*
BDS	3.17	30	0.11				
ABD	0.11	2	0.05	0.84	0.4409	0.3704	0.3693
ABDS	1.89	30	0.06				
CD	5.53	2	2.76	14.79	0.0000*	0.0009*	0.0009*
CDS	5.60	30	0.19				
ACD	0.04	2	0.02	0.19	0.8306	0.6701	0.6699
ACDS	3.33	30	0.11				
BCD	0.04	2	0.02	0.26	0.7706	0.6144	0.6141
BCDS	2.44	30	0.08				
ABCD	0.00	2	0.00	0.01#	0.9944	0.9407	0.9944
ABCDS	1.94	30	0.06				

Table 6 and **7** show that for both time windows of C1 and P1, green and blue do not have difference in potential amplitude; analysis of C1 results in a p-value of 0.1121 (F (1,15) = 2.85) and analysis of P1 results in a p-value of 0.1777 (F (1,15) = 2.00). However, there are statistically significant difference in mean amplitude in the interaction between color and electrodes for both C1 (F (2, 30) = 6.22, p = 0.0239) and P1 (F (2, 30) = 14.79, p < 0.0000). Such statistics support the idea that color may be processed by topography—the existence of a chromatopography. **Figure 9** further illustrates the possibility of chromatopography with difference in ERP responses for color regarding electrodes.

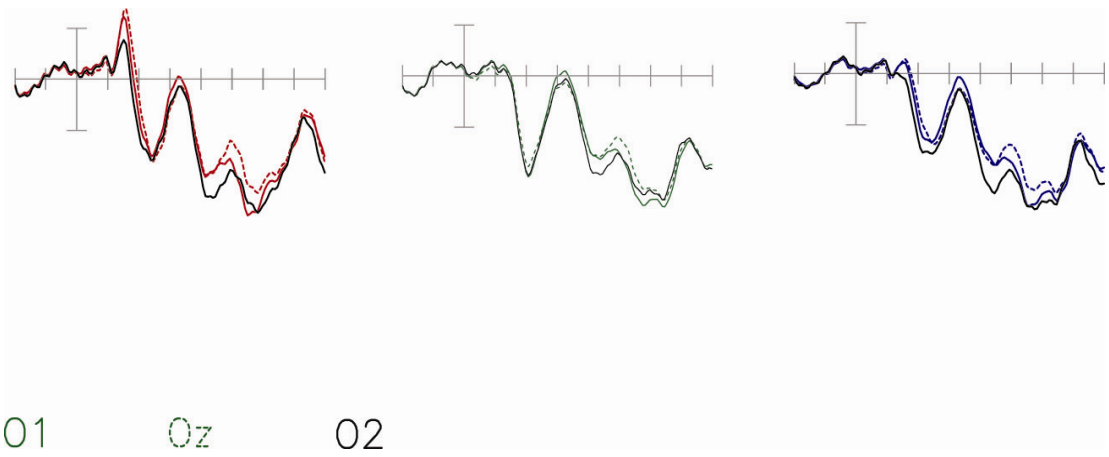

Figure 9: Figure 9: Grand average of ERP (N = 16) of occipital channels for each color, comparing responses from different electrodes. Solid colored line represents ERP response from O1 for that color; dotted line represents ERP response from Oz; black line represents ERP response from O2.

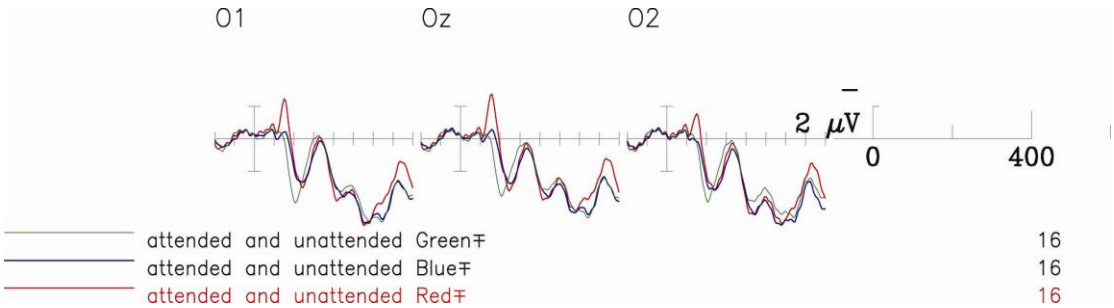

Figure 10: Grand-average ERP (N = 16) of occipital channels for color, averaged across difference luminance and tasks within Task I.

Figure 10 is the grand-average ERP for color, averaged across difference luminance and tasks within Task 1 of color discrimination. ERP responses for colors appear to have differential latencies Peak amplitude latency was analyzed in ANOVA. Both luminance (F (1, 15) = 7.65, p = 0.0144) and color (F (2, 30) = 14.94, p = 0.0010) seem to have different processing time in P1 (**Table 9**). As expected, electrodes did not have different latencies (F (2, 30) = 1.29, p = 0.2698), confirming that neurons around those electrodes do not differ in electrophysiological responses. However, a lack of interaction of both factors (F (2, 30) = 0.25, p = 0.787) even regarding latency is consistent with our previous finding of amplitude potentials. **Table 8** ANOVA of peak amplitude latency at C1 response time implied luminance did not have differential processing time (F (1, 15) = 2.62, p = 0.1266). However, color processing had differential response latencies (F (2, 30) = 14.66, p = 0.0011).

Table 8: ANOVA of peak latency (N = 16) during 60 – 90 ms (C1) of unattended colors of Task I with factors of luminance and color.

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	1579456.75	1	1579456.75	2558.58	-0.0000*		
S	9259.75	15	617.32				
ALuminancer	162.38	1	162.38	2.62	0.1266	0.1266	0.1266
AS	930.88	15	62.06				
BColor	3080.38	2	1540.19	14.66	0.0000*	0.0011*	0.0011*
BS	3152.38	30	105.08				
AB	255.75	2	127.88	2.90	0.0706	0.0737	0.0717
ABS	1323.25	30	44.11				
CElectrodes	421.62	2	210.81	3.70	0.0367*	0.0696	0.0696
CS	1709.75	30	56.99				

Continued...

AC	12.00	2	6.00	0.28	0.7583	0.6027	0.7589
ACS	644.62	30	21.49				
BC	93.25	4	23.31	1.16	0.3393	0.3382	0.3359
BCS	1210.12	60	20.17				
ABC	3.88	4	0.97	0.05#	0.9952	0.9513	0.9850
ABCS	1163.25	60	19.39				

Table 9: ANOVA of peak latency (N = 16) during 90 – 150 ms (P1) of unattended colors of Task I with factors of luminance and color.

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	4112712.00	1	4112712.00	1691.95	-0.0000*		
S	36461.25	15	2430.75				
ALuminancer	1120.25	1	1120.25	7.65	0.0144*	0.0144*	0.0144*
AS	2196.50	15	146.43				
BColor	11796.50	2	5898.25	14.94	0.0000*	0.0010*	0.0010*
BS	11845.75	30	394.86				
AB	98.75	2	49.38	0.24	0.7867	0.7870	0.7868
ABS	6126.00	30	204.20				
CElectrodes	817.50	2	408.75	1.29	0.2896	0.2698	0.2691
CS	9492.25	30	316.41				

Continued...

^LPage 2 Color peak latency 90 - 150 ms unattended Color Frequency Study

AC	214.75	2	107.38	1.02	0.3744	0.3773	0.3762
ACS	3172.50	30	105.75				
BC	178.00	4	44.50	0.40	0.8095	0.7552	0.8095
BCS	6712.75	60	111.88				
ABC	128.25	4	32.06	0.27	0.8964	0.8469	0.8963
ABCS	7135.00	60	118.92				

We noted that the amplitude patterns around C1 and P1 time windows differed for each color; ANOVA regarding time and color was analyzed to see if there was an interaction between the two factors. **Table 10** is the ANOVA with factors of time window (C1 and P1) against colors (unattended colors in Task I). As expected, electrodes did not have statistical difference in each, showing consistent responses regarding stimuli despite time window ($F(2, 30) = 0.04$, $p = 0.8351$). P-value of 0.0011 ($F(2, 30) = 8.85$) confirmed an interaction that occurs for the different time windows regarding colors; there seem to be different patterns of processing for colors

on each compartment of the visual cortex.

Table 10: ANOVA of mean amplitude (N = 16) of unattended colors of Task I with factors of time window (C1 and P1) and colors.

ANALYSIS OF VARIANCE TABLE

SOURCE	SS	DF	MS	F	p	pGG	pHF
MEAN	173.41	1	173.41	1.73	0.2079		
S	1501.72	15	100.11				
ATime	442.98	1	442.98	17.99	0.0007*	0.0007*	0.0007*
AS	369.32	15	24.62				
BColor	54.25	2	27.13	15.49	0.0000*	0.0000*	0.0000*
BS	52.53	30	1.75				
AB	26.82	2	13.41	8.85	0.0010*	0.0011*	0.0010*
ABS	45.48	30	1.52				
CElectrodes	13.71	2	6.86	3.49	0.0435*	0.0766	0.0753
CS	59.02	30	1.97				

Continued...

^LPage 2 Color meana time x hue (unattended color of task I) Color Frequency Study

AC	0.07	2	0.04	0.04#	0.9566	0.8351	0.8350
ACS	24.56	30	0.82				
BC	2.84	4	0.71	5.66	0.0006*	0.0089*	0.0082*
BCS	7.55	60	0.13				
ABC	0.91	4	0.23	5.28	0.0010*	0.0102*	0.0037*
ABCS	2.57	60	0.04				

3.2 Attention

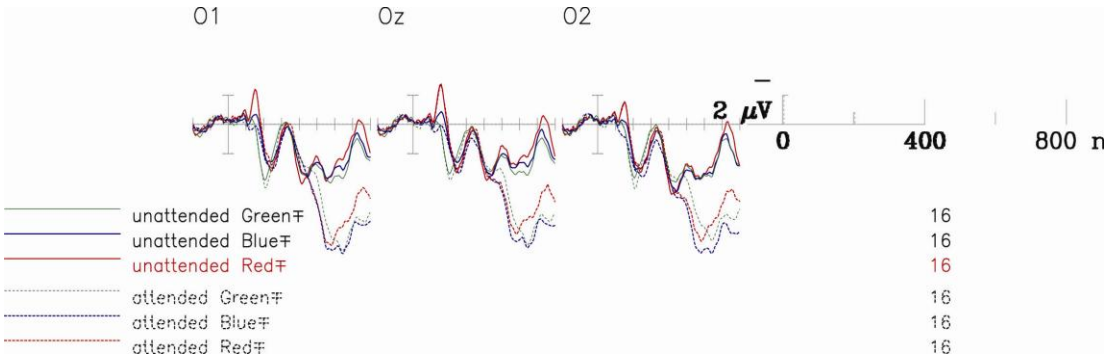

Figure 11: Grand-average ERP (N= 16) of occipital channels for color, averaged across luminance, in different attention conditions of Task I. Solid colored lines represent ERP responses of unattended colors; dotted lines represent ERP responses of attended colors.

To view the effect of attention, we compared trials for responses to colors of attention to responses to colors of inattention. **Figure 11** is the grand-average ERP response from -100 to 400 ms after the stimulus comparing color responses, averaged across luminance, in different attention conditions of Task I. With the addition of statistical comparison from **Table 3** and **Table 4** from previous, we can see that the different attention conditions did not show any interactions with factors of color nor luminance. The negative peaks around 60 – 90 ms for each type of stimulus are similar, implying non-existence of differential response of V1 to attention; while independently each factor shows a main effect, interaction with attention gives p-value of 0.2264 (F (1,15) = 1.59) for luminance and p-value of 0.2765 (F (2, 30) = 34.55) for color. The negative peaks around 90 - 150 ms for each type of stimulus also shows a similar dilemma of no difference in P1 responses for different attention conditions; while independently each factor shows a main effect, interaction with attention gives p-value of 0.0924 (F (1,15) = 3.23) for luminance and p-value of 0.2562 (F (2, 30) = 1.43) for color. **Tables 3** and **4** show ANOVA for statistical

analysis during 60 – 90 ms and 90 - 150 ms, respectively.

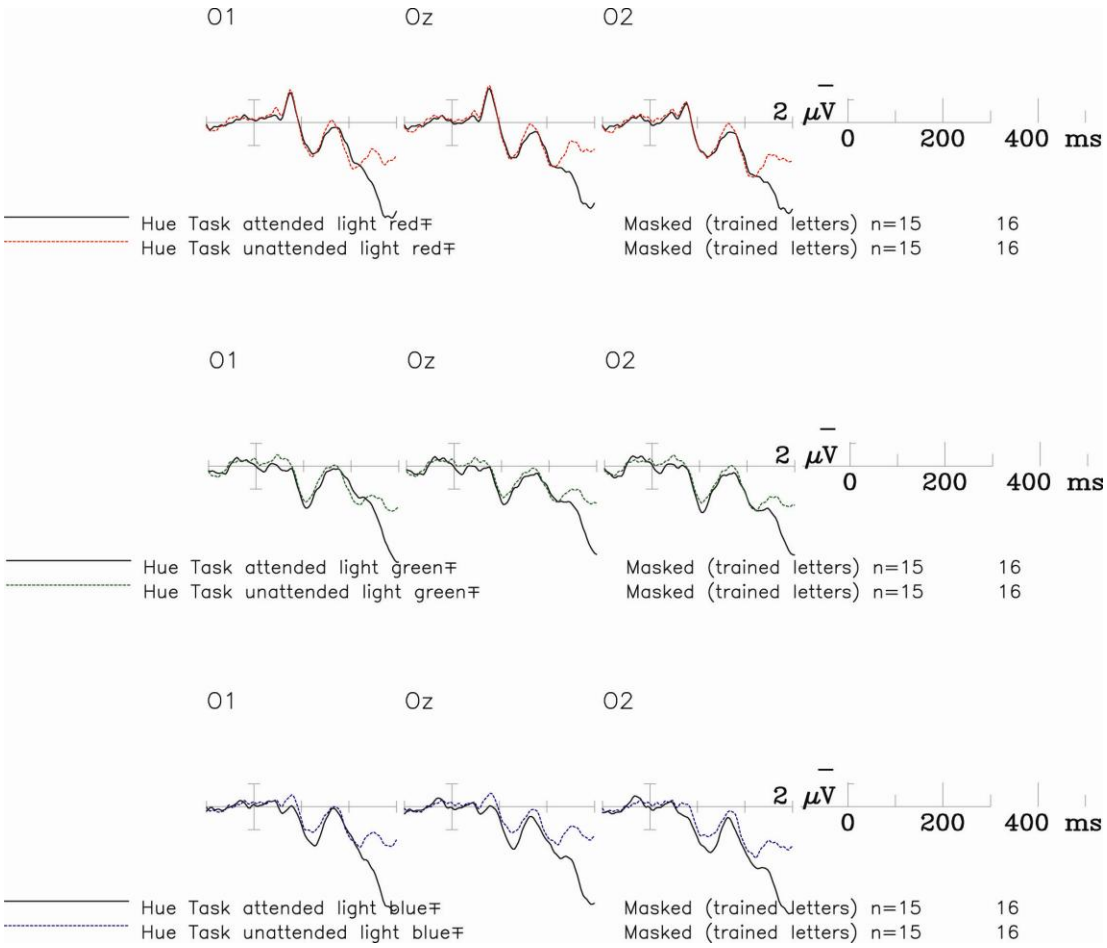

Figure 12: Grand-average ERP (N = 16) of occipital channels at the presentation of colors for different attention conditions during Task I. Solid lines represent the attended color; dotted lines represent the unattended color. There is an absence of statistically significant difference regarding the factor of attention; the ERPs for each color and shade have a consistent response despite the attention conditions. The attended colors produce a more negative peak than unattended.

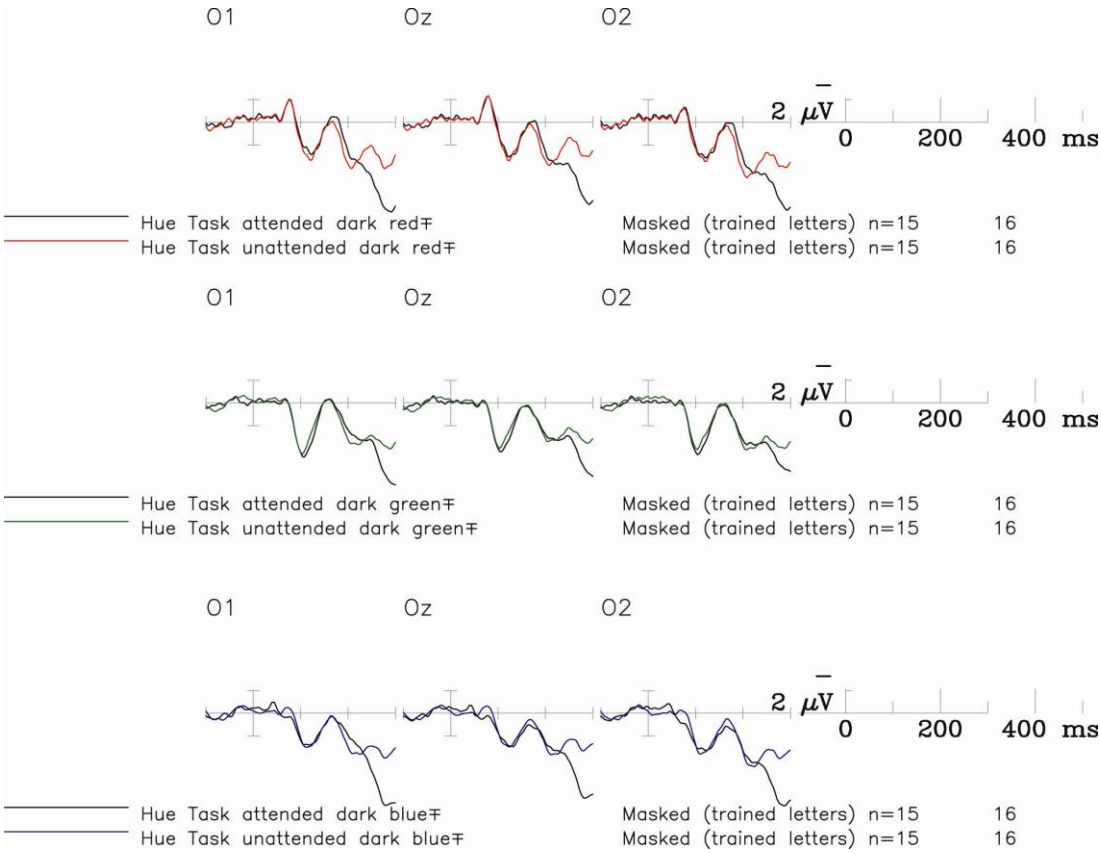

Figure 12: Grand-average ERP (N = 16) of occipital channels at the presentation of colors for different attention conditions during Task I, Continued

Within the same task to attend color, we have compared whether there the factor of attention has caused an effect on processing of color. **Figure 12** represents the ERP comparison of attended versus unattended for each colors of different luminance. Results in Task I show reliably consistent ERPs for each color and shade that is not affected by the different attention conditions. The ERP results were further confirmed by ANOVA analysis of ERPs at time windows.

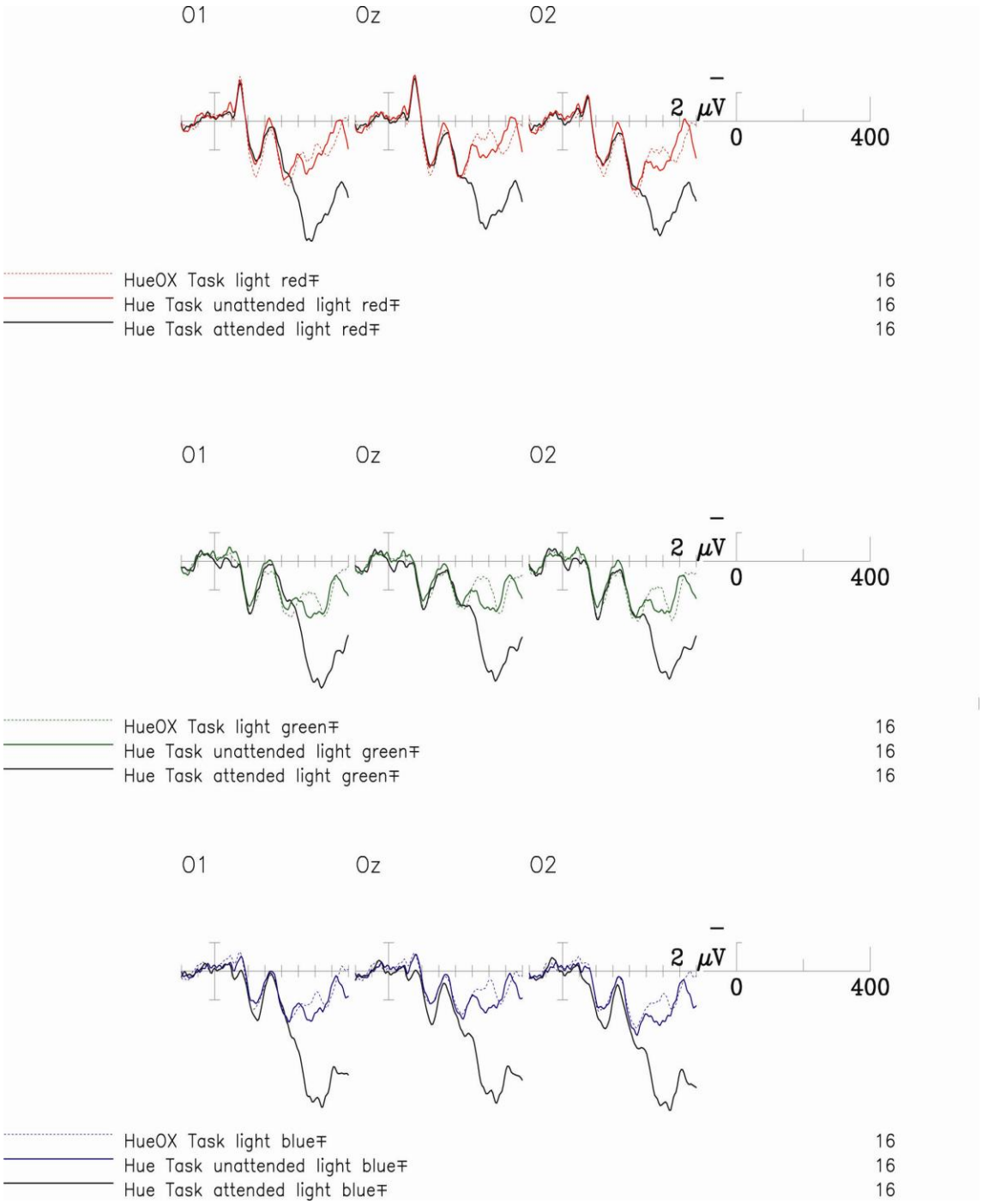

Figure 13: Grand-average ERP (N = 16) of occipital channels for different grapheme and attention conditions of light and dark colors in Task I and Task II. Dotted line represents the response for color (unattended) during a grapheme discrimination task. Solid colored lines represent the ERP during the presentation of a non-focused (unattended) color during a color task. Black represents the ERP for a focused (attended) color during a color task.

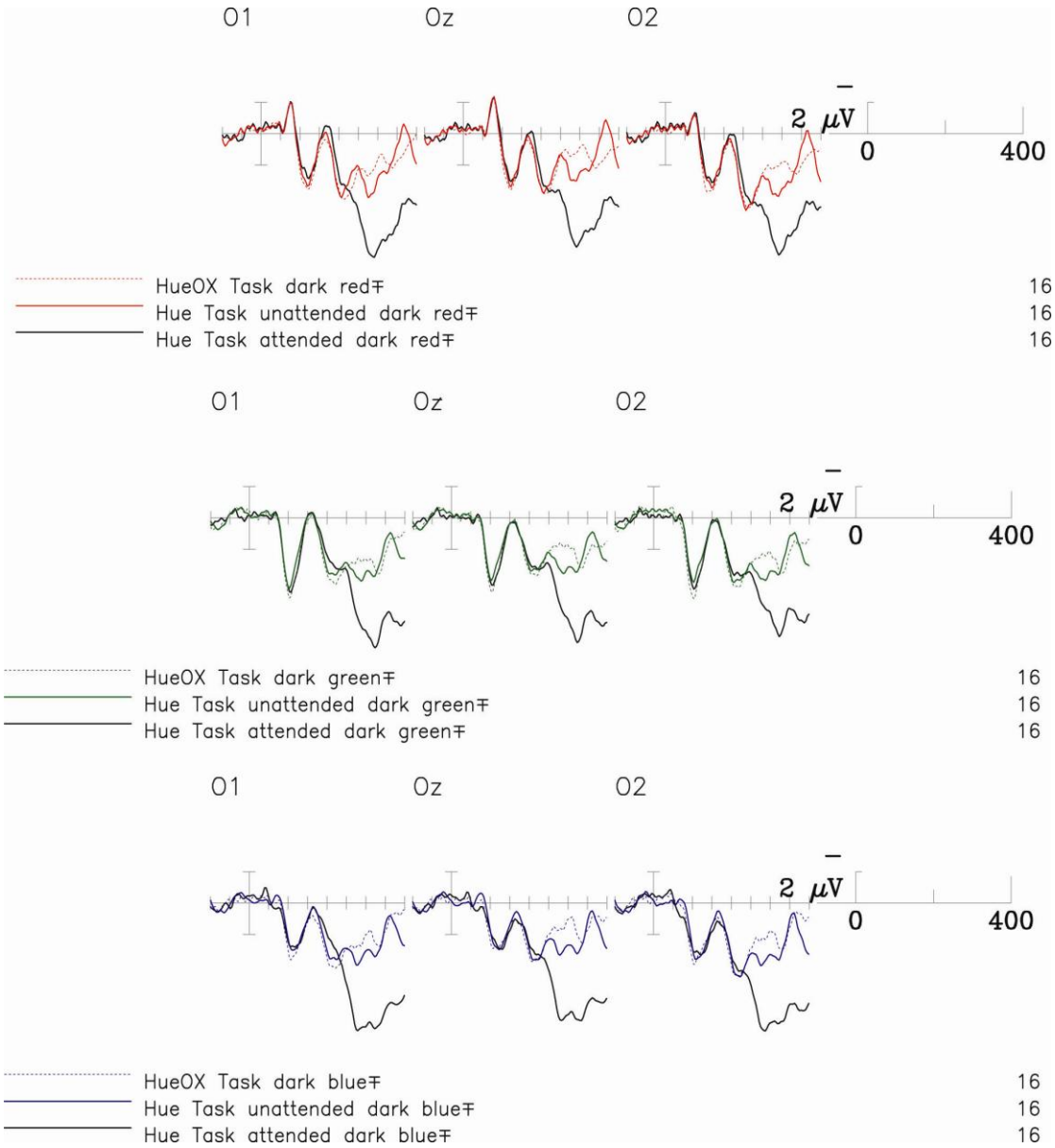

Figure 13: Grand-average ERP (N = 16) of occipital channels for different grapheme and attention conditions of light and dark colors in Task I and Task II, Continued.

To view whether passive viewing of color would be influenced in brain response by paying attention to different components of attention, we compared the unattended color responses from the two tasks of different attention component—color (Task I) versus grapheme (Task II) discrimination. Results were based on the

comparison of ERPs for Task I—color attending task—and Task II—grapheme attending task. **Figure 14** shows the ERPs for both attention conditions of Task I (attended vs. unattended colors), and **Figure 13** contains color ERPs from Task II, which we assumed to be similar in inattentiveness for Task I's unattended color responses.

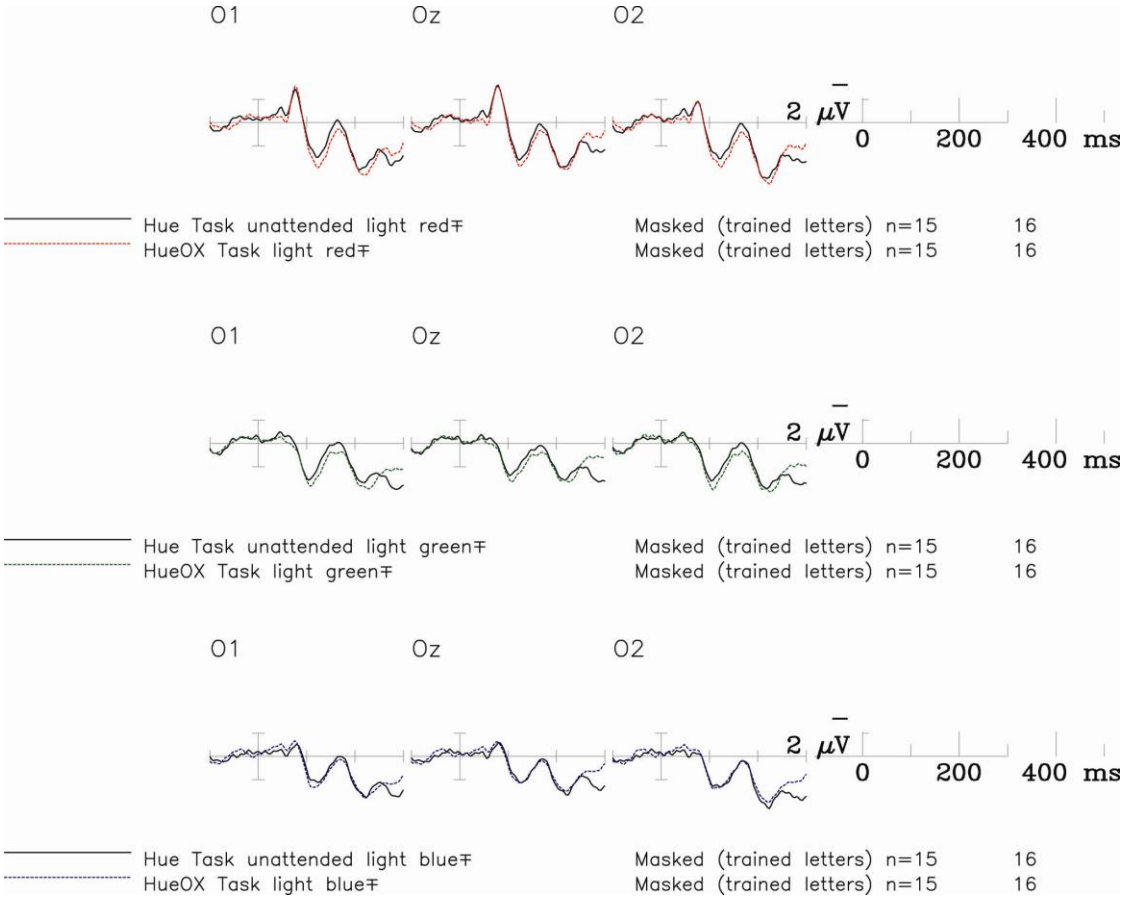

Figure 14: Grand-average ERP (N = 16) of occipital channels for unattended color during different grapheme and attention conditions in Task I and Task II.

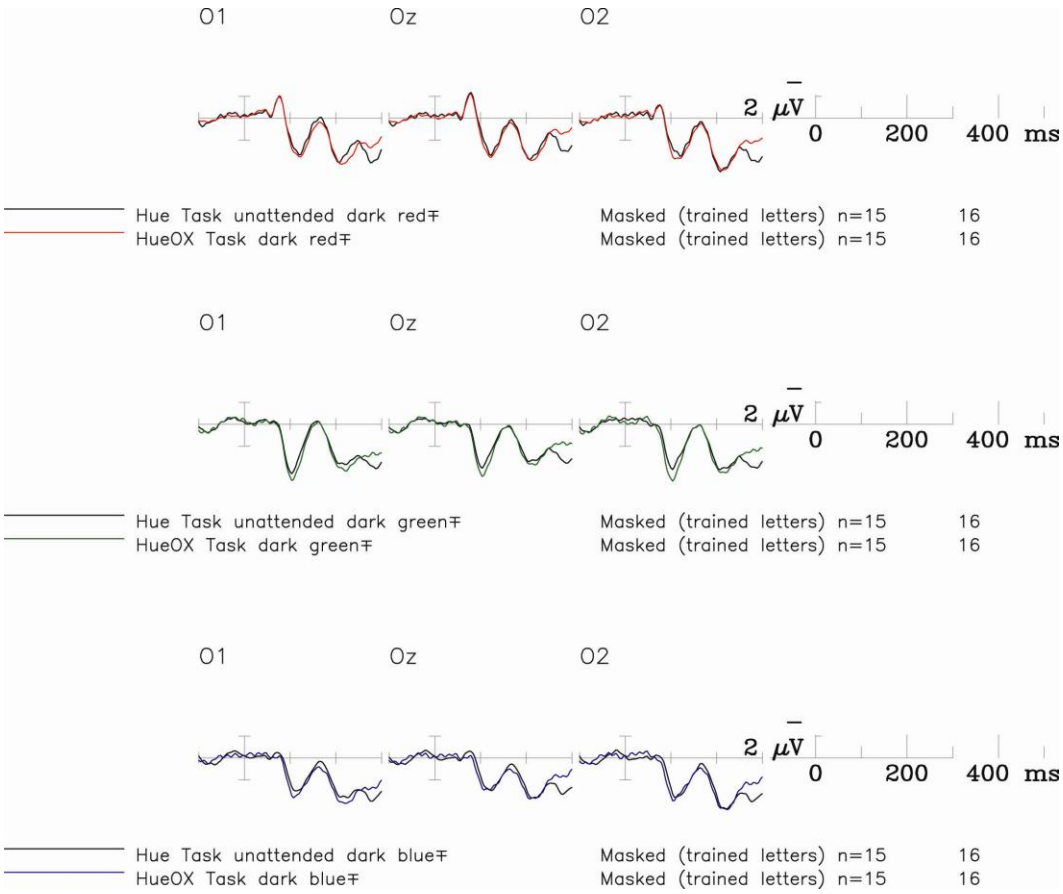

Figure 15: Grand-average ERP (N = 16) of occipital channels for unattended color during different grapheme and attention conditions in Task I and Task II, Continued

Table 11: ANOVA of mean amplitude (N = 16) during 60 – 90 ms (C1) of unattended colors of Task I and Task II with factors of task, luminance, color, and electrodes.

Source	SS	DF	MS	F	P	pGG	pHF
MEAN	81.57	1	81.57	0.64	0.4346		
S	1898.07	15	11.18				
ATask	4.43	1	4.43	0.40	0.5386	0.5386	0.5386
AS	167.66	15	11.18				
BLuminance	43.33	1	43.33	19.91	0.0005*	0.0005*	0.0005*
BS	32.64	15	2.18				
AB	1.70	1	1.70	2.14	0.1641	0.1641	0.1641
ABS	11.94	15	0.80				
CColor	340.70	2	170.35	34.07	0.0000*	0.0000*	0.0000*
CS	150.00	30	5.00				
AC	1.25	2	0.62	0.50	0.6127	0.6132	0.6127
ACS	37.54	30	1.25				
BC	1.18	2	0.59	0.29	0.7480	0.7481	0.7480
BCS	60.48	30	2.02				
ABC	0.79	2	0.40	0.33	0.7247	0.7248	0.7247
ABCS	36.60	30	1.22				
D	32.73	2	16.37	4.67	0.0171*	0.0436*	0.0436*
DS	105.12	30	3.50				
AD	0.16	2	0.08	0.69	0.5086	0.4155	0.4150
ADS	3.47	30	0.12				
BD	0.30	2	0.15	2.36	0.1122	0.1405	0.1398
BDS	1.89	30	3.50				
ABD	0.09	2	0.05	0.71	0.4994	0.4097	0.4097
ABDS	1.93	30	0.06				
CD	8.61	4	2.15	6.21	0.0003*	0.0065*	0.0059*
CDS	20.81	60	0.35				
ACD	0.11	4	0.03	0.43	0.7875	0.6549	0.7337
ACDS	3.68	60	0.06				
BCD	0.73	4	0.18	2.06	0.0968	0.1453	0.1431
BCDS	5.28	60	0.09				
ABCD	0.11	4	0.03	0.46	0.7633	0.6341	0.7104
ABCDS	3.68	60	0.06				

ANOVA (**Table 11**) shows the absence of statistically significant difference amongst different modules of attention in all factors for C1 of 60 – 90 ms. Despite different attention modules, initial C1 responses of 60 – 90 ms from the occipital lobe—V1—are similar in potential amplitude for both color, ($F(2, 30) = 0.5$, $p = 0.6132$), luminance ($F(1, 15) = 2.14$, $p = 0.1641$), and all of their interactions ($F(2, 30) = 0.33$, $p = 0.7247$). Such absence of attentional effect was expected as previous studies showed that C1 is not affected by attention.

Table 12: ANOVA of mean amplitude (N = 16) during 90 - 150 ms (P1) of

unattended colors of Task I and Task II with factors of task, luminance, color, and electrodes.

Source	SS	DF	MS	F	P	pGG	pHF
MEAN	2829.13	1	2829.13	8.64	0.0102*		
S	4914.16	15	327.61				
ATask	23.39	1	23.29	2.56	0.1307	0.1307	0.1307
AS	127.23	15	9.15				
BLuminance	41.57	1	41.57	20.52	0.0004*	0.0004*	0.0004*
BS	30.58	15	2.03				
AB	0.22	1	0.22	0.20	0.6588	0.6588	0.6588
ABS	16.42	15	1.09				
CColor	21.67	2	10.83	3.23	0.0537	0.0537	0.0537
CS	100.63	30	3.35				
AC	1.84	2	0.92	0.45	0.6432	0.6434	0.6432
ACS	61.61	30	2.05				
BC	6.67	2	3.33	2.58	0.0922	0.0947	0.0922
BCS	38.71	30	1.29				
ABC	0.35	2	0.17	0.25	0.7831	0.6252	0.6249
ABCS	21.20	30	0.71				
D	24.66	2	12.33	1.69	0.2025	0.2077	0.2075
DS	219.50	30	7.32				
AD	0.42	2	0.21	0.86	0.4351	0.3660	0.3654
ADS	7.35	30	0.25				
BD	0.34	2	0.17	1.65	0.2082	0.2146	0.2138
BDS	3.12	30	0.10				
ABD	0.07	2	0.03	0.92	0.4084	0.3495	0.3488
ABDS	1.06	30	0.04				
CD	3.01	4	0.75	3.57	0.0112*	0.0411*	0.0395*
CDS	12.65	60	0.21				
ACD	0.61	4	0.15	3.22	0.0183*	0.0331*	0.0310*
ACDS	2.83	60	0.05				
BCD	0.22	4	0.05	0.93	0.4555	0.4055	0.4364
BCDS	3.54	60	0.06				
ABCD	0.05	4	0.01	0.36	0.8336	0.6982	0.6978
ABCDS	2.00	60	0.03				

ANOVA (**Table 12**) from P1 of 90 – 150 ms time window shows similar

absence influences of attention in factors of color ($F(2, 30) = 0.45$, $p = 0.6434$), luminance ($F(1, 15) = 0.2$, $p = 0.6588$), and their interaction ($F(2, 30) = 0.25$, $p = 0.6252$); however, there is a statistically significant interaction with color and electrodes for these different attention modules ($F(4, 60) = 3.22$, $p = 0.0411$); different compoenents of attention (chromatic versus grapheme attention for this case) has effects on different brain regions during later visual processing.

DISCUSSION

4.1 Color

From the public misconception of the homunculus fallacy, the field of neuroscience has made progress toward unraveling the mysteries of perception and sensation. Regarding color vision, many have attempted to elucidate its mechanisms via diverse approaches of Genetics, behavioral psychology, etc.

We have approached this mystery with the psychophysiological method of EEG, in which it has an advantage of fine temporal resolution. EEG coupled with ERP for definite onsets of events (for our study, the presentation of colored squares) allowed us to glance at how the brain processes hues individually. With three electrodes placed around the occipital lobe, we used known activation times for V1 and V4 to measure the brain responses after viewing of colors.

C1 component of ERP responses, which index V1 activation, shows differential responses for both color and luminance of individual effects without an interaction. P1 component with V4 attribution responses to each color also showed individual main effects from color and luminance without an interaction; effects were consistent despite the different luminance levels, yet the responses for each color were unique. These raises a question on whether color vision derives from unique neurons designated for each color or from the network of V4 neurons that may orchestrate different signals for each colors.

Red and green are both passed through the parvocellular path to the visual cortex, yet our data shows a statistically significant difference in the V4 response in terms of power, the amplitude of potential for each stimulus, suggesting different decoding pattern at later neural processes apart from the initial color opponent parvocellular path. Our results also open a new perspective for the dilemma of

dichromatic color perception. Many researchers such as Brettel et al (1997) have attempted to compute how dichromats perceive our colored world. Such studies have been progressed very far, and future studies using ERP to measure the response of dichromats would give confirming evidence to analyze dichromatic in viewing their brain responses to the color perceptual space. For example, the similar or different responses to red and green stimuli by a person with protanopia or deuteranopia would give insights to whether red and green are qualitatively processed similarly or differently at the cortical level. Future studies could be conducted with individuals with flipped L and M photoreceptors on the parvocellular pathway. Such cases are rare but existing; further investigation with these individuals will be a good method to analyze neural processing of color.

As we did see statistical differences in responses among electrodes for each color, the question also derives to whether the location of the neurons account for the perception of color. Amplitude difference in potentials for each color also suggests that a unique pattern of neuronal activation may hold responsible for color perception; the difference in frequencies of neurons or different number of activated neurons may be responsible for the amplitude difference. Amplitude difference in potential can also result from different number of activated neurons. Differential response time of P1 supports a unique color processing in V4 or later visual cortex processes behind the experience of color qualia.

An interesting observation was made during my thesis; color processing seems to differ in pattern at C1 and P1. Heeger et al's fMRI study observed V1 responses to color aligned with color opponency while V4 responses seem to match the perceptual color space, where similar responses were shown with perceptually similar colors. This difference in decoding of color in each compartment was

supported with our study where ERP response patterns for color differed in each C1 and P2 time windows.

From our results, we tentatively conclude that V4 is the location for deriving the richness and diversity of color perception. Three possible explanations or their combinations could be responsible for such experiences: (1) specific neurons designated for each color (2) specific pattern of activation of neurons for each color (3) location of neurons. Based on our results, all three still hold valid and further research into this question will surely be another step toward the advancement of neuroscience.

4.2 Attention

Attention has been known to affect brain responses in terms of spatial discrimination. To study attention effect on color, we set up Task I and compared ERP responses for attended and unattended color. The results were not statistically significant different for ERP responses of different colors during 60 – 90 ms of C1. Also, there is an absence of statistically significant difference for ERP responses during 90 - 150 ms of P1. There is a lack of primordial response to attention; however there is still a later attention response after 200 ms, which is consistent with previous papers from Ito et al.

To study the brain response for color during different attention components, Task II was devised for passive color viewing while discriminating for grapheme—O and X. ANOVA contained unattended color ERP from Task I and Task II. There was a lack of statistically significant difference during 60 – 90 ms, but was present for 90 - 150 ms; C1 response was consistent with previous studies stating that V1 is not modulated by attention. However, later extrastriate (V4) process of color seemed to be

affected by different type of attention. The results imply a lack of attention effect on initial processing of color vision; color perception is a bottom-up process with top-down implication to facilitate detection of feature of interest (color or grapheme). The interaction leads to analysis of individual colors in their response with electrode and attention. However, only blue seems to actually show a pattern change, suggesting that more trials are needed to clarify attention effect.

On the other hand, Zhang et al shows that attention for color has shown ERP modulation within 100 ms. This may be inconsistent with our result since the color stimuli were not isoluminant; our results show luminance affects amplitudes within 100ms as well. However, as our p-value is on the border, $p = 0.0692$ with GG correction while $p = 0.0466$ with HF correction. Future studies with more trials can clean out the signal to noise ratio to give a more clear result. Also, Muller et al study color discrimination task with SSVEP resulted in enhanced SSVEP amplitude for attended colors. However, since SSVEP signals are averaged over time, this cannot identify the initial processing of the visual cortex. Our results are consistent to the conscious experience of color. If one could intentionally control perception by attention, then one would be able to change color perception by will. This is not true as we know that one cannot vividly imagine color.

Conclusion

Color perception is an unconscious process depended on a bottom-up control; however, the difference in attended feature (e.g. whether an individual is looking for a certain color or a certain shape) may influence later processing of color. Our brain seems to have developed a system to process color as we have seen consistent patterns of color in the V1 and V4 despite different levels of luminance. Colors seem to be processed in different decoding manners in each compartment of the visual cortex even in terms of timing. To investigate further to the underlying mechanism behind the differential response—whether the location, frequency, or number of involved neurons--, follow up studies are in the process to be set up with electro-caps with higher density of electrodes by the occipital lobe and subjects with rare conditions of flipped L and M cone connections.

REFERENCES

Andersen, S.K., Muller, M.M., Hillyard, S.A. (2009) Color-selective attention need not be mediated by spatial attention. *Journal of Vision*, 9(6): 2, 1-7

Brang, D., Hubbard, E.M., Coulson, S., Huang, M., Ramachandran, V.S. (2010) Magnetoencephalography reveals early activation of V4 in grapheme-color synesthesia. *NeuroImage*, 53: 268-274

Brouwer, G.J., Heeger, D.J. (2009) Decoding and Reconstructing Color from Responses in Human Visual Cortex. *J. Neurosci.*, 29(44): 13992-14003

Di Russo, F., Stella, A., Spitoni, G., Strappini, F., Sdoia, S., Galati, G., Hillyard, S.A., Spinelli, D., Pitzalis, S. (2011) Spatiotemporal Brain mapping of Spatial Attention Effects on Pattern-Reversal ERPs. *Human Brain Mapping*, 00:000-000.

Foxe, J.J., Strugstad, E.C., Sehatpour, P., Molholm, S., Pasieka, W., Schroeder, C.E., McCourt, M.E. (2008) Parvocellular and magnocellular Contributions to the Initial Generators of the Visual Evoked Potential: High-Density Electrical Mapping of the "C1" component. *Brain Topogr*, 21:11-21

Ito, K., Tomiya, N., Imori, M., Yoshihama, J., and Matsuda, H. (2006) Visual cognitive function in dementia of Alzheimer's type: a comparison of visual event-related potentials and Stroop test. *Psychogeriatrics*, 6: 49–54.

Jacobs, G.H. (1993) The distribution and nature of colour vision among the mammals. *Biol.Rev.* **68,** 413-471

Nida-Rumelin, M. (1996) Pseudonormal Vision: An Actual Case of Qualia Inversion? *Philosophical Studies*, 82:145-157

Proverbio, A.M., Del Zotto, M. Zani, A. (2010) Electrical neuroimaging evidence that spatial frequency-based selective attention affects V1 activity as early as 40-60 ms in humans. *BMC neuroscience, 11:59*

Rowe, M.H. (2002) Trichromatic Color Vision in Primates. *News Physiol Sci*, 17: 93-98

Szatmary, B, Izhikevich, E.M. (2010) Spike-timing theory of working memory. *PLoS Comput Biol.*, 19;6(8)

Zeki, S. (1980) The representation of colours in the cerebral cortex. *Nature*, 284(5755): 412-418

Zhang W., Luck, S.J. (2009) Feature-based attention modulates feedforward visual processing. *Nature Neuroscience*, 12 (1): 24-25.