

COLOR OPPONENCY MODULATES FEATURE INTEGRATION THROUGH BAYESIAN PRIORS

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A THESIS SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

GRADUATE PROGRAM IN BIOLOGY
YORK UNIVERSITY
TORONTO, ONTARIO
AUGUST 2021

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KEYWORDS

attention, Bayesian perception, feature integration, flash-jump effect, visual perception

ABSTRACT

Stimulus color, even irrelevant to the task, has been shown to modulate high-level cognitive functions, producing different behavioural outcomes. However, the effect of color on lower-level perceptual processes remains unclear. To address this gap, we investigated whether color affects feature integration, an early-stage visual process, using the flash-jump illusion. Our results demonstrated that color modulates the integration of color and motion features, as red and blue flashes resulted in more veridical estimates of flash location, compared to green and yellow. We provide a novel interpretation of our current results in respect to a Bayesian perceptual framework, where the color of the flash is inherently assigned different Bayesian weights, resulting in different levels of perceptual shifts. Furthermore, in reviewing pertinent literature and empirical evidence, we have proposed a novel theory outlining three putative mechanisms, predictions and underlying neural circuitry using Bayesian frameworks to explain such color-dependent modulations in visual processing.

ACKNOWLEDGEMENTS AND DEDICATION

Throughout my Masters, I have received a great deal of support and encouragement from so many wonderful people. I would first like to thank my supervisor, Dr. Mazyar Fallah for his expertise, tutelage, and patient support throughout this journey. His friendly, approachable, and ever-smiling personality has made this entire experience very positive. In addition, I would like to express my gratitude to my advisor, Dr. Christopher Bergevin, for his keen interest in my thesis, thoughtful discussions, and enthusiasm. I would also like to give a sincere thanks to Dr. Heather Jordan for lending her knowledge and expertise throughout the research process. In addition, I wish to acknowledge and thank my lab mates from the Visual Perception and Attention Lab for showing me the ropes and providing encouragement. Finally, I wish to acknowledge the love and motivation I received from my family, and friends. Special mention to Simar, Mani, and Jas for patiently listening to my lengthy “stories”. Last but not the least, big thankyou to Becky, Caroline, Daria, Katie and Shir for the newfound friendship, support, and comic relief. Long Live J-Club!

I dedicate this thesis to the memories of my late grandparents; Kashmira S. Saini & Surjit K. Tamber.

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CHAPTER 1

COLOR VISION

1.1 INTRODUCTION

Trichromats are organisms with three independent color channels, allowing for the development of color vision. It has been theorized that color is an important feature of primate vision from an evolutionary perspective, allowing us to differentiate between various food items, detect predators, discriminate ambiguous objects and recognize visual targets (Mollon, 1989; Osorio & Vorobyev, 1996; Gegenfurtner & Rieger 2000, Caine & Mundy 2000; Regan et al., 2001). Some researchers have also suggested that color vision is advantageous for the recognition of faces (Russell & Sinha, 2007), and facilitates non-verbal communication through skin colouration. For example, a flushed face may communicate aggression or embarrassment. In our present world, we seldom consider color as an informative feature. Nowadays, object color is more associated with aesthetic judgments concerning the color of a room, a new toy, or a dress. However, recent developments in the field of color research have demonstrated the modulatory effects of color on human cognitive and psychological functioning. The current thesis examines the effect of color on low-level perceptual processes, and the neural mechanisms that may underlie such color modulations of visual processing.

1.2 COLOR PROCESSING IN THE VISUAL SYSTEM

In the primate brain, the perception of color is a complex computational process carried out in the ventral visual pathway. Color signals are processed in hierarchical stages, with each subsequent stage carrying out more complex computations than the previous. In the pre-cortical stage, cone signals are first integrated in the retina and then relayed to the lateral geniculate

nucleus (LGN) in the thalamus. Cortical processing of color information begins in V1 and continues throughout the ventral visual pathway. Subsequent sections provide a summary of color processing along the ventral stream (see Figure 1 for an overview), followed by a brief overview of feature integration between the dorsal and ventral streams.

1.2.1 Pre-cortical stage: Retina, LGN

Sensory neurons for vision, photoreceptors, absorb light reaching the back of the retina and convert light energy into an electrical signal. There are two types of photoreceptors: rods, which contribute to vision under low illumination conditions (i.e. scotopic vision), and cones, which are responsible for vision under bright light (i.e. photopic vision) (Molday & Mortiz, 2015). Cone photoreceptors also contribute to trichromatic or color vision. Cones are further classified into three types based on their spectral sensitivities. Long (L) cones are maximally sensitive to long wavelengths of light around 564 nm (i.e. red light) (Bowmaker & Dartnall, 1980). Similarly, M and S cones are maximally sensitive to medium (~ 534 nm, green light) and short wavelengths (~420 nm, blue light) of light, respectively (Bowmaker & Dartnall, 1980). Studies investigating the distribution of cones in monkey and human retinas have suggested that L and M cones are found in higher proportions compared to S cones, which are estimated to comprise only 8-10 % of the total (Marc, 1982; Dartnall, Bowmaker, & Mollon, 1983; Kolb & Lipetz, 1991; Mollon & Bowmaker, 1992). The three types of cone signals are processed and subsequently relayed to the LGN via retinal ganglion cells (RGCs) (Masland, 2001). RGC and LGN neurons both have circular receptive fields, which is the area on the retina that activates the cell in response to light in that region. The receptive fields are typically organized into a central circular region, called the center and an annulus called the surround, which are both dependent on the input of many cones. The center responds to the onset or offset of light and the surrounding annulus has the

opposite response. Light falling outside of the surround results in no response from the cell. Information from the retinal ganglion cells arrives in the LGN via parallel segregated channels, color information specifically arrives in the parvocellular layers of the LGN (Dacey & Lee, 1994). LGN cells compute the relative difference in cone activations giving rise to color opponency. The LGN contains three types of color opponent cells. The red/green or L/M opponent cells in the parvocellular layers compare L and M cone signals and are maximally activated by red light and inhibited by green or vice versa (Derrington et al, 1984; De Valois et al., 1958; Wiesel & Hubel 1966; Dacey & Lee 1994; Reid & Shapley, 2002). Similarly, S cone responses are added or subtracted from M and L responses to give rise to blue-yellow axis (Hendry & Yoshioka, 1994; Martin et al., 1997). Yellow/Blue or S/(L+M) opponent cells are excited by yellow light but inhibited by blue (or vice versa) (De Valois & De Valois, 1993). Lastly, light/dark or achromatic cells compute the sum of L, M and S cone inputs to establish a luminance axis. These opposing channels form the two cardinal color axes (R/G, Y/B), which establish the basis for color opponency and a third luminance axis. Parvocellular LGN neurons terminate in layer 4C β of the primary visual cortex (V1) (Livingstone & Hubel, 1988).

1.2.2 Early visual cortex: V1, V2

Visual processing in the early visual cortex is concerned with segmentation and segregation of object properties which are then processed in parallel streams. V1 neurons are tuned for a variety of stimulus properties, including color, form, and orientation. In relation to color vision, information from the LGN color opponent channels arrives in layer 4C β of V1 through anatomically segregated streams (Hubel & Wiesel, 1972; Hendrickson et al., 1978; Blasdel & Lund, 1983; Chatterjee & Callaway, 2003) and projects to color domains in layers 2 and 3 of V1 (Livingstone & Hubel, 1984; Rentzeperis et al., 2014). V1 color “blobs” are clusters of color

selective neurons which are tuned for colors along the color opponent axes (R/G, B/Y), similar to the single opponent cells in LGN (Conway, 2001; Conway & Livingstone, 2006). Single opponent cells found in V1 and LGN are responsible for detecting the color of a region which falls on their receptive fields. Interestingly, color blobs in V1 also contain double opponent cells (Conway, 2001; Johnson et al., 2001; Horwitz et al., 2007), which have larger receptive fields that are antagonistic for both hue and the spatial layout of light. For example, the center of a Red/Green double opponent cell is excited by red but inhibited by green. This pattern is reversed in the surround, which is excited by green but inhibited by red, thus effectively detecting color contrast or color boundaries of an image. Some researchers have suggested that specialized double-opponent color cells in V1 also compute color constancy to some degree (Wachtler et al., 2003). For color constancy to occur, changes in illumination or lighting conditions must be discounted from the light reflected off the object, such that a fixed color may be assigned to a visual target irrespective of illumination. Double opponent cells may achieve this by computing the contrast differences between color opponent receptive fields in both their centers and surrounds (Gegenfurtner, 2003).

Color-tuned neurons from V1 blobs send feedforward convergent input to thin stripes in V2, which are also enriched for color-selective double opponent neurons (Hubel and Livingstone 1987; Gegenfurtner et al., 1996; Ts'o et al., 2001; Shipp & Zeki 2002; Sincich & Horton 2002; Xiao et al., 2003; Lu & Roe, 2008). Some studies have demonstrated the presence of specific color regions in V2 thin stripes, with a columnar organization for neurons with similar hue preferences (Xiao et al., 2003; Lim et al., 2009) and spatially separate regions for luminance (brightness or darkness of a hue) (Wang & Felleman, 2002; Wang et. al, 2007).

1.2.3 Extrastriate Cortex

From V2, color information is projected forward into visual area 4 (V4) (DeYoe et al., 1994; Felleman et al., 1997; Xiao et al., 1999). V4 is an intermediate level area in the ventral stream, and based on the reported predominance of color selective neurons in V4 (Zeki, 1973, 1983), it was thought to be the “color center” in the brain. However, current investigations have demonstrated that V4 cells are receptive to various stimulus features, not just color (Roe et al., 2012). With respect to color vision, V4 “globes” represent the next stage of color processing beyond V2. Color selective neurons found in globes are not affected by luminance changes (Conway et al., 2007). They are arranged into hue maps spanning color space, therefore not restricted to the cardinal color axes (Conway & Tsao, 2006; Conway, et al., 2007; Conway & Tsao, 2009). Li and colleagues (2014) used optical imaging and multiunit recordings in macaques to investigate the organization of color space in V4. They presented a broad range of color stimuli, spanning HSL color space, while the monkeys performed a fixation task. They demonstrated the presence of different hue preferring patches in V4 globes which form clusters with adjacent hues. An increase in saturation (intensity of a hue) of a color led to an increase in activity in its corresponding patch. Furthermore, varying the luminance (lightness or darkness) of the hues resulted in a shift in the hue clusters. As the luminance of the color decreased, its corresponding color-specific patch shifted towards black-preferring patches. Therefore suggesting that luminance and saturation may be integrated into hue representations in V4, whereas these color dimensions appear to be represented separately at earlier stages. In sum, the arrangement of hue clusters modifiable by saturation and luminance provide a basic framework for a 3D color space or map in V4, corresponding to the first representation of perceived color. V4 also plays an important role in achieving color constancy (Zeki, 1983; Heywood et al., 1992;

Kusunoki et al., 2006), however V1 and V2 are also involved in some aspects of color constancy as mentioned previously (Shapley & Hawken, 2002; Gegenfurtner, 2003; Wachtler et al., 2003)

1.2.4 IT Cortex and beyond

In addition to V4, fMRI and imaging studies in monkeys have provided evidence for various color selective regions in the IT cortex, such as posterior TEO, and TE (Conway & Tasao, 2006; Conway et al., 2007, Harada et al., 2009). Sometimes these color selective regions have been collectively termed the PIT cortex, the posterior portion of inferior temporal (IT) cortex. The inferior temporal (IT) cortex, known for its role in creating whole object representations, by combining or integrating independent object features such as color, shape, orientation etc., serves as the final stage of the ventral visual stream and color processing.

Various behavioural studies have implicated the role of IT cortex in color decision making (Komatsu et al., 1992; Conway et al., 2007). For example, Takechi et al. (1997) report stronger activation of IT cortex for a color discrimination task, compared to brightness or position discrimination tasks. Furthermore, some studies have reported that lesions or cooling of the IT cortex leads to deficits in color discrimination (Heywood et al., 1988; Horel, 1994; Huxlin et al., 2000). Moreover, Koida and Komatsu (2007) have demonstrated that neuronal activity of color-selective cells in the IT cortex is modulated by task demands. Taken together, these investigations suggest that IT neurons play an important role in decision making processes related to color vision such as the discrimination or categorization of colors (Dean, 1979; Matsumora et al., 2008) and as an integration site for color and behaviour. This current view is strengthened by the presence of reciprocal connections between IT and prefrontal cortex, an area important for carrying out executive functions and decision making (Webster et al., 1994),

suggesting that color decisions in the IT cortex are modulated by top-down task demands and learning.

1.3 INTEGRATION OF COLOR AND MOTION

The visual system is divided into two hierarchical pathways. The ventral pathway, discussed previously, contributes to the recognition of objects and object features such as color, whereas the dorsal pathway, which is functionally and anatomically distinct, is involved in the processing of motion information and guiding motor behaviours (for a review see; Perry & Fallah, 2014).

The dorsal visual pathway begins in specialized layers of V1, similar to the ventral stream. Starting in layers 4C α and 4B, V1 neurons selective for the motion of simple stimuli such as bars or edges (Hubel & Xiao, 1968; Hubel et al., 1978; Orban et al., 1986) make feedforward connections to neurons in V2 thick stripes (Hubel and Livingstone, 1987; Levitt et al., 1994; Shipp & Zeki, 2002). Next, the middle temporal area (MT) receives motion information from both V1 and V2 (DeYoe & Van Essen, 1985; Felleman & Van Essen, 1991, Born & Bradley, 2005). MT neurons compute local and global information such as depth, motion speed and direction of a moving target (Perry & Fallah, 2014). Although MT neurons are selective for motion, they are blind to color (Maunsell & Van Essen, 1983; Shipp & Zeki, 1985; Gegenfurtner et al., 1994). Motion information from MT is sent to the next stage of the dorsal stream, medial superior temporal area (MST), which is involved in complex motion computations such as 3D motion, velocity, rotation etc. (Perry and Fallah, 2014). From MST, the dorsal stream continues into the posterior parietal cortex where more complex computations such as optic flow, and self-motion occur (Perry & Fallah, 2014).

As mentioned previously, dorsal stream neurons are not selective for color, since color is irrelevant to motion processing and color is processed in an anatomically distinct pathway, the ventral stream. However, there is evidence to suggest “cross-talk” between the ventral and dorsal streams resulting in the incorporation of features from one stream to the other. For example, monkeys viewing 2D moving dot patterns are able to generate a percept of a 3D rotating cylinder and report the direction of its rotation (Bradley et al., 1998). Given that the 2D projection is flat, thus contains no 3D form information, a 3D object representation constructed in the IT cortex is likely being incorporated into motion selective areas in the dorsal stream to allow for the detection of rotation direction. The green-dot or lilac chaser illusion created by Jeremy Hinton is another example reflecting the integration of color and motion information, specifically. The illusion consists of 12 lilac dots in a circular arrangement with a central fixation cross. Each of the lilac discs disappear for a very brief time, in a clockwise fashion. Fixation at the cross results in the perception of an afterimage- a green disc “chasing” each lilac dot as it disappears. Successive afterimages are integrated and perceived as continuously moving in a clockwise fashion. This green afterimage is a consequence of cone adaptation in the ventral stream, however, to perceive the clockwise motion of the afterimage, this ventral stream information must be fed into motion areas such as MT. Some empirical studies have directly provided evidence for the integration of color and motion information, as color was shown to influence various facets of motion processing (Dobkins & Albright, 1994; Croner & Albright, 1997, 1999; Tchernikov & Fallah, 2010; Perry & Fallah, 2012). Croner and Albright (1997) demonstrated that the motion direction of randomly moving dots was easier to discriminate if the coherently moving dots were segregated from the distractors based on color. Similarly, Tchernikov and Fallah (2010) demonstrated that color influences smooth pursuit of randomly moving dots.

Taken together, these investigations suggest that color and motion signals may not be completely independent of one another. Color signals from the ventral pathway are likely incorporated with motion signals in the dorsal pathway, and vice versa. Perry and Fallah (2014) provide a possible location for this integration. They argue that since V4 is the first area to compute perceived color, therefore, color information in the ventral stream must reach V4 before getting incorporated into dorsal stream representations in area MT. Anterograde and retrograde tracer studies have confirmed the presence of bidirectional connections between area MT and V4 (Ungerleider & Desimone, 1986; Ungerleider et al., 2008), thus providing an anatomical basis for this integration (red arrow, Fig. 1).

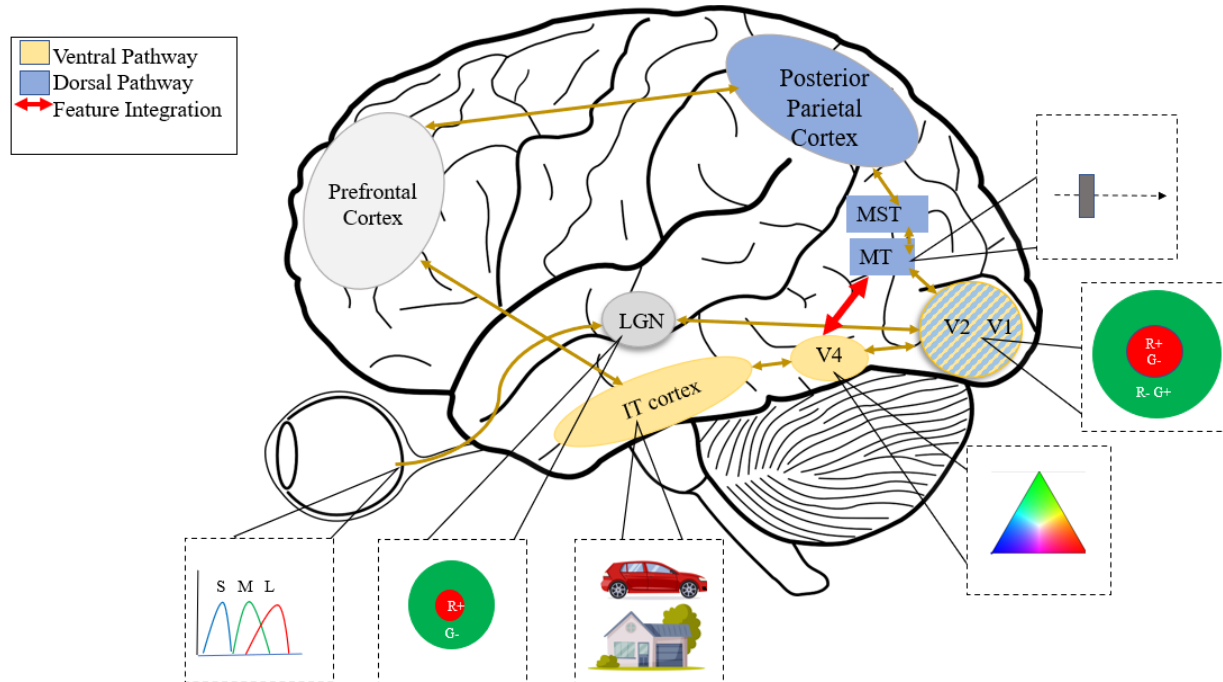


Figure 1. Overview of color processing in the visual system. Key computations or features relevant to color processing within each brain region are depicted as dashed boxes. Color processing in the ventral stream (yellow regions) begins with three types of cone signals (S, M, L) which are processed and relayed to the LGN. The LGN computes relative cone activations giving rise to color opponent cells. This opponent information is then relayed to double opponent cells in areas V1 and V2. Next, area V4 transforms opponent input into a trichromatic color space. The IT cortex creates 3D representations of objects through the incorporation of different features. Dorsal regions (blue) such as MT, MST and the Posterior Parietal Cortex are involved in the motion processing pathway. Areas V1 and V2 are involved in both ventral and dorsal processes. Note that the red bidirectional arrow represents the integration of color and motion information between area V4 and MT.

CHAPTER 2

COLOR DEPENDENT MODULATIONS

2.1 COLOR-DEPENDENT MODULATIONS OF EXECUTIVE FUNCTIONS

The processing of visual information in the cortex has been described to occur in three proposed stages (Marr, 1982). The first stage, low-level, refers to the processing of 2D object features such as; edges, lines, curves and color. In relation to color vision, low level processing of color information begins with color opponent cells in areas V1 and V2. The second, intermediate stage of processing is concerned with incorporating 2D object information from the previous stage with 3D information, which Marr referred to as a 2.5D percept. For example, color selective cells in V4 incorporate 2D color opponent input to create a color space representing perceived color. Higher level processing, the final stage, represents the formation of full 3D object representations at the level of IT cortex and beyond. Executive functions refer to higher-level processes and cognitive capabilities such as attention, decision-making, working memory, inhibition and reasoning, which rely on the whole object (3D) representations created in the ventral visual processing stream (i.e IT cortex).

Recent investigations have suggested that the colour of visual input can intrinsically drive differences in higher level visual processes such as target selection (Tchernikov & Fallah, 2010), visual search (Lindsey et al. 2010; Fortier-Gauthier et al., 2013; Pomerleau et al.,2014), and response inhibition; (Blizzard et al.,2017; Ghasemian et al., 2021), suggesting that all colors may not be processed equally in the visual system. This differential processing of various colors leads to modulations in visual processing which in turn results in different behavioural outcomes based on the color of the stimuli.

Studies investigating the effects of target color in visual search tasks have reported differences in task performance based solely on the color of the targets (Lindsey et al., 2010; Fortier-Gauthier et al., 2013; Pomerleau et al., 2014). As participants search for a colored target among other colored distractors, Lindsey et al. (2010) reported that reddish targets were much easier to find compared to blue/purple targets, represented by faster reaction times for red.

Electrophysiological studies have also supported color-dependent differences in visual search. In an event related potential (ERP) study, Fortier-Gauthier and colleagues (2013) have shown that red targets in a visual search task evoke earlier N2PC waveforms and faster detection times than green targets. This work was extended by Pomerleau et al. (2014), where it was reported that the N2PC waveform appeared earliest for both red or blue stimuli compared to green, and yellow. Furthermore, red stimuli were reported to evoked larger posterior contralateral positivity (Ppc) and positive temporal component (Ptc) waveforms compared to other targets. It has been suggested that the N2PC waveform reflects attentional based filtering of relevant objects (Luck & Hillyard, 1994) and target enhancement (Mazza et al., 2009a, 2009b), whereas the Ptc indicates suppression of distractors after target identification (Hilimire et al., 2011). Given that red stimuli, in particular, result in both greater inhibition of distractors and greater enhancement of the red target itself, these results suggest a greater sensitivity for red stimuli over other colors during visual search.

More recently, response inhibition, which refers to the suppression of context-dependent inappropriate actions mediated by frontal lobe, has also been shown to be modulated by color. The inhibition or execution of motor actions and its behavioral control is studied using a stop-signal task (SST), where observers execute an action (i.e. pressing a button) in response to a go-signal (i.e. visual stimulus on the screen) but inhibit the same action when presented with a stop-

signal (i.e. absence of the go-signal or the onset of a different signal). Blizzard and colleagues (2017) modified this classic task by varying the color of the go-signal on the screen. Their findings showed that varying go-signal colors had no effect on participant reaction times, suggesting that response execution was not modulated by color. However, varying the color of the stop-signal did show a significant effect on response inhibition, where red stop signals facilitated response inhibition (i.e. faster reaction times) than green stop signals. The findings from this study have been recently replicated in monkeys performing a similar stop-signal task (Ghasemian et al., 2021). Asare et al. (in review-a), extended this work by testing for 4 stop signal colors (red, green, yellow, blue). The authors report faster reaction times for red stop signals than green, as previously reported by Blizzard et al. (2017). However, there was no significant difference in reaction times for yellow or blue stop signals, suggesting that response inhibition is specific to red and green only. Asare et al. (in review-b) also investigated the effects of color on another type of response inhibition task, 2-choice discrimination go/no-go. In this study, participants responded to the direction of a white arrow (go trial) but withheld their response if the arrow was red or green (no-go trial). Their findings revealed that red no-go stimuli resulted in an increased accuracy for stopping compared to green. In sum, response inhibition studies investigating the effects of color indicate an advantage for red stop signals compared to green when withholding an action.

Taken together, these previous color investigations suggest that the color of a visual input has a modulatory influence on visual processing and can drive differences in various higher-order executive functions. Differential behavioural outcomes based on the color of a visual stimulus will be referred to as color-dependent modulations here on in. The exact mechanisms behind such color-dependent modulations are currently unknown.

2.2 PUTATIVE MECHANISMS OF COLOR MODULATIONS

Although the exact neural mechanisms underlying color-dependent modulations are unknown, the hierarchical nature of the visual system provides various opportunities for such modulations to occur. Color signals may be differentially processed at one or more stages in the ventral visual pathway resulting in the differential modulation of the cognitive process at hand.

Firstly, color opponent signals at the earliest stages of the ventral stream provides one putative mechanism. Differences between L, M, S cone signals are computed by LGN opponent cells, giving rise to red-green and blue-yellow color axes (De Valois et al., 1958; De Valois & De Valois, 1993). Each type of opponent cell is maximally activated by one color and inhibited by its complementary color. Therefore, this antagonistic circuitry inherently leads to differential processing of color within each opponent pair.

In contrast, Tchernikov & Fallah (2010) reported hierarchical color effects, instead of differences between opponent pair colors. They demonstrated that in the absence of any task demands, which colored random-dot-kinematograms (RDKs) surface was selected and pursued with eye movements, depended on a hierarchy of colors, with red selected and tracked over > green> yellow> blue. They have suggested that this color hierarchy may drive differences in attentional capture and allocation, resulting in the modulation of attentional resources during a visual task. Tchernikov & Fallah's (2010) attentional hierarchy provides yet another putative mechanism for color- dependent modulations.

Lastly, color- dependent modulations of cognitive functions may also arise due to learning of specific color associations and meanings (Elliot & Maier, 2007). Given that color processing computations can be modulated by top-down influences from the prefrontal cortex (Koida &

Komatsu, 2007), learning and experience-based changes to visual processing can underly color modulations of various behavioural tasks.

In sum, color opponency, attentional hierarchy, and color associations may provide insight and enhance our understanding of how various perceptual and cognitive tasks can be modulated based on color. As much is unknown about the neural mechanisms and circuitry involved in color-dependent modulations, many questions are still unanswered. For example, which of the three proposed mechanisms is supported by empirical data? What are the neural correlates for each mechanism? Are these mechanisms task-dependent? Is the color-dependent modulation of a given task a result of one mechanism or an interplay of multiple mechanisms? Is there a different mechanism entirely?

2.3 BAYESIAN MODELS OF PERCEPTION

Sensory input feeding into the visual system can be ambiguous and noisy. For example, different stimuli can result in the same retinal image or the same stimulus can generate different retinal images depending on viewing angle. A small retinal image of a tree can be interpreted as a large tree in the distance or a small tree closer to the observer. Despite the ambiguity, the human visual system is quite good at creating accurate representations of objects and object properties in our visual field. One central question that arises is how? Helmholtz (1867) offered a solution suggesting that our brain generates accurate perceptions by unconsciously inferring or assuming information based on prior experience or knowledge. For example, the same object may appear a different color under different illumination conditions, but our brain can discount the effects of illumination by inferring properties of light.

There is growing support for the theory that visual perception is based on such Bayesian inferences, where sensory input is integrated with prior experience or knowledge to create accurate representations about the world around us. Bayesian models of perception are derived from Bayes Rule, a mathematical formula for calculating conditional probabilities (i.e. the probability that event A occurs given event B). Bayesian models can be used to estimate object properties under ambiguous or uncertain conditions conditioned on the sensory input (i.e retinal image) (Kersten & Yuille, 2003; Kersten et al., 2004; Feldman, 2012). Given sensory data, D, that can be interpreted as a variety of distinct possible perceptions or perceptual alternatives (A_1, A_2, \dots, A_n), the probability of a given perception, A_i , being true based on the sensory input, called the *posterior probability*, $p(A_i|D)$, is proportional to the *likelihood*, which is the probability of the data, D, given A_i is true, $p(D|A_i)$, multiplied by the *prior probability*, which is the probability of a given perceptual belief, A_i , being true, $p(A_i)$.

$$p(A_i|D) \propto p(D|A_i) p(A_i)$$

Simply put, the posterior probability is the product of the likelihood, which arises from fit of the image data and the priors, which represent prior knowledge or predispositions about object regularities independent of the sensory input (Kersten et al., 2004) (Figure 2). For example, when viewing shaded objects, we typically assume illumination from above. This light source prior may be the result of our experience with the sun's natural placement in the sky as well as the typical placement of artificial lights (Kersten et al., 2004). As more sensory data accumulates or as the data becomes less ambiguous, the posterior probability is biased towards the likelihood function, whereas, insufficient, highly ambiguous or noisy sensory data biases the posterior probability towards the prior distribution (Feldman, 2012). The observer then selects the most

likely interpretation or perception for that sensory stimulus based on posterior probability of each interpretation/perception.

Bayesian models have been used to understand and gain insights into various aspects of feature processing such as color (Brainard & Freeman, 1997; Brainard et al., 2006; Brainard, 2009), motion estimations (Weiss et al., 2002), as well as, the integration of different features within one sensory modality or the integration of multisensory signals from different modalities (Battaglia et al., 2003; Deneve & Pouget, 2004; Sundberg et al., 2006). For example, when localizing the position of a stimulus in space, visual and auditory localization signals may get integrated together in a Bayesian manner (Battaglia et al., 2003; Deneve & Pouget, 2004). The optimal or predicted location of the object is the product of the location estimate based on visual signals and location estimate based on auditory signals (Deneve & Pouget, 2004), however, the predicted location (posterior probability function) is more dominated by the visual information due to our bias towards using visual cues to localize objects, thus the visual signal distribution has a higher prior weighting (Battaglia et al., 2003). Similar Bayesian approaches have also been applied to the integration of visual and proprioceptive cues when reporting hand location (van Beers et al., 1996, 1998, 1999, 2002). Recently, Sundberg et al. (2006) applied a Bayesian approach for the integration of motion and color information within one sensory modality, vision.

As underlying mechanisms are currently unknown, a Bayesian perceptual framework, which in the field refers to incorporating prior information with sensory input to produce the perceptual experience, may be helpful in understanding how the color of a visual signal can differentially influence visual processing, resulting in color dependent modulations of attentional or perceptual processes in the visual system. The color of a visual signal may vary the weights of

the priors such that the prior distribution is weighted more during the calculations of posterior probability. The posterior probability may be shifted based on the differential weightings of the color priors, thus resulting in differential outcomes based on color alone. For example, previous work has demonstrated a bias for red such that red facilitates stopping (Blizzard et al., 2017; Ghasemian et al., 2021). This modulatory effect of red is possibly due to stronger priors for red stop signals due to our experience with red, given that in our modern world, red is commonly used to signal stopping (traffic signs, red traffic light etc.). Therefore, different weighting of priors based on the color of the signal may provide a basis for color-dependent modulations reported in the literature. This Bayesian framework can be used as a foundation for color-dependent modulations reported in the literature.

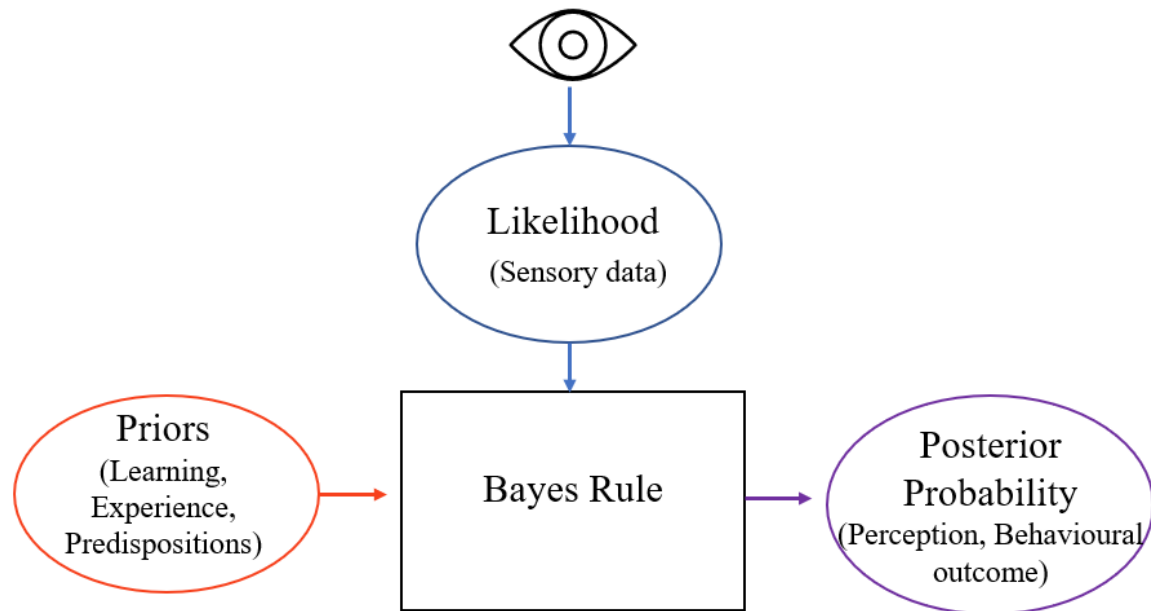


Figure 2. Schematic depicting a basic Bayesian framework for perception. Within a Bayesian framework, sensory input from the retina (likelihood) is integrated with previous learned or innate predispositions about objects and object properties (priors) to create accurate perceptions of the world, as the sensory input can be ambiguous, noisy or incomplete.

2.4 COMPARATIVE COLOR PREFERENCES ACROSS SPECIES

In addition to humans, many other animals also see the world in color. The mechanisms behind vertebrate color vision are diverse, allowing for animals to adapt to their respective environments. Despite the differences, all color systems require a minimum of two different types of cones/cone pigments and a neural circuit to compare their relative activations which allows for wavelength discriminability. In general, the more types of cones with slightly different spectral sensitivities, the better the color discrimination capabilities. Comparative genetics have revealed that cone photopigments in modern vertebrates evolved from the ancestral jawless fish some 500 million years ago (Bowmaker, 2008), where four cone types; long-wavelength (red,

490-570 nm), middle-wavelength (green, 480-535 nm), short-wavelength (blue-violet, 410-490 nm), and UV-selective (355-440 nm); evolved from a single photopigment through a series of gene duplications (Bowmaker, 2008). Modern vertebrates have retained these cone families, with some lineages losing cone classes, while others have gained cone classes to better suit the demands of their environments.

From an ecological perspective, color discrimination is advantageous for many tasks such as detecting prey or predators, mate selection, and foraging, therefore, animal species may also have color preferences or innate color biases similar to humans. The subsequent sections provide an overview of evidence for such color preferences in three different lineages; non-human primates, birds, and fish.

2.4.1 Non-human primates

The mammalian lineage lost UV-selective and middle-wavelength cone classes and became dichromatic (Wakefield et al., 2008), and therefore most mammals today are dichromatic with only two functional cone classes: short-wavelength selective (blue) and long-wavelength selective (red). However, primate ancestors re-evolved a third cone pigment to gain trichromatic vision (Hunt et al., 1998). Old world monkeys (and humans) developed trichromacy through a duplication of the ancestral X-linked long-wavelength opsin gene (LWS). The LWS opsin gene duplicated and diverged into two spectrally distinct photopigments, creating L (red-sensitive) and M (green-sensitive) photopigments, in addition to the evolutionarily conserved short-wavelength selective opsin gene (blue) located on autosomal chromosome 7 (Carvalho et al., 2017).

Therefore, in old world primates, trichromacy was achieved through each cone expressing one of three distinct opsin genes (S, M, L). L and M opsin genes are located on the X-chromosome in a tandem array, sharing 98% sequence homology (Carvalho et al., 2017), differing only at three

key amino acid sites (Neitz et al., 1991), which underlies the shift in spectral sensitivity of the two photopigments. This homology increases the likelihood of recombination errors at the L and M gene locus during meiosis, resulting in red-green color deficiencies, especially in males as males only have one copy of the X chromosome (Carvalho et al., 2017).

In contrast, the molecular mechanisms underlying trichromacy in new world monkeys (Americas) are slightly different as the two ancestral groups evolved separately from one another after the landmass split 65 MYA. In new world monkeys, the LWS gene is polymorphic with different alleles of the gene having slightly different spectral sensitivities (Carvalho et al., 2017). As a result, male monkeys are dichromatic as only one type of LWS allele is expressed per X chromosome. Females, heterozygous at the LWS locus, are trichromatic as they express two different alleles of the LWS gene, in addition to the short-wavelength opsin gene.

The evolutionary drives which underlie this re-evolution of trichromacy in primates are debated. Some researchers have argued that primates developed trichromacy for communication using skin colorations (Changizi et al., 2006). Hiramastus et al. (2017) provided empirical support for this hypothesis, showing that trichromatic color vision is useful for detecting changes in skin coloration compared to dichromatic vision, thus aiding communication among primates. Several studies have shown that red facial coloration is used for intrasexual dominance and status signalling in many different non-human primate species (Gerald, 2001; Bergman et al., 2009; Marty et al., 2009; Grueter et al., 2015; Petersdorf et al., 2017). Furthermore, there is evidence to suggest that skin coloration may also be used in intersexual signalling. For example, Dubuc et al. (2014) reported that red facial coloration in males is attractive to female macaques (*Macaca mulatta*), such that more proprioceptive behaviours were exhibited towards redder male monkeys and by a greater number of females. Despite the behavioural evidence, phylogenetic studies

(Fernandez & Morris, 2007) suggest that red-green color vision evolved before the use of skin color signalling in primates. Therefore, color signalling/communication may not have driven the emergence of trichromacy, instead, color vision and the improved ability to discriminate between long-wavelengths of light may have acted as a prerequisite for red color signalling. In light of this emerging evidence, improved foraging has been proposed as an alternative to the color signalling theory. The development of improved red-green discrimination may have evolved to help primates forage, to better differentiate between red fruits against green foliage (SurrIDGE et al., 2003; Gerl & Morris, 2008). Skalnikova et al. (2020) demonstrated evidence for this foraging hypothesis by investigating color preferences in macaques. Their results show that monkeys had stronger preference for red colored food items compared to other colored foods, but no such preference for red non-food items. Moreover, in the context of food, red coloration usually indicates fruit ripeness, therefore this bias for red food items may also be explained through context dependent learning and association. More recently, Ghasemian et al. (2021) provided evidence for an innate color-stopping bias in monkeys, where red stop signals were shown to facilitate stopping faster than other colors, similar to the red response inhibition bias observed in humans (Blizzard et al., 2017). However, the test subjects (monkeys) had no previous experience with red as a stop signal (i.e stop signs, traffic lights etc), therefore these results suggest that non-human primates developed color associations through innate, evolutionarily conserved color preferences, which is not surprising given the similarities between human and non-human primate color vision and color processing.

2.4.2 Birds

Similarly, many species of birds have been known to use color for food preferences and mate selection. Most birds are dimorphic, where the males have bright coloration on their feathers and

plumage, whereas the females are generally lighter in color. Given these differences, male plumage has been hypothesized to play a key role in mate selection by female birds (Hill, 2006). For example, a field study (Siefferman & Hill, 2003) revealed that male eastern bluebirds (*Sialia sialis*) with brighter UV-blue plumage paired earlier in the mating season and produced more offspring, suggesting that plumage coloration is correlated with reproductive success. This relationship has also been observed in red-capped robins (*Petroica goodenovii*) where male robins with red plumage have highest number of offspring in a season (Dowling & Mulder, 2006), as well as house finch (Hill, 1990), cardinals (Wolfenbarger, 1999) and widowbirds (Pryke et al., 2001). Some researchers have suggested that plumage coloration is an indicator of mate health and quality (Doucet, 2002), therefore acts as an intraspecific signal to females, who associate brighter coloration with better mate health. Red, yellow and orange plumage colorations are produced by carotenoid pigments which are supplemented through diet and cannot be synthesised in the body (Olson & Owens, 1998). Given the role of carotenoids in immune and antioxidant responses (Bendich, 1993; Paiva & Russell, 1999), only healthy males with good nutrition should be able to divert such an important resource to plumage coloration, therefore acting as a reliable health signal.

In addition to mate selection, birds have also been shown to use color for food preferences. Rothery et al. (2017) reported a higher preference for silver and green seed feeders in several species of garden birds, measured by the number of bird visits. More interestingly, when birds are presented with the same food differing in color, a strong preference for red colored foods have been observed in three North American bird species (Willson et al., 1990), as well as New Zealand robins (Hartley et al., 1999), perhaps due to the association of red with ripe fruits. Stronger evidence for associative learning in birds comes from an experimental study

investigating flower preference in hummingbirds (Meléndez-Ackerman et al., 1997). Meléndez-Ackerman and colleagues (1997) reported that hummingbirds have a bias for selecting red colored *Ipomopsis* flowers over white. Through their investigations, the authors discovered that the red flowers contain more nectar, explaining hummingbird preferences. In their subsequent experiments, they manipulated the flowers so that nectar reward for red and white flowers was equal, and still observed a preferential bias of hummingbirds for red flowers because of their past experience with red flowers and high nectar reward. However, when the nectar reward was switched such that white flowers contained more nectar, the birds quickly learned the new color association and visited more white flowers. Therefore, suggesting that flower color preference in hummingbirds is associated with nectar reward based on prior learning and experience.

These color preferences in birds are made possible by high acuity color vision. Birds have more advanced color discrimination capabilities due to the presence of four types of cones (UV, S, M, L), (tetrachromatic) (Bowmaker, 2008; Kelber, 2019), whose spectral sensitivities are further fine tuned by colored oil droplets in the inner segments of the photoreceptors (Vorobyev, 2003; Bowmaker, 2008). These oil droplets further filter light to reduce the effective overlap between cone spectral sensitivities therefore improving color discrimination. Some bird species such as raptors also have high acuity, rod-free zones in the retina similar to the human fovea (Mitkus et al., 2017). Although the retinal organization of photoreceptors and their sensitivities are well documented in birds, color processing at the cortical level is not yet well understood.

2.4.3 Fish

Similar to birds, many species of fish have also been known to use carotenoid coloration for sexual signaling and mate selection as carotenoids are costly and diet dependent (Sefc et al., 2014), therefore acting as a reliable signal for mate health in fish as well (Milinski, 2014). Color

preferences have been well studied in teleost fish such as cichlids, where female cichlids have been shown to prefer red-yellow colored males (Kodric-Brown, 1985; Maan et al., 2004) with females spending more time and mating more often with the red-yellow males compared to other males (Bourne et al., 2003). In a freshwater teleost fish, *Puntius titteya*, both males and females have been shown to use red-yellow carotenoid colorations for mate selection (Mieno & Karino, 2009), where females with redder carotenoid coloration spawned larger eggs, suggesting that males may also use carotenoid coloration of females to assess mate health. Other studies have suggested that red-yellow colorations in males is also used for intrasexual dominance signaling in male-male competitions (Evans & Norris, 1996; Dijkstra et al., 2005; Ogita & Karino, 2019), in addition to intersexual signaling, as observed in other animal species. Generally, most fish species are tetrachromatic, with four types of cone classes, however, within the teleost family, gene duplication events and subsequent divergence of opsin genes have expanded the number of cones classes especially in the long-wavelength range (Bowmaker & Loew, 2008), providing a physiological link for red-yellow sexual selection, as the divergence of the long-wavelength detecting opsin genes confers improved color discrimination in the red-orange range (Watson et al., 2011).

More recently, innate color biases have been reported for another species of fish, zebrafish (*Danio rerio*), possessing tetrachromatic color vision (UV, S, M, L) (Nawrocki et al., 1985), similar to many other fish species. Park et al. (2016) placed zebrafish larvae in acrylic mazes with different colored sections, and measured the location of the free swimming larvae every two minutes for 30 minute periods. Their results revealed a hierarchy of color preference, with zebrafish larvae preferring blue regions over red, red over green and green over yellow (B > R > G > Y). This pattern of results was corroborated by a second study (Peeters et al., 2016), where

both zebrafish adults and larvae preferred blue and avoided yellow, with red and green falling in between. Furthermore, the avoidance for yellow was mitigated with the administration of anti-anxiety drugs suggesting that yellow may evoke fear or anxiety in zebrafish, however the exact reasoning behind this blue-approach and yellow-avoidance preference is currently not well understood.

In summary, color preferences, biases and associations have been observed in many other vertebrate species, reflecting the importance of color cues in ecological contexts. These observations further suggest that the differential processing of color signals is not unique to humans. And finally, given differences in ecological pressures, retinal and visual system circuitry, the neural mechanisms behind such color processing may be different across species.

CHAPTER 3

MOTION INDUCED POSITION SHIFTS

3.1 THE FLASH-LAG EFFECT

Motion-induced position shifts, first reported by Ramachandran & Anstis (1990), are perceptual illusion of motion wherein the movement of an object influences its perceived location. The flash-lag effect is one such well known example. A static object is momentarily “flashed” in physical alignment with a moving target (i.e. rectangular bar). Although, both the moving and stationary targets are in veridical alignment, observers perceive the moving target ahead of the stationary object at the time of flash onset (Figure 3A). In other words, the flashed object appears to “lag” behind the moving target.

The flash-lag effect was first reported by Wolfgang Metzger (1932), but it was Romi Nijhawan (1994) who sparked widespread scientific interest in this motion illusion. After Nijhawan’s rediscovery, literature devoted to understanding the mechanisms and variables that affect the flash-lag illusion increased exponentially. A large number of studies have investigated the effects of different observer and stimulus variables on the perception of the flash-lag illusion (for a review, see Hubbard, 2014). For example, Nijhawan (2001) reported that the illusion is eliminated if the observers track the moving target, thus fixation is necessary for the illusion to occur. Moreover, various stimulus properties such as distance (Vreven & Verghese, 2005), speed (Nijhawan, 1994; Krekelberg & Lappe, 1999; Wojtach et al., 2008) and presentation timing (Eagleman & Sejnowski, 2000; Watanabe, 2004) have also been reported to influence the magnitude of the perceived lag. For example, as the speed of the moving target increases, the magnitude of the illusory shift also increases (Nijhawan, 1994; Krekelberg & Lappe, 1999;

Wojtach et al., 2008). The timing of the stationary flash relative to the moving target is another well investigated variable. When the onset of the flashed object terminates the motion of the moving target, such that the flashed object and the moving target disappear simultaneously, this presentation is called flash-terminated. When the flashed element appears at a point during the moving object's trajectory, such that it does not align with the moving target's onset or offset, this condition is called flash-continuing (depicted in Figure 3A). Eagleman & Sejnowski (2000) reported that the flash-lag effect is abolished or reduced in the flash-terminated condition, but persists in the continuing condition. This important finding has been corroborated with many versions of the flash-lag effect (Moore & Enns, 2004; Watanabe, 2004; Kessler et al., 2010).

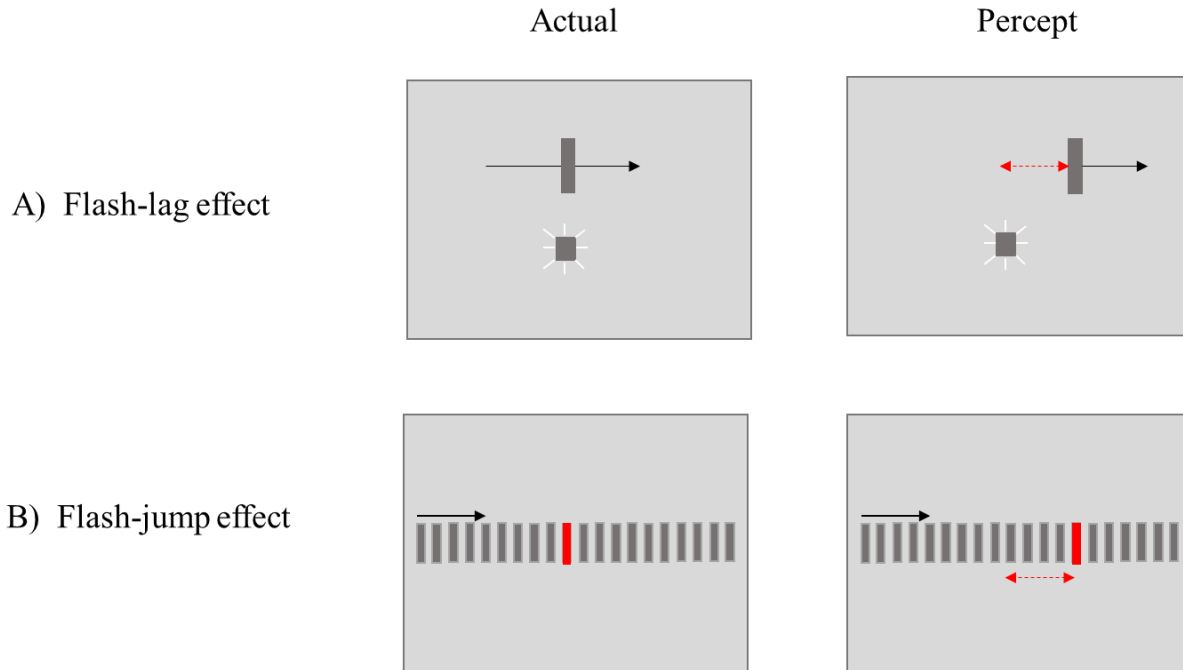


Figure 3. Illustration of the (A) flash-lag and (B) flash-jump effects. The discrepancy between the actual presentation of stimuli versus perception is depicted. The black arrows represent the direction of motion and trajectory of the moving target. The red arrows depict the magnitude of the illusory shift or mislocalization (exaggerated for the purpose of illustration). **A)**

The flash-lag effect occurs when a stationary target (i.e. grey square) is briefly presented in physical alignment with a moving target (i.e grey bar), resulting in a forward illusory shift in the perception of the moving target's location when the flash occurred (note the flash itself is not mislocalized). **B)** The flash-jump effect occurs when a moving target (i.e grey bar) changes color at a single position along its trajectory, and the color change is misperceived to occur further along the bar's trajectory at a later occurring bar position.

3.2 THE FLASH-JUMP EFFECT

The flash-jump effect, sometimes called feature-flash, is another phenomenon related to motion-induced position shifts. When a moving target (i.e. rectangular bar) changes color at a single

position along its trajectory of motion, the color flash is perceived to occur farther along the target's trajectory (Cai & Schlag, 2001a, 2002) (Figure 3B). In other words, the color change appears to “jump” forward in the direction of motion. The presentation timing of the flashed element can be manipulated to give rise to the flash-terminated or flash-continuing conditions, similar to flash-lag. In the flash-terminated sequence, the onset of the color flash results in the termination of the motion sequence of the bar such that both the color change and the bar disappear simultaneously. Therefore, the flashed bar is the last bar in the apparent motion sequence. In the flash-continuing condition (depicted in Figure 3B), the color change appears at one location during the bar's motion sequence, then the bar reverts back to its original color and continues along its trajectory. Behavioural data indicates that observers report less of a mislocalization or diminished illusory shift (therefore, more veridical location estimates of the flash) in the flash-terminated condition (Cai & Schlag, 2001a & b; Sundberg et al., 2006), similar to studies on the flash-lag effect.

This mislocalization has been proposed to be a result of feature integration (Cai & Schlag, 2001b; Sundberg et al., 2006). Given that this illusion involves features within one object (i.e. motion and color), the location of the color flash is estimated through the integration of color and motion signals, which are processed in different visual pathways. Cai and Schlag (2001b) proposed that the motion and color systems operate at different rates; therefore, information relevant to these features is processed at different times, resulting in asynchronous feature binding. As the color change of the flashed element is processed later (Moutoussis & Zeki, 1997a & b; Viviani & Aymoz, 2001) it is integrated to a later occurring bar position in the motion sequence, ultimately giving rise to the flash jump effect. In the flash-terminated condition, the absence of motion cues after the flash allows for a more veridical prediction of

flash location as there are no subsequent bars to misbind color to. Sundberg and colleagues (2006) replicated the findings of Cai & Schlag (2001a) in human observers and monkeys. In recording the response of color selective V4 neurons in monkeys, Sundberg et al. (2006) report neural correlates of this flash-jump illusion in area V4, as the receptive fields of color selective V4 neurons shifted forward along the direction of motion for both the flash-terminated and flash-continuing conditions. Although a physiological retinotopic shift in V4 activity was observed for both conditions, behavioural human data indicated the absence of a perceptual shift, thus, more veridical estimation of flash location in the flash-terminated compared to flash-continuing condition. The authors propose a Bayesian framework to explain this perceptual discrepancy between the two conditions. The authors suggest that the mis-localized representation of the flash, observed as retinotopic shifts in V4 neurons (red curve, Fig. 4), is integrated with a representation of all the possible bar locations (dotted curve, Fig. 4) through a later stage Bayesian process likely occurring in a color-insensitive area. This Bayesian process determines the location of the shifted flash (from V4 responses) relative to the presented bar locations (from a color-insensitive area). In the continuing condition, all bar locations were presented, therefore, the resultant joint probability function (black curve, Fig. 4) is shifted forward, resulting in our perception of a large flash “jump”. However, in the terminating condition, bars after the flash are not presented as the motion sequence terminates, therefore the color-insensitive area represents bar locations before the flash only. When the shifted flash representation from area V4 is integrated with this representation of terminated bar locations, the resultant joint probability estimate is constrained to the veridical location, resulting in the absence of a perceptual shift, thus explaining the perceptual discrepancy between the two motion conditions, although mis-localized V4 responses were observed for both.

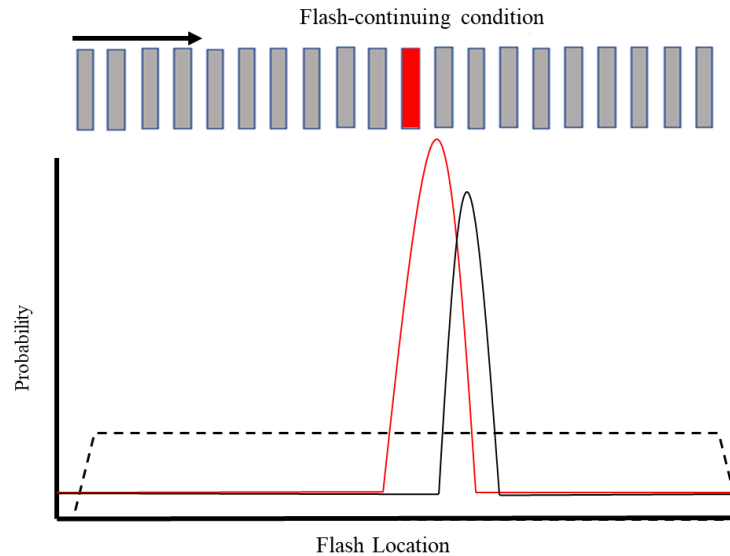


Figure 4. Schematic of Bayesian framework proposed to underlie the flash-jump illusion.

The red curve depicts the estimate of flash location at the onset of the flash in area V4. Note that this estimate is shifted forward due to the mis localized responses of color selective V4 neurons, as reported by Sundberg et al. (2006). A second non-color selective area such as area MT, represents the distribution for the motion of the bar at all presented bar locations (dotted curve). It has been previously proposed that the shifted V4 responses (red curve) are integrated with the representation of presented bar positions (dotted curve), giving a joint probability estimate of the color flash relative to all bar locations (black curve), which corresponds to our perception of an illusory shift in the continuing condition, and the absence of an illusory shift in the terminating condition. Note that this illustration depicts the flash-continuing condition with the bar moving in the rightward direction. Adapted from “A motion-dependent distortion of retinotopy in area V4,”

by Sundberg, K.A., Fallah, M., & Reynolds, J.H, 2006, *Neuron* 49 (3), 447–457. © 2006

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3.3 PROMINENT THEORIES

Over the years, various alternatives have been proposed to explain motion induced position shifts, most of which have been based on studies investigating the flash-lag effect. Despite years of debate, a complete, all encompassing theory is absent from the literature, as many of major hypotheses fail to adequately explain all conditions or variables. A list of prominent theories is summarized in Table 1.

In rediscovering the flash-lag effect, Nijhawan (1994) revealed an important real-world implication of motion based mislocalization errors. When we observe a moving object such as a ball, it takes several milliseconds for the retinal information to reach the visual cortex (axonal delay). Furthermore, it takes additional time for processing and the subsequent generation of a motor output to catch the ball (processing delay). By the time the visual information about the position of the ball is transmitted and processed, the ball would have changed locations, resulting in a catching error. Without any compensatory mechanisms in place, this would result in mislocalization of moving objects in the real-world. To compensate for such delays, Nijhawan (1994) proposed that the visual system extrapolates the position of the moving object forward based on its previous course. In relation to the flash-lag effect, this extrapolation creates the percept of the moving bar as farther ahead. Since the flashed object has no previous course or motion history, its position is not extrapolated, leading to our perception of the flash-lag effect. The motion extrapolation account fails to explain the observed presence of a lag during random changes in direction (Whitney & Murakami, 1998; Eagleman & Sejnowski, 2000), because unpredictable or random changes in the direction of the moving target cannot be extrapolated accurately. In addition to random directional changes, Nijhawan's hypothesis also fails to explain the absence of flash-lag effect in the terminated conditions. The motion of the moving target

terminates with the onset of the flash, however, due to neural delays in processing, this termination is processed after a short delay, meanwhile the compensatory extrapolation mechanisms overshoot the location of the moving target forward, beyond the termination point, predicting a perceptual illusory shift even in the terminated condition, which is inconsistent with empirical data (Eagleman & Sejnowski, 2000; Moore & Enns, 2004; Watanabe, 2004; Kessler et al., 2010).

Whitney and Murakami (1998) proposed another alternative explanation, called the differential latency hypothesis which posits that latency differences between moving and stationary objects underlie the flash-lag effect. This theory suggests that moving objects are processed faster, with shorter neural delays, than static objects (Cai and Schlag, 2001b; Jancke et al., 2004; Subramaniyan et al., 2018), therefore, at the time of the flash, the flashed object is processed slower compared to the moving object. And by the time the flashed object is perceived, the moving bar is perceived to be farther along its trajectory. The differential latency theory also isn't without its inconsistencies. For example, some studies have reported no such latency difference between moving and static objects (Chappell et al., 2006; Fouriezos et al., 2007), furthermore, some researchers have argued that flashed objects are actually processed faster than moving objects (Nijhawan et al., 2004). The differential latency account also fails to explain the presence of the illusory shift in flash-initiated conditions, where the time of onset for the flashed and moving targets is the same, thus they come into view at the same time. At the time of the flash, $t=0$, when both the moving and static targets are presented together at the beginning of the motion sequence, it is unlikely that the visual system is able to distinguish which of the two stimuli is the moving target vs. the static object, and subsequently process the moving target faster, leading to a illusory position shift.

The post-diction or motion-biasing hypothesis, proposed by Eagleman & Sejnowski (2000, 2007) postulates that position information of a moving target continues to be collected for a brief period after the flash, and the triggering event (i.e. the flash) resets the integration of target positions. In other words, at flash onset, the position of the moving target is computed based on motion signals that continue to arrive over the next ~80 ms following the flash. Therefore, the prediction of target location at an instance (i.e. onset of flash) is biased forward by motion information that is collected after the flash, resulting in the flash-lag effect. Recently, Eagleman & Sejnowski (2007) extended the post-diction theory to provide a unified explanation of other motion-induced position shifts such as flash-jump. They demonstrated that Cai & Schlag's (2001b) asynchronous feature binding theory cannot account for the flash-jump effect, as observers mislocalized the color change of a moving bar to a later position which was not physically presented in the motion sequence (i.e. a position somewhere between two actual bar positions). Thus, mis-binding of the color change to a later occurring bar position, misaligned in time, was ruled out. Instead, they suggest that the instantaneous position judgement of the color change is shifted forward by motion signals that follow the triggering event (i.e. color change), offering a spatial rather than a temporal mechanism. Critics of the post-diction hypothesis have argued that if the triggering event (i.e. flash) resets the integration of target position, then the presentation of a flashed object every 80 ms along the motion sequence of a moving target should result in the moving object not being perceived at all since its location estimate is reset each time (Whitney & Cavanagh, 2000). Furthermore, given that the post-diction hypothesis is contingent on events after the flash, pre-flash cues or information should not affect the position estimate, however this is not the case (Baldo et al., 2002; Chappell & Hine, 2004).

More recently, the discrete sampling hypothesis, by Schneider (2018), suggests that visual input is sampled into discrete moments or time intervals, each with a time duration, D . The position of a given object is recorded as its last known position at the end of each sampling interval, comparable to still images taken in rapid succession. A moving object's last known position corresponds to its most recent, updated position within the moment. Therefore, if a static object is flashed at the beginning of the sampling interval, there is a large time gap between the registered position of the moving vs. static stimuli, leading to a large flash-lag effect. If the static flash is presented towards the end of the sampling window, the registered position of the flash aligns with the position of the moving target thus, no perceptual shift is observed. Schneider (2018) argued that the flash-jump effect is also a consequence of discrete sampling. Within one sampling interval, the color change of the moving object is registered at a single point in time, however, the position of the moving object is recorded as its final position within that interval, leading to a displacement of the color change by $D/2$ from its onset time. Although discrete or periodic sampling has been implicated in some aspects of visual perception (Chakravarthi & Vanrullen, 2012; Chota & Vanrullen, 2019), future studies of flash-lag or flash-jump, which directly test Schneider's predictions are needed in order to evaluate the empirical validity of this new model.

Table 1. Prominent theories of the flash-lag effect.

Theory	Summary	Exemplary Evidence
Motion Extrapolation	Perceived location of moving target is extrapolated forward	Nijhawan, 1994; Maus & Nijhawan, 2008; Nijhawan, 2008
Differential Latency	Moving target processed faster compared to static target, the moving target is perceived farther along	Whitney & Murakami, 1998; Whitney et al., 2000; Ögmen et al., 2004
Post-diction	Instantaneous position of a moving target is biased by motion information collected after the triggering event	Eagleman & Sejnowski, 2000, 2007
Discrete Sampling	Visual information is sampled periodically, therefore flash-lag is the result of a discrepancy between the real vs. sampled position of the stimuli	Schneider, 2018

CHAPTER 4

OBJECTIVES AND HYPOTHESES

Previously, color has been shown to influence higher level visual processing (Lindsey et al., 2010; Tchernikov & Fallah, 2010; Fortier-Gauthier et al., 2013; Pomerleau et al., 2014; Blizzard et al., 2017; Ghasemian et al., 2021), suggesting that color can intrinsically modulate attentional and cognitive processes and drive differences in later stage decision making processes. For example, previous investigations have provided evidence for color dependent modulation of executive functions in the prefrontal cortex such as response inhibition, where red stop signals were shown to facilitate stopping more than green (Blizzard et al., 2017), likely due to our associations of red with stopping. Similarly, the processing of information in the parietal cortex has also been shown to be modulated by color information. Studies investigating the influence of color on oculomotor processes have reported hierarchical color differences in pursuit target selection, and saccade execution (Tchernikov & Fallah, 2010; Kehoe et al., 2018). However, color differences in the ventral visual pathway have not been investigated. Although there is strong evidence for color modulation of higher stages of the visual processing hierarchy (i.e. prefrontal and parietal processes), whether or not these color differences can be found earlier in the visual system is currently unknown. As higher-level visual functions require complete objects representations, it is unclear whether color influences the processing of information after objects are fully represented in the visual system, (as the prefrontal and parietal color studies may suggest) or it can influence visual processing before an object is represented fully. For example, if color can modulate the processing of visual information before complete representations of objects are formed, this would suggest that these color effects are ubiquitous from the earliest stages of the visual processing hierarchy and feedforward into higher level

processing, thus modulating later stage visual functions as reported previously. The overarching goal of this current thesis is to investigate the effects of color on low-level visual processes, i.e. whether or not color can influence low level perception before objects are fully represented in the visual system.

To test this, we explored feature integration, a low-level visual process wherein various object features are first processed independently of one another and then integrated together to create the perception of an object as a whole (Treisman & Gelade, 1980). Specifically, we investigated the integration of color and motion signals using the flash-jump paradigm, a visual illusion composed of both color and motion features (Chapter 5). We hypothesized that the color of the flash would differentially affect the magnitude of the illusory shift observed in the flash-jump illusion, indicating that the integration of color and motion information, at the earliest stages of visual processing is modulated by color. Furthermore, the pattern of findings would distinguish which of the three proposed neural mechanisms drives color-dependent modulation of feature integration, and low-level visual processes in general. For example, color opponency suggests processing differences within each opponent pair, such that red and green signals are processed differentially, as well as blue and yellow signals, thus we would expect to see significant differences in illusory mislocalizations between red and green flashes, as well as blue and yellow flashes. The attentional hierarchy (Tchernikov & Fallah, 2010), in contrast, predicts a hierarchical pattern of mislocalizations, where the illusory shift for every flash color is significantly different from one another. Lastly, visual or learned associations predict a significant difference between red and green flashes. As red and green colors are commonly associated with stop or go-signals, they may effectively advantage or disadvantage the observer's

prediction of the flash location. In sum, all three mechanisms predict different patterns of color effects, allowing for an effective way to empirically distinguish between them. .

Given that many aspects of visual perception follow a Bayesian framework, we also sought to determine how color processing integrates into a Bayesian framework, ultimately giving rise to color dependent modulations of visual processing (Fig. 5). Bayesian models of perception have previously suggested that visual information from the retina is incorporated with our prior knowledge or predispositions about objects and object properties to create our perception of the world. From this Bayesian perspective, we proposed that differential behavioural outcomes based on color (color dependent modulations) are likely a result of different prior weightings given to each color, which are automatically incorporated into the computations for a given cognitive or perceptual task, producing different behavioural outcomes. In consideration of the flash jump effect, specifically, we hypothesized that colors associated with stronger attentional capture, i.e., red (Tchernikov & Fallah, 2010; Fortier-Gauthier et al., 2013), would have stronger weights. The resultant estimation for flash location would be biased towards the veridical location of the flash, resulting in a decrease in the mislocalization error of the flash. We proposed an extension of Sundberg et al.'s (2006) Bayesian model to describe how differential weighting of color priors may explain the color-dependent modulation of the flash-jump effect, and feature integration in general (Chapter 5).

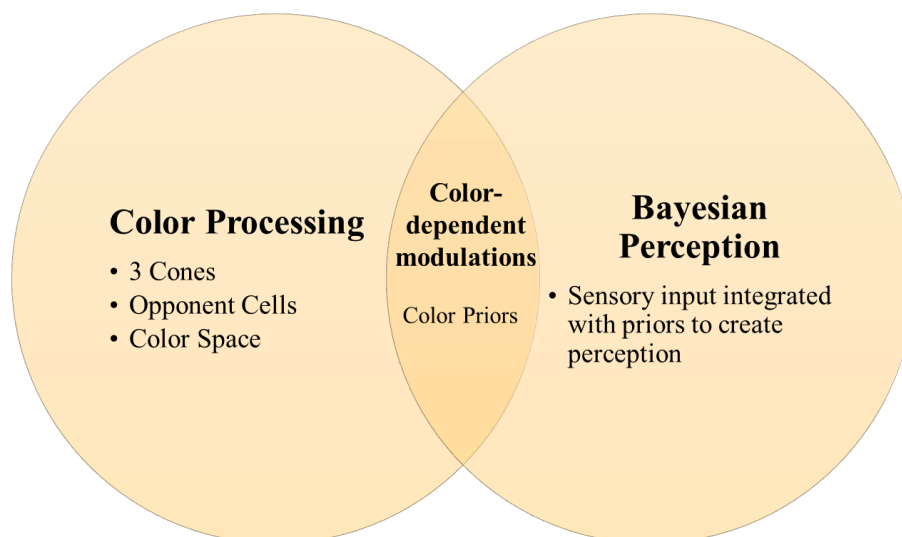


Figure 5. Venn diagram illustrating the overlap between color processing in the visual system and Bayesian perception. The inherent processing of color within the visual system can produce modulatory effects on perception as a result of color dependent modulations through differentially weighted color priors. Priors, based on innate or learned color differences get integrated into visual processing and modify a given perceptual or cognitive process.

The results from our first study (Chapter 5) implicated color opponent mechanisms in the modulation of visual processes at the low-level stage and given the hierarchical nature of the visual processing pathway, this would suggest that color processing mechanisms also build on one another, with color opponency influencing the earliest stages of color processing in the visual cortex (see Fig. 6 for overview). Color opponent cells in LGN compute the relative activations of cone photoreceptors to compare red versus green and blue vs yellow signals. This opponent information would then feed into a color space representation in V4, which in turn leads to the formation of color associations in the prefrontal cortex. Therefore, these three mechanisms can modulate different stages of the visual processing hierarchy in a feedforward manner. However, current studies on color dependent modulations have not applied this

feedforward approach to explain how and where color differences arise in the visual system. In our second paper (Chapter 6), we attempted to place all reported color effects in the attention and perception literature into this feedforward color modulation model based on the predictions made by each color processing mechanism. To our knowledge, this is the first attempt to organize and evaluate the empirical validity of the proposed mechanisms. Based on the functional and structural organization of the visual system, we proposed putative brain areas and underlying neural circuitry that may provide a physiological basis for each mechanism. Furthermore, we developed a theory on how each color mechanism may get incorporated into a Bayesian framework of perception to modulate various processes in the visual system (Chapter 6).

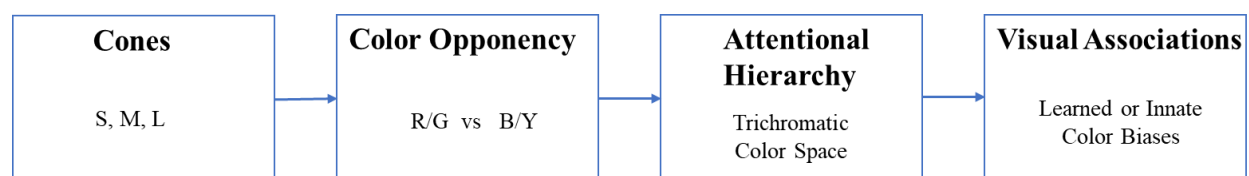


Figure 6. Schematic depicting the interplay between the three -color processing mechanisms. Color information from the three cone types is computed into relative activations of red versus green, and blue versus yellow, giving rise to the two color-opponent channels. Color opponent information is transformed into a color space representation, giving rise to the attentional hierarchy, which is used to build visual color associations.

In summary, the purpose of the current research was to answer the following questions: Are low level visual processes also modulated by color? If so, by which mechanism? From a Bayesian perspective, how do visual processes get modulated by color? And lastly, how do these color processing mechanisms underlie or contribute to color dependent modulation of the visual system more generally?

CHAPTER 5

COLOR MODULATES FEATURE INTEGRATION

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This manuscript has been published in **Frontiers in Psychology**. HS wrote the manuscript, collected, and analyzed the data. HJ designed the experiment and data analysis, programmed the experiment, and revised the manuscript. MF designed the experiment and data analysis and revised the manuscript.

Saini, H., Jordan, H., & Fallah, M. (2021). Color modulates feature integration. *Front Psychol*, 12:680558. <https://doi.org/10.3389/fpsyg.2021.680558>

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5.1 ABSTRACT

Bayesian models of object recognition propose the resolution of ambiguity through probabilistic integration of prior experience with available sensory information. Color, even when task-irrelevant, has been shown to modulate high-level cognitive control tasks. However, it remains unclear how color modulations affect lower-level perceptual processing. We investigated whether color affects feature integration using the flash-jump illusion. This illusion occurs when an apparent motion stimulus, a rectangular bar appearing at different locations along a motion trajectory, changes color at a single position. Observers misperceive this color change as occurring farther along the trajectory of motion. This mislocalization error is proposed to be produced by a Bayesian perceptual framework dependent on responses in area V4. Our results demonstrated that the color of the flash modulated the magnitude of the flash-jump illusion such that participants reported less of a shift, i.e. a more veridical flash location, for both red and blue flashes, as compared to green and yellow. Our findings extend color-dependent modulation effects found in higher-order executive functions into lower-level Bayesian perceptual processes. Our results also support the theory that feature integration is a Bayesian process. In this framework, color modulations play an inherent and automatic role as different colors have different weights in Bayesian perceptual processing.

KEYWORDS

attention, Bayesian perception, visual perception, feature integration, flash-jump effect

5.2 CONTRIBUTION TO FIELD STATEMENT

Studies have reported that color modulates higher-level cognitive processing, e.g. we respond to red stop signals faster than non-red stop signals. We investigated how ubiquitous color effects could be by reaching back down to the level of feature integration, examining whether the color of an object influenced its binding of non-color features.

Observers commonly mislocalize a feature change at a single position of an apparent motion stimulus, reporting that it occurred further along the motion path (flash-jump illusion). We found that the color (red, green, blue, yellow) influenced both the magnitude of the illusion and the precision of its spatial representation. This is the first report of between-color differences in their integration with another feature (i.e. motion), and that these automatic color modulations occur in an early stage of object processing, long before higher order executive functions.

We propose a Bayesian perceptual framework as the underlying mechanism for color and motion integration, providing a new approach to the understanding of color influences on perceptual representations and attentional processes. This has implications for computational and cognitive models of feature integration and selection of objects, and the role of colour in interface design, accessibility, and neuromarketing.

5.3 INTRODUCTION

Our ability to recognize and interact with objects relies heavily on visual perception. However, images of real-world stimuli can be highly complex and ambiguous. Despite ambiguous, incomplete or noisy input, the human visual system is able to perceive objects and object properties with great accuracy. Helmholtz (1867) theorized that the visual system makes unconscious deductions or “inferences” about object and scene properties to resolve this ambiguity, resulting in accurate perception. In recent decades, Helmholtz’s theory of unconscious inference has been formalized into models of Bayesian perception. Bayesian models of visual perception suggest that the resolution of ambiguity occurs through probabilistic integration of prior experience or knowledge (priors) with available sensory information (likelihood), giving rise to a probability distribution of the object property in question. With noisier sensory input, there is increased reliance on prior knowledge (Kersten et al., 2004).

Color is an important source of information in a wide variety of daily tasks ranging from object perception to response control. The specific color of an object aids in object recognition, such as the color of an apple distinguishing between varieties. When driving, a red traffic light alerts the driver to stop the vehicle. However, recent studies have shown task-irrelevant color can also intrinsically modulate cognitive functions such as attentional selection (Tchernikov & Fallah, 2010), visual search (Lindsey et al. 2010), and response inhibition; (Blizzard et al., 2017).

Tchernikov and Fallah (2010) demonstrated that smooth pursuit target selection was dependent on an intrinsic attentional hierarchy of red (strongest), followed by green, then yellow, and blue (weakest) when saccading to two superimposed random-dot kinetograms. In the absence of any task demand to follow a particular color, red was automatically selected and pursued over other colors; green was marginally selected and pursued over yellow and blue, and yellow was

selected and pursued over blue; whereas, blue was not selected over any of the other colors. Similarly, Lindsey et al. (2010) reported that red targets were faster to find in a visual search task compared to other colored targets. Blizzard et al. (2017) reported that response inhibition was facilitated by red more than green stop signals in a stop-signal task (SST). Electrophysiological studies have also provided support for color modulations of executive functions. In a visual search task, red and blue targets evoked earlier N2pc waveforms compared to other colors, suggesting that the deployment of attention may occur faster for red and blue (Fortier-Gauthier et al., 2013; Pomerleau et al., 2014). In addition, Racey et al. (2019) performed an fMRI study which demonstrated that the posterior midline cortex (PMC), which is involved in preferences and value judgements of stimuli (Kable & Glimcher, 2007; Grueschow et al., 2015), was modulated by color features, even if color was irrelevant to the orientation judgment task, which supports different colors having different values or weights. Taken together, these investigations suggest that the color of visual input can intrinsically modulate attentional and cognitive processes, driving differences in later stage decision making processes which ultimately modulate behavioral control. We propose that this color dependent modulation of visual processing can be explained by Bayesian models of perception. In a Bayesian framework, the relative strength of a given color would vary the weight of the priors, biasing the joint probability distribution, and potentially produce different behavioural outcomes based on color.

In the present study, we sought to investigate whether such color-dependent modulations are dependent on Bayesian perceptual processes in the visual processing streams. We focused on feature integration using the flash-jump effect, a visual illusion of color and motion integration first described by Cai and Schlag (2001a). Sundberg et al. (2006) found neural correlates of the flash jump effect in area V4 and propose that a Bayesian framework for motion and flash

integration underlies this illusion. In the flash jump illusion, a moving stimulus such as a rectangular bar changes color at a single position along its trajectory. Observers perceive the flash as occurring farther along the trajectory of motion, than at its veridical position, thus mislocalizing the flash to a later occurring bar in the sequence. This is a mislocalization of feature integration between color and motion information. If the flashed element is the last element in the sequence (terminating condition), the flash location is perceived veridically. Sundberg et al. (2006) recorded the responses of color selective V4 neurons as monkeys viewed the flash jump illusion. In the classic continuing motion condition, the receptive fields of V4 neurons that were selective for the color of the flash shifted along the trajectory of motion, which matched psychophysical data in humans viewing the same stimuli. Interestingly, when the flash terminated the motion sequence, the retinotopic shift in V4 persisted, supporting a mislocalization of the color and motion feature integration. However, humans reporting the flash location in the terminating condition did not mislocalize the flash. Previous studies have used Bayesian frameworks to account different aspects of real and illusory motion processing (Jacobs, 1999; Weiss et al., 2002; Lisi & Cavanagh, 2015, Gershman et al., 2016; Hui et al., 2020; Yang et al., 2021). Building on those studies, Sundberg et al. (2006) suggest that this motion dependent mislocalization in the continuing but not terminating condition is consistent with a Bayesian model of sensory integration (see: Knill, 2007; Vilares & Kording, 2011), supported by the retinotopic mislocalization in area V4 neurons. The position of the color flash in area V4 and the positions of the moving bars in motion areas such as MT are integrated together to give a joint probability estimate of the color flash in relation to the motion sequence. Sundberg et al. (2006) posit that the presence or absence of a shift, observed in the continuing and terminated conditions is a result of this integration, where the representation of the flash (V4 responses) biases the joint

estimation in the continuing condition resulting in large perceptual shifts. However, in the terminating condition, there are no representations for any further bar positions and thus the joint estimation results in a veridical representation of the flash location.

In the present study, we investigated whether varying the isoluminant color (red, green, yellow, or blue) of the flash affected its mislocalization. We hypothesized that in a Bayesian framework, colors associated with stronger attentional capture, i.e., red (Tchernikov & Fallah, 2010; Fortier-Gauthier et al., 2013), would have stronger weights resulting in a decrease in the mislocalization error of the flash. Furthermore, the pattern of color shifts would distinguish which underlying mechanism drives perception: the intrinsic color hierarchy (Tchernikov & Fallah, 2010) which requires color space representation, or ‘pop-out’ visual search color advantages for red and blue (Pomerleau et al., 2014), which are likely dependent on color opponency effects.

5.4 METHODS

5.4.1 Participants

Twenty-four undergraduate students (17 females and 7 males; 18-43 years) completed the study for course credit. The study was approved by the York University Human Participants Research Committee. All participants were naïve to the purpose of the study, had normal or corrected-to-normal acuity and normal color vision (Ishihara, 2006). All participants gave written informed consent prior to participation.

5.4.2 Paradigm

Participants were seated in a dimly lit room with their heads resting on a chin rest 84 cm from an 18” CRT monitor (60 Hz refresh, 1024 x 768). Eye position was tracked using an infrared eye-tracking system (ISCAN, Inc. ETL-400), and experimental control was handled by Presentation

(Neurobehavioral Systems). The background was dark gray (CIE $x = 0.35$, $y = 0.56$; 0.365 cd/m^2) with a light gray fixation cross (0.34° by 0.34° CIE $x = 10.83$, $y = 16.25$; 11.93 cd/m^2) at the center of the display.

The stimulus consisted of an array of 20 bars (3.3° by 0.3°), spaced 0.8° apart, presented 4° below the fixation cross (Fig. 7). Apparent motion sequences were produced by bars sequentially appearing for 2 frames, with 2 frames of blank time in between, moving either leftwards or rightwards. The inducing bars were light gray, matching the fixation cross, (CIE $x = 10.83$, $y = 16.25$; 11.93 cd/m^2). The target, a colored bar selected from one of four photometrically isoluminant colors (12 cd/m^2 ; Red $x = 27.57$, $y = 1.804$; Green $x = 6.007$, $y = 2.516$; Yellow $x = 12.24$, $y = 2.379$; Blue $x = 27.08$, $y = 139.3$) appeared at one of the 11 central positions (Fig. 7A). Consistent with prior studies of color modulations of visual or cognitive processing, photometric isoluminance was necessary to determine the modulatory effects of individual colors as, perceptual isoluminance would have incorporated these effects (as well as others) into the resulting perceptual luminance for each color.

In the terminating condition, once the colored bar appeared, the motion sequence was terminated such that this flashed element was the last bar presented (Fig. 7B). In the continuing condition, the bar appeared at all 20 positions (Fig. 7B). If the participant broke fixation during stimulus presentation, the trial was terminated with an auditory warning and shuffled back into the same block.

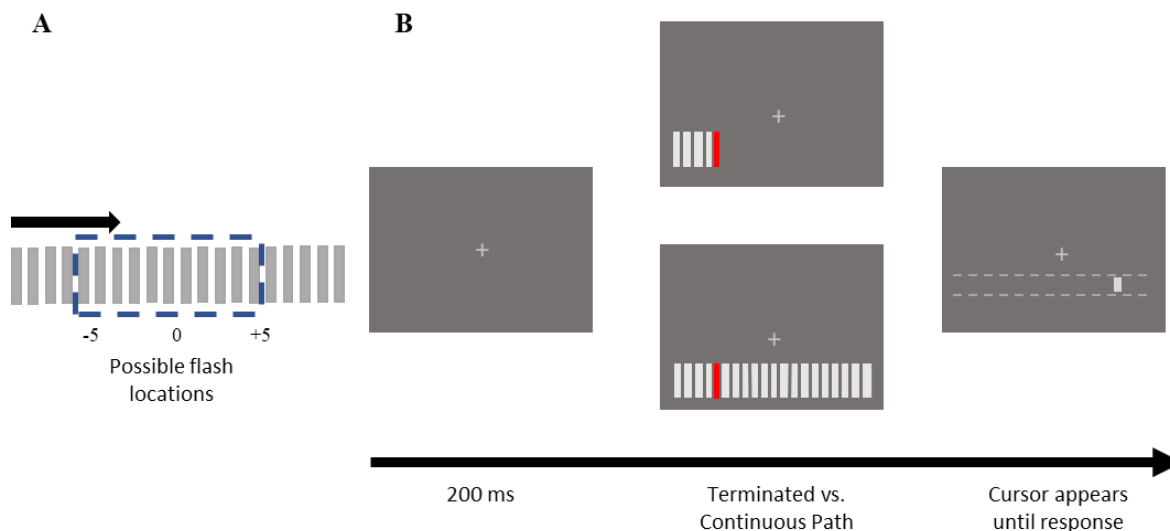


Figure 7. Stimulus schematic and sample trial presentation. (A) An apparent motion sequence comprised of 20 grey, rectangular bars, moved either in a leftward (not depicted) or rightward direction. One of the central 11 positions was presented in one of 4 isoluminant colors (red, green, yellow, and blue). (B) Experimental protocol of trials depicting sample terminating vs. continuing motion path trials. For each motion path (terminating or continuing), each of the 11 central bar positions were tested, using both directions, and all 4 colors. Participants reported the colored flash location by clicking with a mouse, that could only move horizontally along the motion path. Note that the dotted white lines did not appear on the screen.

At the end of the apparent motion sequence, if fixation was maintained successfully, a light grey cursor bar (0.55° by 0.3°) (CIE $x = 10.83$, $y = 16.25$; 11.93 cd/m^2) appeared 4° below fixation.

The mouse could shift the cursor horizontally, but not vertically. The cursor's initial location was randomized along the length of the stimulus array (-12.29° to $+12.29^\circ$). Using the mouse, participants reported the position of the colored target flash by moving the cursor to the perceived location and clicking. Participants did not receive any feedback on the accuracy of their responses.

Participants completed 4 blocks of trials with eye-tracking calibration at the beginning of each block, and as required during the experiment. In each block, participants completed 176 trials, one for each of the 11 target flash locations crossed with each of the 4 target colors, 2 motion paths (terminating vs. continuing), and both motion directions (leftward vs. rightward).

5.4.3 Data Analysis

To examine the effects of color on the magnitude of the flash jump effect, the horizontal distance (dva) of between the location the target flash and the perceived location was computed such that a positive discrepancy was forward, and a negative discrepancy backward along the direction of apparent motion. The discrepancy between target location and response was collapsed separately for terminating vs. continuing conditions across all 11 possible flash positions and both directions of motion. Population means were derived from median shifts in perceived flash locations for each participant. One-sample, one-tailed t-tests, corrected for multiple comparisons using an incremental application of the Bonferroni method (Benjamini & Hochberg, 1995), were used to investigate whether mean flash location shifts were significantly mislocalized forward from zero. To investigate color differences in the precision of localization responses, we computed 95% confidence intervals (CI) of the distribution of position responses (horizontal position) for each motion path and flash color, by participant, as has been done previously in eye movement and reach targeting studies (Henriques et al., 2003; Khan et al., 2005; Ren et al., 2006; Blohm & Crawford, 2007). The upper bound was subtracted from the lower bound of the 95% CI to give an estimated width or range as a metric of response precision. See Fig. 8 for a schematic depiction of analytical metrics. Mean differences in mislocalization shifts and precision metrics were analyzed separately using 4 flash color (red, green, yellow, blue) X 2

motion path (terminating, continuing) repeated measures ANOVAs. Benjamini-Hochberg (1995) corrections were applied to post-hoc tests to control for multiple comparisons.

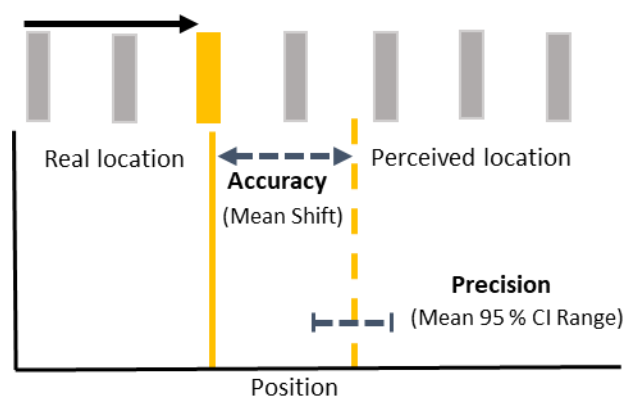


Figure 8. Analytical metrics. For each motion path and flash color, response accuracy was measured as the mean shift between the real location (solid line) and the perceived location (dashed line) of the flash. Response precision was measured as the mean range (upper- lower bound) of 95% confidence intervals for the perceived shifts. Accuracy and precision depicted here is based on mean metrics for yellow flashes in the continuing condition. Note that spacing between bars is exaggerated for illustration.

5.5 RESULTS

The mean difference between the veridical and participants' perceived locations were calculated for each flash color in the continuing and terminating conditions, listed in Table 2 and shown in Figure 9. One-sample one-tailed t-tests showed that the reported flash locations were consistently and significantly mislocalized forward along the path of motion for all colors in the continuing path condition (all large effect sizes by Cohen's d) as well as the terminating path condition (all corrected p 's $< .05$, red and yellow: small effect sizes, green and blue: medium effect sizes).

Table 2. Mean shift (dva) in flash location and significance values (corrected p-value, Cohen's d) for each motion path.

	Flash color	Mean shift (dva)	T-test Sig.(1-tailed)	Cohen's d
Continuing (1.33 dva)	Red	1.23	< .001	1.490
	Green	1.43	< .001	1.595
	Yellow	1.45	< .001	1.809
	Blue	1.21	< .001	1.493
Terminating (0.2 dva)	Red	0.14	.043	.366
	Green	0.21	.01	.575
	Yellow	0.19	.029	.434
	Blue	0.27	.006	.690

To determine whether the magnitudes of the flash-jump mislocalizations were modulated by color, a 4 (Flash Color: red, green, blue, yellow) X 2 (Motion Path: terminating, continuing) repeated measures ANOVA was carried out.

Consistent with prior studies of the flash-jump illusion, we found a significant main effect for motion path [$F_{(1,69)} = 60.504$, $p < .001$, $\eta_p^2 = 0.725$], with a much smaller mislocalization in the terminating ($M (SD) = 0.20 (0.39)$) compared to the continuing ($M (SD) = 1.33 (0.83)$) motion condition. Supporting our hypothesis, there was a main effect for flash color [$F_{(3,69)} = 7.709$, $p < .001$, $\eta_p^2 = 0.251$], showing that the isoluminant color of the flash affected the magnitude of the jump. There was a significant interaction between motion path and flash color [$F_{(3,69)} = 9.731$, p

< .001, $\eta_p^2 = 0.297$], resulting from a stronger color modulation on flash localization in the continuing motion path than in the terminating motion path.

To investigate this further, separate one-way ANOVAs were carried out on each motion path condition. In the continuing path condition, there was again a significant main effect of flash color, $F_{(3,69)} = 11.000$, $p < .001$, $\eta_p^2 = 0.324$. Mislocalization was smaller for red ($M (SD) = 1.23 (0.82)$) and blue ($M (SD) = 1.21 (0.81)$), than for green ($M (SD) = 1.43 (0.90)$) and yellow ($M (SD) = 1.45 (0.80)$) flashes. Planned pairwise comparisons with Benjamini- Hochberg corrections show no significant differences between red and blue (corrected $p = .86$) or green and yellow (corrected $p = .822$), but all other color differences were significant (corrected p 's < .003) (Fig. 9). This pattern of results was robust across individuals, as 19 out of 24 participants produced smaller shifts for red compared to green flashes, and 21 out of 24 participants produced smaller shifts for blue compared to yellow flashes.

In the terminating path condition, where the overall flash-jump effect was small ($M (SD) = 0.20 (0.39)$), there was still a significant main effect of flash color, [$F_{(3,69)} = 4.190$, $p = .009$, $\eta_p^2 = 0.154$]. The smallest shift was observed for red ($M (SD) = 0.14 (0.37)$), followed by yellow ($M (SD) = 0.19 (0.43)$), green ($M (SD) = 0.21 (0.37)$), and blue ($M (SD) = 0.27 (0.39)$) flashes. Planned pairwise comparisons show a significant difference between red and both green (corrected $p = .009$) and blue flashes (corrected $p = .009$). None of the other contrasts were significantly different (all corrected p 's > .05) (Fig. 9). Therefore, the pattern of results across the four colors differed between the continuing and terminating conditions (see Fig.10 for a summary of color differences).

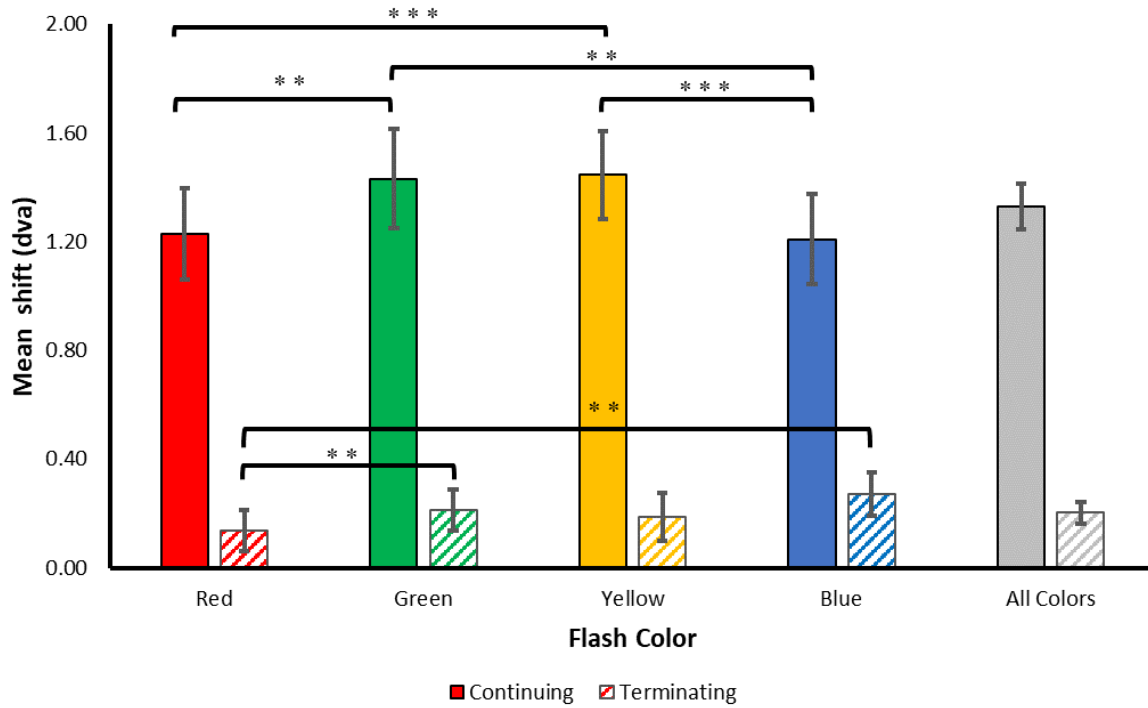


Figure 9. Perceived shifts. The mean \pm SEM shift (dva) in the perceived flash location for both terminating and continuing motion paths. Positive values correspond to a forward shift along the direction of motion. Corrected ** $p < .01$, *** $p < .001$.

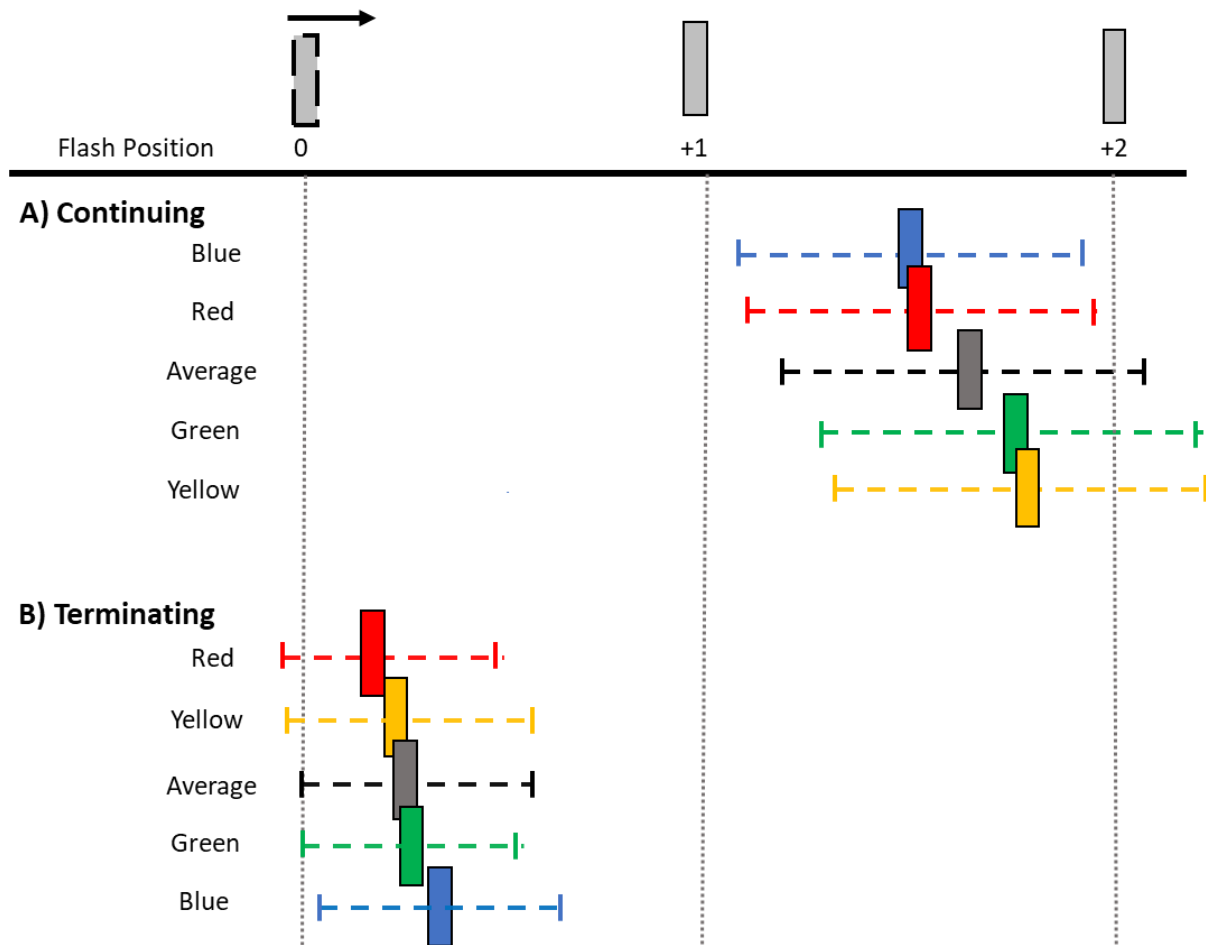


Figure 10. Perceived shifts in flash location relative to bar positions. The mean shift (colored bar) and mean 95% CI range (colored dashed line) for each flash color and overall average for both (A) continuing and (B) terminating motion paths. Note that the flash appears at bar position 0 and the apparent motion sequence moves rightwards. Spacing between bars is exaggerated for illustration purposes.

To examine the effect of flash color on the variability of responses, i.e. participants' precision in localizing the flash, mean 95% CI ranges were calculated for each flash color in the terminating and continuing conditions (Fig. 11). A 4 (Flash Color: red, green, blue, yellow) X 2 (Motion Path: terminating, continuing) repeated measures ANOVA was conducted on this precision metric. There was a significant main effect of motion path [$F_{(1,69)} = 89.269, p < .001, \eta_p^2 = 0.795$],

with larger 95% CI ranges for the continuing ($M (SD) = 0.72 (0.24)$) compared to the terminating ($M (SD) = 0.46 (0.21)$) motion condition, suggesting more precise representation of the flash location in the terminating condition. Unlike in the perceptual shifts, there was no statistically significant differences in mean 95% CI ranges based on flash color [$F_{(3,69)} = 2.283, p = .087, \eta_p^2 = 0.090$] or a statistically significant interaction between motion path and flash color [$F_{(3,69)} = 2.256, p = .09, \eta_p^2 = 0.089$].

As with the perceptual shift analysis, we next carried out separate one-way ANOVAs for each motion path. In the continuing path condition, there was a significant main effect of flash color, [$F_{(3,69)} = 2.879, p = .042, \eta_p^2 = 0.111$], with less response variability for red ($M (SD) = 0.695 (0.25)$) and blue ($M (SD) = 0.690 (0.23)$) flashes, versus more response variability for green ($M (SD) = 0.77 (0.25)$) and yellow ($M (SD) = 0.74 (0.25)$) flashes. Qualitatively, the pattern of color effects matches the pattern observed in the perceptual shifts, wherein, red and blue flashes resulted in more precise representations of the flash location, compared to green and yellow. This pattern of results was robust across individuals as 17 out of 24 participants produced more precise estimations of flash location for red compared to green flashes, and 18 out of 24 participants produced more precise estimations for blue compared to yellow flashes. Post-hoc tests with Benjamini-Hochberg corrections for multiple comparisons revealed no significant difference in 95% CI ranges for all flash colors (all corrected $p \geq .054$). Given the significant main effect of flash color on response precision, how the pattern qualitatively matches the perceptual shifts, and the higher variability in the precision metric itself, uncorrected pairwise comparisons were also conducted to discern the role of statistical power. We found a significant difference in 95% CI ranges between red and yellow (uncorrected $p = .043$) and green and blue flashes (uncorrected

$p=.009$), while all other contrasts were not significant (uncorrected $p > .05$), supporting the qualitative pattern of color modulations (Fig. 11).

For the terminating motion path, the main effect for flash color on response variability was not statistically significant [$F_{(3,69)} = 1.481$, $p = .227$, $\eta_p^2 = 0.061$]. We conducted planned pairwise comparisons finding no significant difference between the mean 95% CI ranges for all color contrasts (corrected p 's $> .05$) (Fig. 11). Similar to the perceptual shift results, the pattern of color modulations on response variability differed between the two motion paths.

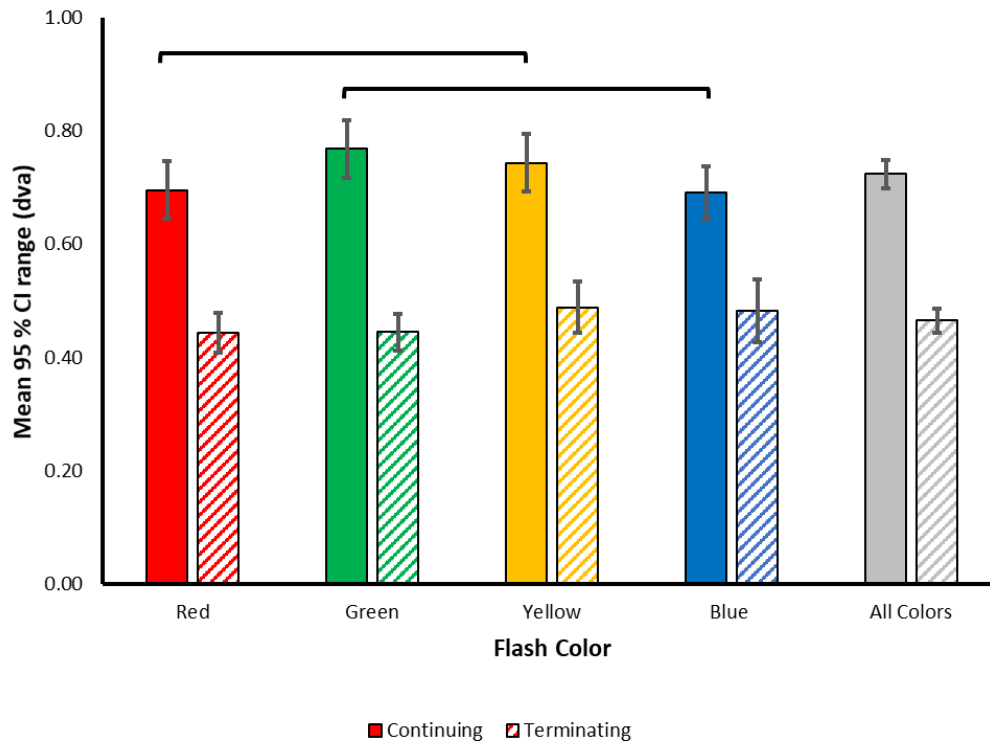


Figure 11. Color modulation of response variability in the flash jump illusion. Precision in responses was measured as the mean 95% CI range \pm SEM and plotted as a function of flash color for each motion path. Lines represent color differences unadjusted for multiple comparisons.

5.6 DISCUSSION

We found a larger shift in the flash mislocalization in the continuing compared to the terminating condition, consistent with a prior study of the flash jump effect (Sundberg et al, 2006). These findings are consistent with other studies of motion-induced position shifts such as the related flash-lag illusion, where the effect is not observed or reduced in the flash-terminated condition, but persists if the flash occurred at the beginning or during the motion sequence (Khurana & Nijhawan, 1995; Eagleman, & Sejnowski, 2000; Kanai et al., 2004; Nijhawan et al., 2004;

Watanabe, 2004). The absence of motion cues after the flash in the terminating condition allows for a more veridical prediction of flash position as there are no subsequent bars. Previously reported color modulations of cognitive functions have suggested that color can intrinsically modulate attentional and cognitive processes in the absence of a task demand (Tchernikov & Fallah, 2010; Lindsey et al. 2010; Blizzard et al., 2017; Fortier-Gauthier et al., 2013; Pomerleau et al., 2014). In the current study, we sought to investigate whether such color-dependent modulations are dependent on Bayesian perceptual processes in the visual system or whether these color modulations are a result of associative learning for specific higher-order executive functions only. We hypothesized that if different colors had different weights in terms of Bayesian priors, then color would modulate the strength of the flash jump effect.

Consistent with this hypothesis, the color of the flash had a significant impact on its perceived location. Participants demonstrated both improved accuracy (i.e., more veridical reports of the flash location) and improved precision (i.e., less variability in responses) in localizing the flash when it was red or blue compared to green and yellow. Comparing across the colors, the smaller the mislocalization the greater the precision in determining where the flash occurred, suggesting that the color of the flash modulated the strength of its representation in the visual system. This proposed advantage in representational strength is consistent with the advantage found for red or blue pop-out targets in visual search (Lindsey et al., 2010). There was also a slight advantage of terminating red flashes over other colors such as blue and green, as participants were more veridical in reporting their location as well. This small improvement in accuracy for red flashes in the terminating condition may arise from a stronger weight for red signals in stopping, as has been shown in studies investigating response inhibition (Blizzard et al., 2017; Ghasemian et al., 2021). The lack of significant differences between the other colors in the terminated condition

may be due to the smaller magnitude of the perceptual shifts when the flash terminates the motion sequence. Overall, red and blue flashes in the continuing motion condition produce more precise and veridical representations of the flash location than green or yellow, which is the focus of subsequent discussion sections.

5.6.1 Underlying mechanism for color modulation effects

Next, we consider various mechanisms that could give rise to the color modulation of the flash jump effect. Tchernikov and Fallah (2010) described an intrinsic color hierarchy, where when participants automatically pursued one of two superimposed surfaces differing in isoluminant color, the color determined which surface was selected and the speed of the smooth pursuit. For target selection, the strength of the colors is greatest with red, followed by green, yellow, and blue, while pursuit speed was based on the distance between the two colors in color space, a property of the color representation in area V4 (Li et al., 2014). As the flash jump illusion is also reflected in the responses of area V4 neurons (Sundberg et al., 2006), it would not be surprising to find that the color hierarchy determines the perceptual shift and precision of localizing the flash in the flash jump illusion. However, participants in the current study showed a different pattern than the color hierarchy, as their perceptual shifts were smaller for both red and blue than for green and yellow continuing flashes. Therefore, the color hierarchy does not reflect the differential strengths of the colors when integrated with motion in the flash jump illusion.

As both red and blue produce more veridical and precise localization of the flash over green and yellow, this may instead reflect opponent-process theory (Hering, 1964), based on opponent color channels; red versus green and blue versus yellow, where each color of the pair inhibits the other. However, color opponency does not inherently predict which color of each pair would be the stronger. The results of this study are consistent with opponent-process theory, and further

suggest that red is dominant over green and blue over yellow. Consistent with this finding, the advantage for red over green has previously been found for response inhibition in the stop-signal task (Blizzard et al., 2017), however green and yellow were not tested. It is interesting to note that the ratio in perceptual shifts between red and green (0.86) is qualitatively similar to the difference between blue and yellow (0.83) suggesting that each opponent pair may be weighted similarly. However, future studies will be necessary to fully understand the relative weightings of the colors in each opponent pair. Since V4 is the last stage that receives color opponency information (Conway, 2009), this input is likely modulating the color-selective neuronal responses giving rise to the perceptual shift in the flash jump illusion.

5.6.2 Motion-induced position shifts

The flash jump illusion is one of many phenomena related to motion-induced position shifts; other related examples include the flash-lag (Nijhawan, 1994; Whitney & Murakami, 1998; Eagleman & Sejnowski, 2007; Khoei et al., 2017), flash-grab (Sinico et al., 2009; Cavanagh & Anstis, 2013), flash-drag effects (Whitney & Cavanagh, 2000; Murai & Murakami, 2016).

Multiple explanations have been proposed to explain such motion-based mislocalization errors, including the differential latency, discrete sampling, motion biasing, and motion extrapolation hypotheses; for a review of prominent theories, see, Nijhawan, 2002; Hubbard, 2014. The results of the current study provide an opportunity to distinguish between these hypotheses, supporting those that could integrate color modulation effects and refuting those that could not.

The differential latency hypothesis proposed by Whitney and Murakami (1998) posits that moving targets are processed faster, with shorter neural delays, than stationary flashed targets (Cai and Schlag, 2001b; Jancke et al., 2004; Subramaniyan et al., 2018). In consideration of the *flash-lag* effect, by the time the static flash is perceived, the moving bar is perceived to be further

along its trajectory. Previous studies have reported temporal processing differences between color and motion systems (Moutoussis & Zeki, 1997a & b; Viviani & Aymoz, 2001). However, for the differential latency hypothesis to explain color modulation of the *flash-jump* effect, the latency difference between color and motion would need to vary depending on the color of the flash, which would require that different colors be processed with different latencies. Indirect evidence contrary to this account comes from Blizzard et al. (2017), where it was demonstrated that reaction times were not differentially modulated based on the color of the go signal, both when the color was task-irrelevant or color was used as the discriminator for response selection. The range of mislocalization differences between red/blue and green/yellow flashes is 0.2-0.24°, which corresponds to latency differences between the colors of ~17-20 ms. While neurophysiological approaches have revealed no differences of that magnitude in neuronal latencies for different colors in area V4 (e.g. Chang et al., 2014), future neurophysiological studies would need to precisely measure color latencies in multiple areas along the ventral visual stream to further test the differential latency hypothesis.

More recently, Schneider (2018), proposed the discrete sampling hypothesis which posits that the visual system samples input into discrete moments or time windows, each with a duration, D . This discrete sampling hypothesis suggests that, during the flash-jump illusion, the color change occurs at a point in time during one moment or sampling window; however, the location of the moving target is recorded as its final position within that time window. By this hypothesis, the color flash would be displaced by $D/2$ from its actual time of onset. The discrete sampling hypothesis is a modification of the differential latency theory, as both suggest temporal processing differences for color and motion information. However, the discrete sampling hypothesis compartmentalizes color and motion information into discrete moments based on

these latency differences. If the latency difference between two events (i.e. color change and motion) is small, they are registered in the same moment, thus perceived together, but, if there is a large latency difference between color and motion, then these two events are registered into different moments, leading to the flash jump effect. Based on the speed of the apparent motion sequence, the average flash jump effect of 1.33° corresponds to a latency difference of ~ 111 ms, which would be consistent with discrete sampling. However, the discrete sampling hypothesis does not currently predict differences in perceived position shifts based on flash color, as the sampling differs between modalities, rather than between individual colors. For this theory to explain color-dependent modulation of the perceived shift in flash location, as the duration of each perceptual moment would not vary based on the color of the flash, there would need to be latency differences between the different color flashes that would shift green and yellow into a later discrete moment than red and blue. While there is no current evidence for varying latencies for the different colors (Chang et al., 2014; Blizzard et al, 2017), if future neurophysiological studies find latency differences in color opponent areas, and those differences are large enough to cause different color flashes to fall into different moments, then the discrete sampling hypothesis could potentially account for the color dependent modulation of the flash-jump effect.

Temporal integration theories of motion-induced position shifts in the flash-lag illusion (Brenner & Smeets, 2000; Eagleman & Sejnowski, 2000) suggest that position estimates are computed based on information that is collected over a period of time after the flash. This post-diction or motion-biasing hypothesis postulates that the flash triggers the start of the motion integration window where information about the position of a moving target is collected for another ~ 60 ms (Brenner & Smeets, 2000) to ~ 80 ms (Eagleman & Sejnowski, 2000, 2007) after the flash. Therefore, the final position of the colored flash is shifted along the trajectory of motion by

signals that arrive in the next ~60-80 ms. For this hypothesis to account for color-dependent modulations of the flash jump effect, different colors would need to either initiate the start of the integration window at different times or produce different integration window durations. Given that colors have been shown to modulate attentional resources (Tchernikov & Fallah, 2010), the attentional strengths of different colors could similarly modulate the integration window. In terms of the attentional color hierarchy, red is the strongest and blue is the weakest of the four colors tested (Tchernikov & Fallah, 2010). A color-dependent attentional modulation of the integration window would then predict less of a shift for red than green or yellow, as was found in this study, but also that blue would produce the largest shift. In contrast, the current study showed that blue (as well as red) produced smaller shifts than green and yellow. Therefore, the incorporation of the attentional color hierarchy into the postdiction hypothesis cannot explain the current results.

The motion extrapolation account posits that the perceived position of a moving target is extrapolated forward along its trajectory, based on its previous history, to compensate for neural delays in processing (Nijhawan, 1994). More recently, Bayesian frameworks for object localization have been used to explain motion extrapolation (Lisi & Cavanagh, 2015; Khoei et al., 2017; Hui et al., 2020). For example, Lisi & Cavanagh (2015) proposed that the previously perceived location of a moving object becomes a Bayesian prior for the estimate of its upcoming motion. Similarly, the parodiction hypothesis proposes that the visual system predicts an object's final position as its most probable position (Khoei et al., 2017). These are both Bayesian models, which integrate sensory information with an internal a priori distribution to give a probability distribution function of the object's position. Next, we will describe how extensions of these

Bayesian models provide a framework by which color can modulate the degree of the flash-jump effect.

5.6.3 Bayesian framework

Bayesian models of perception suggest that if the input is sparse, variable, or noisy (visual or perceptual noise), the visual system makes a prediction by biasing its perception towards typical objects or representations based on priors (Knill & Richards, 1996; Rao et al., 2002; Kersten & Yuille, 2003; Kersten et al., 2004; Feldman, 2012). As there is already work supporting Bayesian frameworks for motion processing (Jacobs, 1999; Weiss et al., 2002; Lisi & Cavanagh, 2015, Gershman et al., 2016; Hui et al., 2020; Yang et al., 2021), Sundberg et al. (2006) proposed a similar Bayesian approach for the estimation of flash location relative to bar locations in the flash-jump paradigm. The authors observed a retinotopic shift in color-selective V4 neurons for both the terminating and continuing conditions and proposed that this retinotopic shift in V4 cells provides a physiological basis for our perception of the flash-jump effect. Although a retinotopic shift was observed for both conditions, perceptually, human observers do not report large mislocalizations in the terminating condition. Therefore, to explain this discrepancy, Sundberg et al. (2006) proposed a Bayesian model of sensory integration, wherein the shifted representation of the flash (V4 responses) is integrated with a representation of all presented bar positions (likely occurring in a later stage color-insensitive area), giving rise to a joint probability estimate of the flash relative to actual bar locations. In the continuing condition, color-insensitive areas maintain the location of all bars in the sequence, since all locations were presented, therefore, the resultant joint probability function represents the shifted position signaled by the mislocalization in the V4 neurons. However, in the terminating condition, bars beyond the flash are not presented, therefore there are no representations for any further bar positions in color-

insensitive areas. When the shifted flash representation from area V4 is integrated with this representation of the terminated condition bar locations, the resultant joint probability estimate is restricted to the veridical location, resulting in the absence of a perceptual shift in the terminating condition.

We propose a modification of this Bayesian framework to explain how the representation of the flash in the color selective area (e.g. area V4) is mislocalized and how color modulates the magnitude of this shift. We propose that the V4 mislocalization reported by Sundberg et al. (2006) is produced by an earlier Bayesian framework for feature integration, where the motion extrapolation signal is combined with the color signal that is weighted differently depending on the color priors.

Figure 12 shows hypothetical probability distributions for the flash locations in the continuing condition for red, green, blue, and yellow flashes. The dashed black curve illustrates the estimate for motion position at the onset of the flash, arising from a motion selective area such as MT. Note that the estimate for motion position is further ahead along the direction of motion at the time of the flash due to the motion extrapolation prior (Nijhawan, 1994; Sundberg et al., 2006; Lisi & Cavanagh, 2015; Khoei et al., 2017; Hui et al., 2020). Anterograde and retrograde tracer studies have confirmed the presence of bidirectional connections between area MT and V4 (Ungerleider & Desimone, 1986; Ungerleider et al., 2008). This motion information feeding into V4 has also been shown to modify the selectivity and responses of V4 neurons (Tolias et al., 2005). Therefore, we suggest that the mislocalization in V4 responses (Sundberg et al., 2006) arises from the integration of incoming motion signals with incoming weighted color opponency information. At flash onset, a representation of the bar's motion (from motion selective areas) which is shifted forward due to motion extrapolation (black dashed curve in Figure 12) is

integrated with a representation of the color flash (from color opponent cells) at its veridical location (colored dashed curve in Figure 12), giving rise to a posterior probability distribution (solid colored curve in Figure 12) that is shifted forward. The color-dependent modulation of the flash jump effect is dependent on the representation of the flash (color dashed curve) being weighted differently by color. The dashed colored curve illustrates the estimation of the flash location (i.e. color selective area) at the onset of the flash for each of the red, green, blue, or yellow flashes, with the height of the curve representing the weighting of that representation. Based on our results, a higher weighting is given for the stronger colors (red and blue) than the weaker ones (yellow and green). The difference in weighted priors for these colors are likely due to color opponency input, wherein red in red vs green, and blue in blue vs yellow are the stronger colors of the pairs, even at isoluminance. The resultant probability density function (depicted as solid colored curves in Figure 12) is less shifted forward for red and blue resulting in a predicted flash location closer to its veridical location, but is more shifted for yellow and green, resulting in a larger mislocalization or jump of the flash. The integration of the motion and color opponency signals thus produces the mislocalized responses in area V4 neurons, meaning that the integrated probability distribution functions from our model (solid-colored curves) correspond to the shifted V4 color signal in the model proposed by Sundberg et al (black curves in Figure 5 of Sundberg et al., 2006). As Sundberg and colleagues proposed, this shifted V4 signal is then integrated with actual bar locations (represented in a later stage color-insensitive area) in a second Bayesian process to give an estimate of flash location relative to the continuing or terminated conditions. As we observed small mislocalizations in the terminated condition as well, we propose that similar to the continuing condition, the representation for the final bar position in the terminated condition would also be slightly shifted forward due to motion

extrapolation (Lisi & Cavanagh, 2015; Khoei et al., 2017). Then, when the color weighted flash information is integrated with this motion estimate, the probability density function would be color modulated around a slightly shifted mislocalization, consistent with our perceptual results. Since the flash-jump mislocalization is found in the responses of area V4 neurons (Sundberg et al., 2006), this proposed mechanism predicts that color modulation would also be reflected in area V4, where the mislocalization would vary based on the color of the flash, although further studies would be needed to confirm it. More generally, these results provide further support that perception and feature integration follow a Bayesian framework.

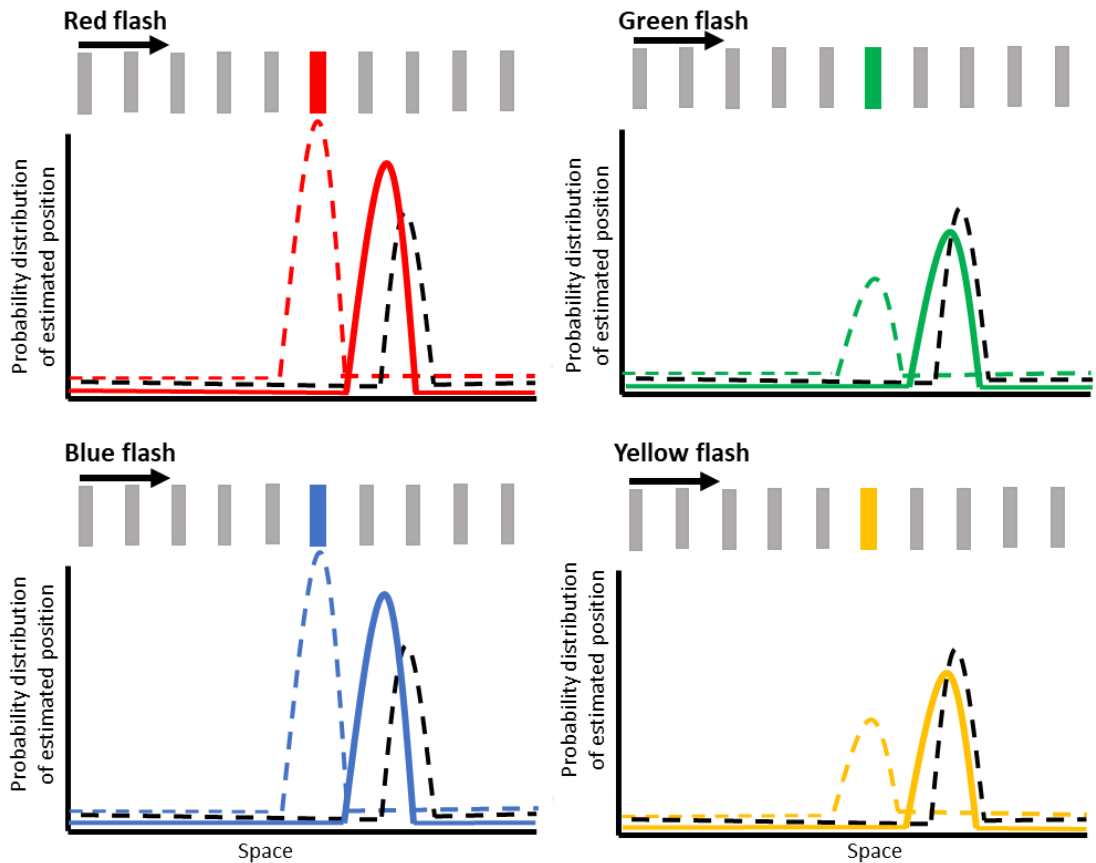


Figure 12. Illustration of the Bayesian model of color modulation. The dashed black curve depicts the motion extrapolation-dependent position representation for the moving bar at the onset of the flash. The dashed colored curve depicts the estimation of the flash location at the onset of the flash for red, green, blue, and yellow flashes, with the height representing the weight of that estimation. The integration of these two signals is depicted by the solid-colored curve, which represents the probability density function for the mislocalization of the flash, as represented by V4 neuronal responses. Note that this illustration depicts the flash-continuing condition with the bar moving in the rightward direction and the spacing between bars has been exaggerated for illustration purposes.

5.7 CONCLUSION

These results show that the color of the flash modulates its perceived location in the flash jump illusion, affecting both accuracy and precision metrics. Specifically, red and blue flashes in the continuing motion path are localized both more precisely and with less of an illusory shift than green and yellow, likely based on color opponent mechanisms which provide input into area V4, an area previously shown to encode the mislocalized position of the flash. We propose a Bayesian framework that integrates color opponency priors and motion extrapolation priors to give rise to the flash jump illusion. The color of the flash biases the weight of the priors; resulting in different levels of mislocalizations based on inherent strengths of different colors, where red and blue have stronger representations than green and yellow. This is further support for perception and feature integration being dependent on Bayesian mechanisms.

AUTHOR CONTRIBUTIONS

HS wrote the manuscript, collected, and analyzed the data. HJ designed the experiment and data analysis, programmed the experiment, and revised the manuscript. MF designed the experiment and data analysis and revised the manuscript.

FUNDING

This work was funded by a Vision: Science To Applications (VISTA) Master's scholarship to HS, and a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to MF.

CHAPTER 6

THE INFLUENCE OF COLOR ON COGNITIVE PROCESSING

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This manuscript has been submitted to **Nature Reviews Neuroscience**. HS designed the theory, reviewed the literature, placed the findings into the theory framework and drafted the article. MF designed the theory, provided feedback on the framework, and revised the written draft.

6.1 ABSTRACT

Considerable recent work has demonstrated the influence of color on cognitive functions, suggesting that the color of a stimulus can modify attentional or perceptual processes, resulting in different behavioral outcomes. For the first time, we propose how three separate putative neural mechanisms; color opponency, attentional hierarchy, and visual associations explain how and where such color-dependent modulations occur in the visual system. Furthermore, we describe a novel theoretical approach to understanding how these color mechanisms can modulate visual processing through Bayesian frameworks, wherein, the modulatory effect of color on a cognitive or perceptual process is due to differences in prior weights for each color, set by one of the underlying color processing mechanisms.

KEYWORDS

color, color opponency, attentional hierarchy, visual associations, Bayesian perception

6.2 INTRODUCTION

Over the course of millions of years, the primate visual system evolved from achromatic to color vision. From an evolutionary standpoint, color is an important characteristic of human vision, allowing us to differentiate between food items, detect predators, and recognize visual targets (Mollon, 1989; Osorio & Borovyeb, 1996). Recent developments in the field of color research have also demonstrated the modulatory effects of color on human cognitive and psychological functioning. There is strong evidence to suggest that different colors can intrinsically alter visual processing in the brain, ultimately modulating behavioral outcomes, even if object color is irrelevant to the task at hand. Therefore, it is critical to consider the impact of everyday color decisions on various aspects of psychological functioning. Much of the research in this field has focused on answering applied questions such as the link between color and consumer behavior (for a review see, Paul & Okan, 2011), food consumption (Shankar et al., 2009; for reviews, see Shankar, Levitan, & Spence, 2010; Spence et al., 2010), productivity (Kwallek, Lewis, & Robbins, 1988; Hatta et al., 2002; Kwallek, Soon, & Lewis, 2007; Küller, Mikellides, & Janssen, 2009, for a review, see, Savavibool, 2016) and attraction (for a review see, Elliot & Maier, 2014). Previous review articles on color and psychological functioning have focused on specific areas of research, such as attraction, providing evaluations of theoretical and empirical developments, as well as recommendations for future research (Elliot & Maier, 2014; Elliot, 2015, 2019), but have not taken into consideration possible underlying neural mechanisms or circuitry to explain such modulations. In our present paper, we propose and describe how each of the underlying color processing mechanisms can give rise to color-dependent modulations of visual and cognitive processes, with supporting empirical evidence from prior studies. Due to the

broad encompassing applications of color research, we have limited our focus primarily to research on color and attention.

6.3 MECHANISMS OF COLOR-DEPENDENT MODULATIONS

Color-dependent alterations in psychological functioning and cognition may be attributed to differential processing of colors within the visual system. The value of a color may influence different stages of visual processing depending on the task and stage in the visual processing hierarchy. Herein, we propose three mechanisms that allow stimulus color to alter attentional or perceptual processes at various stages of the visual system (see Table 3 for an overview, as well as representative examples).

6.3.1 Color opponency

The existence of three cone types, proposed by Young (1802) and Helmholtz (1866), combined with the opponent organization first proposed by Hering (1964) gave rise to the opponent-process theory, which posits that cone photoreceptors from the retina are arranged together to form three opposing color mechanisms; red versus green, blue versus yellow, and achromatic (black vs white). This theory states that we can detect only one of the opposing color pairs at a time because activation of one member of the pair inhibits the other. Information from cones is projected onto ganglion cells, and ultimately reaches the parvocellular layers of the LGN, where opponent cells compute the relative difference between various cone activations. Short (S) opponent responses are either added or subtracted from medium (M) and long-wavelength (L) units to give rise to the red-green and yellow-blue axes (De Valois & De Valois, 1993).

Parvocellular axons from the LGN terminate in V1 (Hubel & Wiesel, 1972; Blasdel & Lund, 1983), having influence on early visual processing stages. Opponent mechanisms would allow

for color-dependent modifications of early visual processes by advantaging one color from its competitive pair, while simultaneously disadvantaging the other. Therefore, we would expect to find differential processing of colors within opponent pairs, but no differences between pairs as the opponent channels are independent of one another. In other words, color opponency would predict a significant difference between red and green as well as between blue and yellow signals.

Based on recent studies where the contribution of hue on attention and perception was evaluated, there is some empirical evidence supporting the modulatory effects of color opponent mechanisms. Recent studies employing visual search tasks have reported differences in task performance based on the hue of targets (Lindsay et al., 2010; Fortier-Gauthier et al., 2013; Pomerleau et al., 2014). When comparing electrophysiological responses between red and green targets in a visual search task, Fortier- Gauthier et al. (2013) reported that red targets evoked an earlier N2pc waveform, and faster detection responses than green targets, indicating a processing difference between isoluminant red and green signals, as predicted by color opponency theory. A second study also evaluated lateralized event-related potentials (ERPs) of various colored targets during a comparable visual search task (Pomerleau et al., 2014). Their analyses revealed that the N2pc waveform occurred earlier for red or blue, compared to green or yellow targets, further corroborating previous ERP findings (Fortier-Gauthier et al., 2013) and the color opponency theory. Based on the link between the N2pc waveform and contralateral attention deployment (Luck, 2014), and its neural correlate in intermediate visual processing areas such as the extrastriate cortex (Hopf et al., 2000), these results suggest that in a visual search task, attention may be deployed to red and blue stimuli faster than other colors, based on color opponency input.

Further support for opponent processes comes from Saini, Jordan & Fallah (2021), where they investigated the effect of task-irrelevant color on motion-induced position shifts (i.e., flash jump effect). In their study, an apparent motion sequence composed of grey rectangular bars flashed a color at one position along its trajectory, and subjects were tasked with reporting the location of this color change. Results from this study revealed a significant effect of flash color on the perceived location of the flash, such that observers were more accurate and precise in their predictions of flash location for red and blue, compared to green and yellow flashes. The authors posit that the color dependency observed in the flash jump paradigm may arise as a result of color opponent mechanisms, wherein red and blue appear to be the advantaged opponent colors in their respective pairs.

Although color opponency predicts a significant difference within opponent color pairs, it does not make predictions about the relative weighting of colors in their respective pairs, i.e., which color from the pair is advantaged. Current studies (Fortier- Gauthier et al., 2013; Pomerleau et al., 2014; Saini et al., 2021) suggest that red signals are advantaged over green and blue signals are advantaged over yellow, however, future investigations are necessary to fully understand how and why these opponent weightings arise, and whether this pattern of color effects (red > green and blue > yellow) is supported by other low-level visual tasks as well.

6.3.2 Attentional color hierarchy

In 2010, Tchernikov & Fallah demonstrated that color features intrinsically bias target selection and pursuit speed when observers execute smooth pursuit eye movements to two superimposed random-dot-kinematograms (RDKs), segmented by color, and moving in opposite directions. The selection and subsequent pursuit of one of two isoluminant colored surfaces was modulated by an intrinsic hierarchy of red, followed by green, yellow and blue. Furthermore, the authors

reported an increase in pursuit speed as the distance in color space between the two isoluminant colors increased. The attentional color hierarchy assigns relative weights to each color, wherein red signals > green > yellow > blue. Therefore, depending on the color of a visual signal, this attentional color hierarchy drives differences in attentional capture and allocation, resulting in changes in the strength or speed of processing of that signal, giving rise to different outcomes based on color alone.

More evidence for the attentional color hierarchy comes from studies investigating the effect of color on additional oculomotor behaviors. Kehoe et al. (2018) investigated color space representations in the oculomotor system by measuring saccade curvatures during a memory-guided saccade task with color targets and distractors. They demonstrated that saccade curvatures were modulated by CIE (x,y) color space distances between the colored target and distractors. More importantly, their analyses revealed hierarchical differences between color targets for various metrics of saccade target selection and encoding such as color selection, saccadic reaction times, precision and proportion of errors. Similar to the hierarchical color effects reported by Tchernikov and Fallah (2010), Kehoe and colleagues report a hierarchy of selection for specific colors such that red targets were selected more frequently compared to green and yellow, and marginally selected more frequently than blue, regardless of task instructions. Moreover, the authors reported that saccades directed to red targets were faster, more precise, and performed with less errors compared to green and yellow. In sum, these findings suggest a hierarchical structure of inherent priority given to various colors. Studies exploring the link between color and attentional adhesion have also revealed an attentional biasing effect for red, wherein, red targets increase attentional capture, resulting in greater

attentional adhesion, especially in an emotionally valanced context (Buechner et al., 2014; Kunjecki et al., 2015; Xia et al., 2018).

It should be noted that evidence for the color hierarchy comes from various aspects of dorsal stream processes involving the oculomotor system such as target selection, saccade accuracy, saccadic reaction time, and pursuit speed (Tchernikov and Fallah, 2010; Kehoe et al., 2018). As the dorsal stream is not in itself selective for color (Baker et al., 1981; Maunsell & Van Essen, 1983; Dobkins & Albright, 1994; Gegenfurtner et al., 1994), that color information must arrive from elsewhere. There is strong empirical evidence suggesting that color information from the ventral stream gets incorporated into dorsal stream processes, as color can influence various aspects of motion processing. For example, Croner & Albright (1997) reported that discrimination of motion direction of randomly moving dots is improved when the distractor dots are segmented by a known color. More recently, Perry & Fallah (2012) demonstrated that segmentation of two RDK surfaces by color reduced the time needed to process and encode the motion direction of the two surfaces. Therefore, these color effects can be explained by feature integration of color space representations from V4 into dorsal stream object files used by areas MT, MST, and LIP (for review see, Perry & Fallah, 2014). We propose that V4 neurons establish a color hierarchy, which is then integrated into dorsal stream object representations (red arrow, Figure 13), resulting in observable color differences in dorsal stream processes. We hypothesize that similar attention color hierarchy effects will be seen for ventral stream visual processing. However, the attentional color hierarchy is yet to be corroborated for ventral stream processes directly, which should be the focus of future studies.

6.3.3 Visual associations

As we grow and experience the world around us, we learn to “form implicit associations between repeated pairings of colors and specific messages” (Elliot & Maier, 2007). Some researchers posit that color associations may be physiologically defined (Goldstein, 1942; Ott, 1979), or may have evolved to reflect emotion through changes in skin coloration (Changizi, Zhang, & Shimojo, 2006; Hill and Barton, 2005), while others suggest that they are a result of both biological and social sources (Elliot & Maier, 2012). In the modern context, red is most commonly utilized as a stop signal in stop signs and traffic lights, alerting us of danger. In contrast, green is associated as a go-signal, communicating safety or success. A driver approaching a red traffic light will bring their vehicle to a sudden stop, whereas a driver approaching a green signal on the same traffic light will continue driving. Therefore, associative learning arising from experience can modulate our cognitive and behavioral response differentially based on the color of a visual signal.

Several studies have demonstrated evidence for color-dependent modulations of higher-order executive functions. Blizzard and colleagues (2017) evaluated task performance on the classic stop-signal task (SST) by varying the color of the go and stop- signals. In studies 1 and 2, the color of the go-signal varied to investigate the influence of color on response execution. The authors report no significant difference in reaction times or response accuracy for task-irrelevant or task-relevant go-signal colors. In a third study, the authors examined the effect of stop-signal color on response inhibition. Participants were tasked with responding to the direction of a white go -signal arrow, which was followed by an iso-luminant color change to either red or green, signaling participants to withhold their response. Mean reaction times for red stop signals were faster than green, suggesting that response inhibition, but not response execution (i.e.,

experiments 1 & 2), networks are sensitive to the color of the visual signal, with red stop signals facilitating response inhibition more than green stop signals. This work was extended by Asare et al. (in review-a), where they used a modified SST with a spatially separated stop signal. Their results revealed faster reaction times for red stop signals than green, corroborating previous SST findings (Blizzard et al., 2017). Furthermore, the study reported no significant difference in reaction times for blue and yellow stop signals, suggesting that response inhibition modulation is specific to red and green only. Even though red and green have strong associations (i.e., red = stop, green = go) in our modern world, the facilitatory effect of red on response inhibition could arise either from nature or nurture.

Recent work has provided insight into this nature versus nurture argument. Ghasemian and colleagues (2021) have found evidence for evolutionarily persevered visual associations, suggesting that meaningful connections between visual stimuli can be innate. They replicated the color SST task (Blizzard et al., 2017), in macaque monkeys and similarly found that red stop signals facilitated response inhibition compared to green, corroborating the findings in human studies. The discovery of color dependent modulations in monkeys demonstrates an inherent, evolutionarily preserved bias for red as a stop signal, where red may have evolved to be associated with danger or threat as it is the color of blood and many venomous or poisonous animals/fruit. It should be emphasized that, experience dependent learning may modify such innate biases. In this case, humans have supported the relationship between red and stopping by incorporating this association into our modern world (i.e. red stop signs, red traffic lights), thus reinforcing this red-stopping bias with experience. However, other innate color biases may diminish over time as they are weakened or “overridden” by new experiences and associations when their use in the modern world is incongruent. It is worth noting that the aforementioned

study provides evidence for an innate red-stopping bias only, whether other color associations are learned or innate is currently unknown, thus requiring future investigations.

In contrast, evidence supporting the nurture argument, i.e. role of experience, environment and learning comes from other studies investigating the effect of red on cognitive performance. In the Chinese stock market, red signifies an increase, whereas green signifies a decrease in stock prices. Due to their unique experience with red and green, stockbrokers associate red with financial gain/success, and green with financial loss/failure, which is contrary to typical associations for red and green. Zhang and Han (2014) demonstrated that a red stimulus, compared to green, impaired performance on an IQ test in college students. In contrast, the opposite was true for stockbrokers, where red improved test performance, consistent with its positive learned association from their work experience. Therefore, color-dependent modulations can also result from learned color associations, based on unique personal experiences, which affect higher-level cognitive functions differently.

Color-in-Context theory

Some researchers have theorized that contextual information also plays a vital role in the formation of learned associations. The physical or psychological context of a colored signal can give rise to diverse learned associations, resulting in different meanings and behavioral responses for the same visual signal (Elliot & Maier, 2012). The color red is a particularly good example. Despite mixed results (Mehta & Zhu, 2009; Elliot & Arts, 2011; Meyer & Bagwell, 2012; Steele, 2014; Shi, Zhang & Jiang, 2015; Rezaeian, Motealleh, & Etemadi, 2015; Arthur, Cho, & Muñoz, 2016), proponents of this theory argue that red undermines cognitive performance in achievement contexts due to its association with failure and avoidance motivation (Elliot et al. 2007; Maier et al., 2008; Elliot et al., 2009). A recent meta-analysis (Gnambs, 2020) reported a

small negative effect of red on reasoning tests, while performance on anagram and knowledge tests was not impaired. *Color-in-Context* theory suggests a negative effect of red in achievement contexts; however viewing red in a romantic context has a favorable attraction enhancing effect (Elliot & Niesta Kayser, 2008; Elliot et al., 2010; Niesta Kayser, Elliot, Feltman, 2010; Pazda, Elliot, & Greitemeyer, 2012), again with mixed results (Schwarz & Singer, 2013; Young, 2015; Peperkoorn et al., 2016). It is worth noting that methodological differences may account for mixed findings as the studies utilized various methods of stimulus presentation (e.g., computer screens, printer paper) and task types.

In addition to research on achievement and attraction, several studies have investigated the context dependent effect of red on the assessments of emotion and physical health. Specifically, the color red is consistently associated with negative emotions such as anger (Jonaskaite et al., 2019) and facilitates the perception and identification of angry facial expressions (Palmer et al., 2013; Young et al., 2013; Wiedemann et al., 2015; Nakajima, Minami, & Nakauchi, 2017; Minami, Nakajima, & Nakauchi, 2018; Peromaa & Olkkonen, 2019) as human and primate faces often flush when angry (Drummond, 1997; Drummond & Quah, 2001; Montoya, Campos, & Schandry, 2005). However, when assessing physical health, a red facial tinge is an indicator of good blood flow and oxygenation (Stephen et al., 2009 a, b), hence, good health, resulting in different meanings of a flushed face depending on the context that it is viewed under. It is important to note that, the *Color- in- Context* theory stems from learned associations but hypothesizes differential behavioral outcomes for the same-colored stimuli depending on the context (i.e., achievement vs. romantic).

Table 3. Overview of color-modulation mechanisms and supporting empirical findings.

Mechanism of color modulation	Summary	Exemplar evidence	References
Color opponency	Red vs Green Blue vs Yellow	<ul style="list-style-type: none"> • Visual search task • Flash-jump paradigm 	Lindsay et al., 2010 ; Fortier-Gauthier et al., 2013 ; Pomerleau et al., 2014 ; Saini et al., 2021
Attentional Hierarchy	Red > Green > Yellow > Blue	<ul style="list-style-type: none"> • Smooth pursuit target selection • Memory-guided saccade task 	Tchernikov & Fallah, 2010; Kehoe et al., 2018
Visual Associations	Implicit associations between repeated pairings of colors and specific messages (learning/experience/ or innate)	<ul style="list-style-type: none"> • Stop Signal Task • Two-choice discrimination go-no-go task • Negative effect of red on cognitive performance • Positive effect of red on attraction • Facilitatory effect of red on the perception of anger and physical health 	Blizzard et al., 2017 ; Ghasemian et al., 2021 ; Asare et al., in review-a ; Elliot et al., 2007 ; Gnambs, 2020 Elliot & Niesta Kayser, 2008 ; Elliot et al., 2010 Palmer et al., 2013 ; Young et al., 2013 ; Stephen et al., 2009 a, b

6.4 CIRCUITRY AND BRAIN REGIONS

We propose that the value of a color may influence different stages of visual processing depending on the level the task is performed at. The early stages of the visual stream encode color as red-green and blue-yellow opponent cells along a segregated stream from the LGN to

V1 (Chatterjee & Callaway, 2003) and up to intermediate visual processing areas such as V4 (Conway, 2009). Therefore, color opponent mechanisms provide an opportunity for color to modulate low-level visual processes at the earliest stages of the visual processing hierarchy. Color selective neurons in V4 transform the color opponent input into a color space representation, which gives rise to the attentional color hierarchy. This provides for color-dependent modulations of attentional processes based on V4 output at intermediate stages of the visual hierarchy. Finally, visual associations (innate or learned) can influence later stages of the visual processing hierarchy through long-range, top-down signals from the prefrontal cortex (PFC) (Watanabe, 1992; Asaad et al., 1998; Miller, 1999). The PFC is known to have strong feedback connections with the anterior inferior temporal (IT) cortex in particular (Webster et al., 1994), and V4 (through FEF; Pouget et al., 2009), thus it is well positioned to influence visual processing through these connections. Visual associations may also alter processing of other executive functions carried out within the frontal lobe, such as response inhibition (Blizzard et al., 2017; Ghasemian et al., 2021, Asare et al. (in review)). In sum, based on the hierarchical nature of the visual system, we propose that color opponency, attentional hierarchy and visual associations modulate attentional and perceptual processes in a sequential manner (see Figure 13 for an overview). As visual processing is a sequential process, it is possible that more than one color mechanism is at play for a given task/cognitive process, which would require the mechanisms to build on one another.

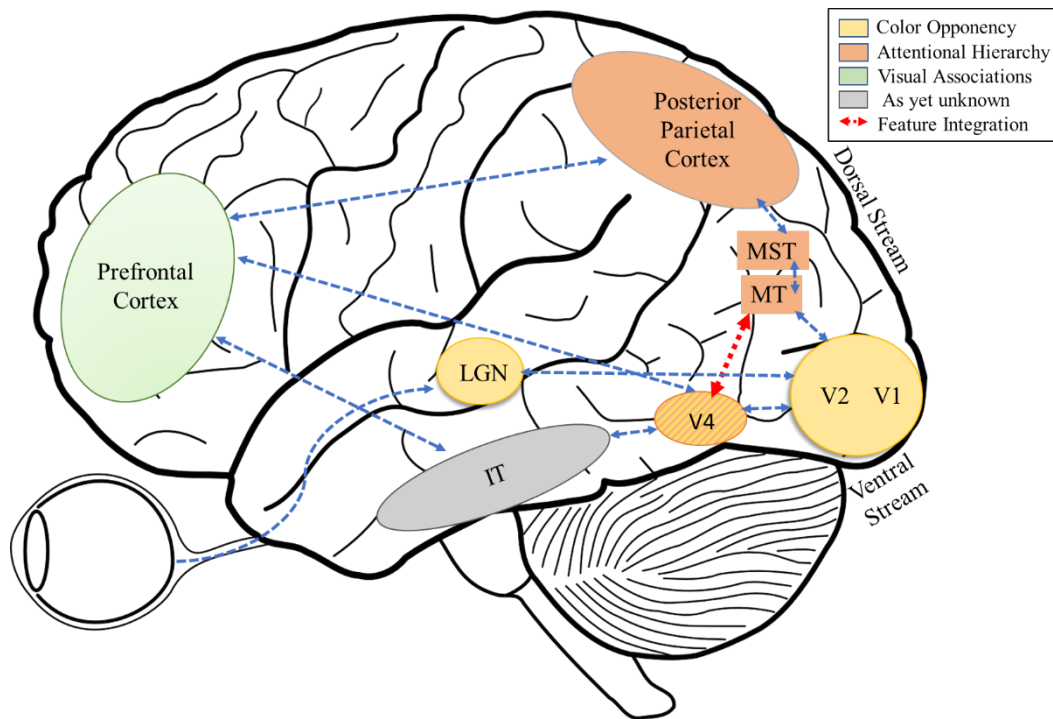


Figure 13. Mechanisms of color-dependent modulations in the visual system. Colored regions represent the location and stages of visual processing, which are modifiable through one of three mechanisms: color opponency (yellow), attentional hierarchy (orange), and visual associations (green). Connections among brain regions are depicted as dotted blue arrows. Red/green and blue/yellow opponent information from LGN is projected to V1 and then V2, allowing for opponent mechanisms to modulate early visual processing. V4 is both yellow and orange since it receives color opponent information from lower- visual areas and transforms it into a color space representation, giving rise to the attentional hierarchy. This mechanism can modify intermediate stages of the ventral pathway, as well as dorsal stream processing through the integration of color information into dorsal stream object representations (red arrow). Finally, color associations established in the prefrontal cortex can modify later stages of the visual processing hierarchy.

6.5 BAYES THEORY OF COLOR-MODULATION

Given the hierarchical structure of the visual system, we propose that these different color mechanisms occur sequentially in the visual system depending on level at which the task is performed and modulate visual processing through a Bayesian framework of perception. In this framework, the visual system can modulate cognitive processes through the probabilistic integration of prior knowledge or predispositions (priors) and sensory input (likelihood) (Kersten & Yuille, 2003; Kersten et al., 2004; Feldman, 2012). In consideration of color-dependent modulations, the weight of the Bayesian priors being incorporated would change depending on the attentional strength of a specific color. The posterior probability distribution, resultant from this Bayesian computation would be biased differentially, producing different responses or outcomes on the same task depending on object color.

As mentioned previously, bottom-up color opponency information, based on the antagonistic organization of opponent cells advantages one color from its competitive pair, while simultaneously disadvantaging the other. Therefore, from a Bayesian perspective, one color in each opponent pair has a higher prior weighting than the other, driving differences in the resultant posterior probability distribution. This Bayesian approach has been recently used to explain how color-opponent input can modulate perceptual processes such as feature integration.

One such example arises from color modulation of the flash-jump illusion, wherein Saini et al. (2021) proposed a Bayesian framework for the color-dependent modulation of feature integration. In this Bayesian approach, color opponency information defines the weights of the colored stimuli when integrated with other object features such as motion (Figure 14, taken from Saini et al., 2021). The representation of the expected forward motion (black dashed curve in Figure 14) of the moving bar is integrated with the representation of the colored flash (dashed

colored curves, Fig. 14) which is weighted differently based on the color of the flashed bar, as depicted by the height of this curve. Their behavioural results indicate that both red and blue flashes reduce the illusory shift observed in the flash-jump illusion, indicating that both red and blue colors are weighted higher in comparison to their respective opponent pair colors, with green and yellow being the weaker colors. The resultant posterior probability function (solid colored curve, Fig. 14) corresponding to the perceived shift in flash location, is less shifted forward for both red and blue flashes since the higher weighting of the color representation biases the posterior probability curve towards the veridical location of the flash. Although, color opponency theory does not make direct predictions about the relative weighting of each color in a pair; results from the aforementioned study and other previous investigations suggest that red signals are weighted higher than green (Fortier-Gauthier et al., 2013; Saini et al., 2021) and blue signals are weighted higher than yellow (Pomerleau et al., 2014, Saini et al., 2021), which would then differentially bias the Bayesian posterior probability function of a given perceptual or cognitive task.

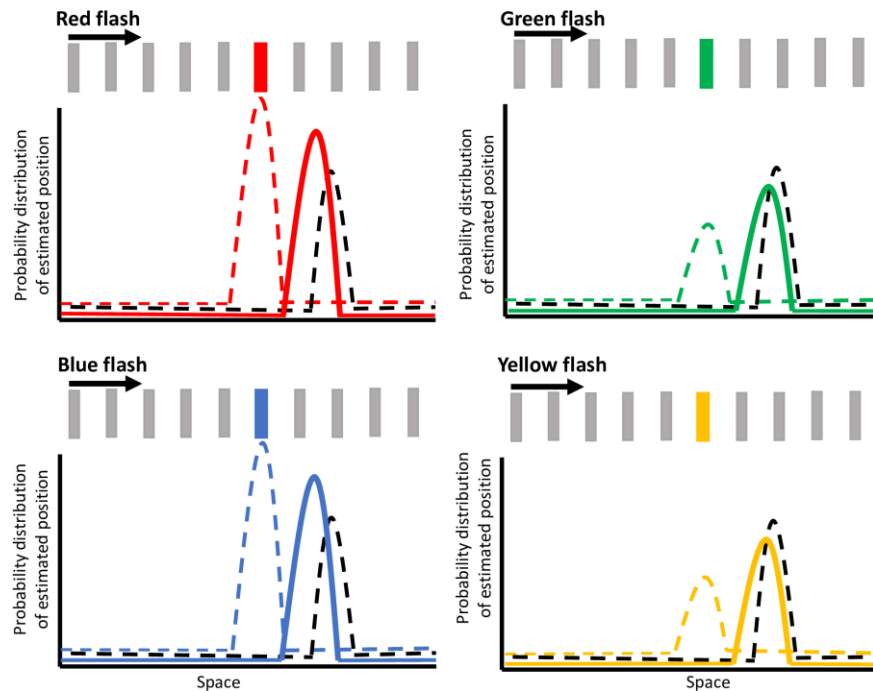


Figure 14. Illustration of the Bayesian framework of color dependent modulation of feature integration. In relation to the color dependent modulation of the flash jump illusion, the dashed black curve depicts the motion extrapolation-dependent position representation for the moving bar at the onset of the flash, represented in motion selective areas such as MT. The dashed colored curve depicts the estimation of the flash location at the onset of the flash for red, green, blue, and yellow flashes in color selective areas such as V4, respectively. Saini et al. (2021) propose that color opponent input feeding into V4 defines the weight of the colored stimuli, with stronger opponent weights for red and blue flashes compared to green and yellow (as depicted by the height of the dotted colored curves), as red and blue flashes were found to reduce the illusory shift. The integration of these two signals is depicted by the solid-colored curve, which represents the probability density function for the mislocalization of the flash, as represented by V4 neuronal responses. This perceived estimate of flash location is less shifted

for red and blue compared to green and yellow flashes. Note that this illustration depicts the flash-continuing condition with the bar moving in the rightward direction and the spacing between bars has been exaggerated for illustration purposes. Taken from: “Color modulates feature integration,” by Saini, H., Jordan, H. and Fallah, M., 2021, *Frontiers in Psychology*, 12, p. 9 (DOI: 10.3389/fpsyg.2021.680558). © Saini, Jordan, Fallah 2021.

We hypothesize that the attentional hierarchy can also differentially assign weights to various colors based on their location in trichromatic color space. A given point in trichromatic color space would have a prior weight based on its distance to each of the unique hue corners (red, green, yellow, blue) (Figure 15, taken from Kehoe et al., 2018) and cone proportions. For example, a reddish point in color space will be closer to the red corner and given that red has 1.6 times the number of cones as green, the reddish hue will have a higher weight than a greenish point that is the same distance away from the green corner. Therefore, based on the distance and cone proportions in color space, red signals are weighted more than green > yellow > blue signals (Tchernikov & Fallah, 2010; Kehoe et al., 2018), setting the color dependent weights in the Bayesian model for later stage processes affected by the attentional color hierarchy.

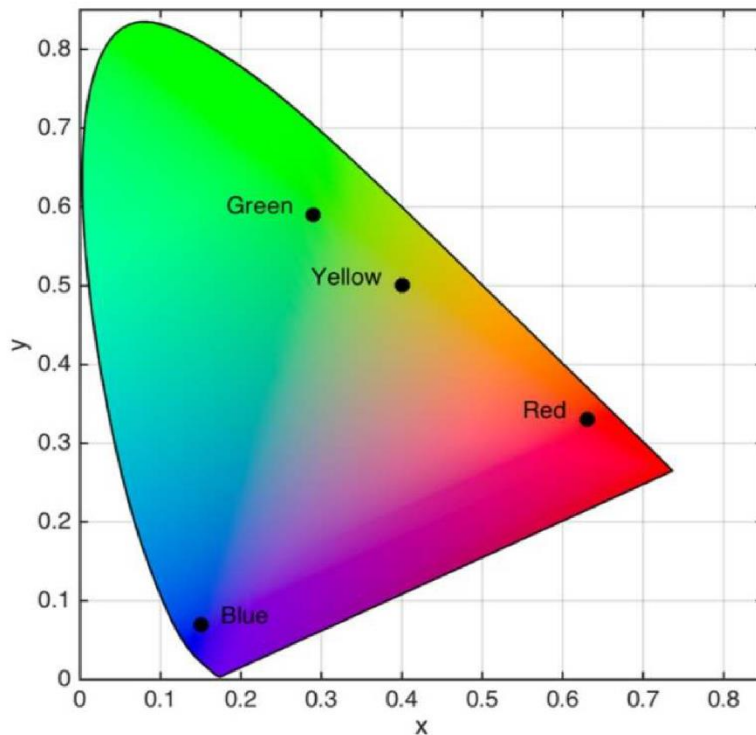


Figure 15. Location of isoluminant red, green, blue, yellow colors in CIE (x,y) color space.

The attentional hierarchy assigns prior weights to each color based on the distance of the color from the unique hue corners in color space (depicted as black dots) and cone proportions. In other words, colors closer in distance from its respective corner will have a higher prior weight.

Furthermore, given the proportions of cone photoreceptors in the retina, $L > M > S$, reddish colors have the highest weights, followed by green and then blue. Taken from: “Perceptual color space representations in the oculomotor system are modulated by surround suppression and biased selection,” by Kehoe D.H, Rahimi, M., and Fallah, M. (2018), *Frontiers in System Neuroscience*, 12(1). p.4 (DOI:10.3389/fnsys.2018.00001). © Kehoe, Rahimi, Fallah 2018.

The color modulation of a given perceptual task such as pursuit target selection can be best explained using an accumulator model for decision making (Palmer et al., 2005), where the noise and the slopes underlying the walk-to threshold get modulated by stimulus color based on

Bayesian weights (Fig. 16). For example, the pursuit of one of two moving RDK surfaces, segmented by color (Tchernikov & Fallah, 2010) occurs through the accumulation of motion information in motion selective areas of the dorsal stream. However, the selection of a given surface over the other is modulated by color information (i.e. attentional color hierarchy) which is integrated into dorsal stream object files. A higher Bayesian weight for one color over the other would result in a reduction in the noise in the walk-to threshold for that colored surface, compared to the second colored surface. This noise reduction results in the higher weighted color reaching the decision threshold faster. Therefore, based on the Bayesian weights established by the attentional hierarchy, we propose that, a red RDK surface reaches threshold first, followed by green, yellow and then, blue (Fig. 16). When making a perceptual decision between a red and a green RDK surface, the red surface is selected first and pursued over green. Similarly, a green surface would be selected and pursued over yellow, and a yellow surface is selected over blue, which is consistent with the hierarchical pattern of color effects observed for pursuit target selection (Tchernikov & Fallah, 2010). Furthermore, that study showed the speed of pursuit of a given surface was dependent on the distance in color space between the colors of the two surfaces. This provides further support for weighted color priors, as an unweighted average of the opposite directions would result in no pursuit, but instead the pursuit speed is dependent on color space distance. Therefore, the attentional color hierarchy provides automatic weighting for colors in color space and these attentional weightings for color drive target selection and competitive motion processing.

A similar Bayesian modification of the accumulator model can also give rise to the color-dependent modulation of other oculomotor processes such as saccadic eye movements. Recently, Kehoe et al. (2018) have reported that saccade curvatures to colored targets in a memory-guided

saccade task are modulated by CIE (x,y) color space distances between the colored target and the distractors, with red targets automatically selected more frequently than green and yellow in the absence of any task demands. Furthermore, the authors report faster latencies and fewer errors for saccades directed to red targets compared to green and yellow. This inherent, hierarchical structure of color effects can be explained by faster decision thresholds and noise reduction in the information accumulation process for stronger colors, similar to the color modulation of pursuit eye movements described above (Tchernikov & Fallah, 2010). Given the relationship between saccade curvatures and CIE (x,y) color space, it is likely that weighted color input (set by attentional hierarchy established in color space) modulates the decision making process such that red targets reach threshold faster with less interference compared to other colors. Once again, the attentional color hierarchy assigns different Bayesian weights to specific colors which then drives the information accumulation process.

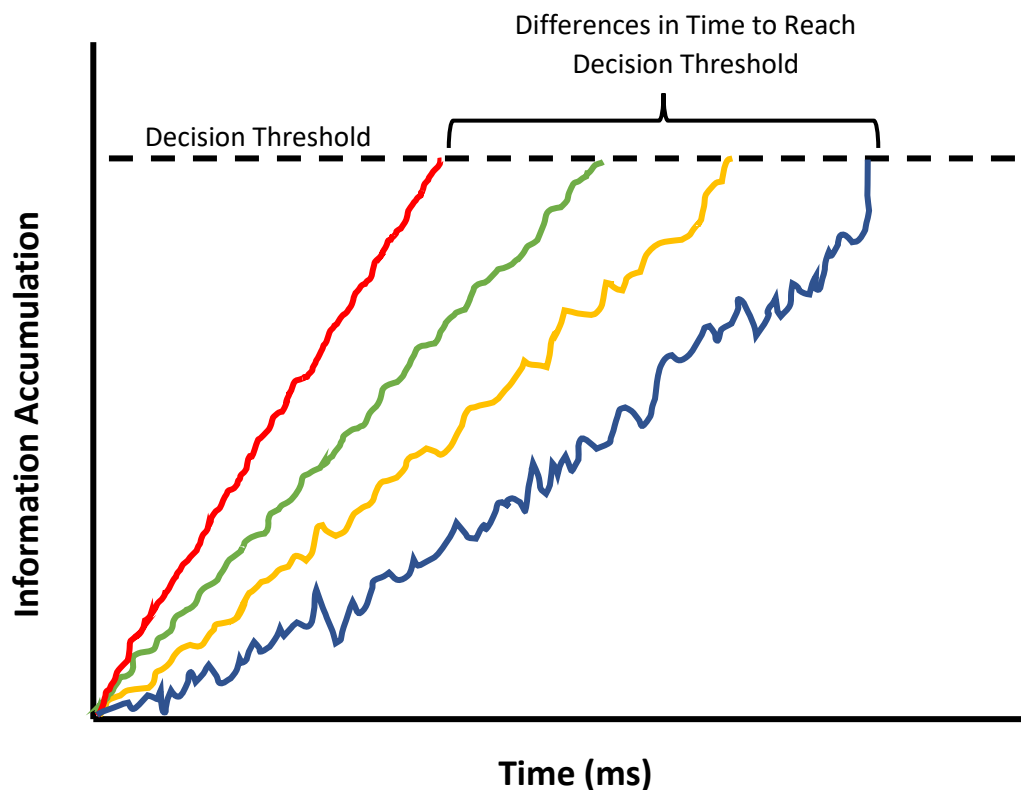


Figure 16. Hypothetical accumulation decision making model. When observers are asked to make pursuit eye movements to one of two colored, moving RDK surfaces, pursuit target selection is modulated by the color of the surfaces. Motion areas in the dorsal stream accumulate information to reach a decision threshold, where the slope and noise in the walk-to threshold is modulated by differentially weighted color priors. Stronger Bayesian priors for one color results in a reduction in the interference in the walk to threshold for that colored surface, resulting in the higher weighted color reaching the decision threshold faster. Based on the Bayesian weights set by the attentional hierarchy, a red stimulus reaches threshold first, followed by green, yellow and blue, resulting in the selection and subsequent pursuit of a given RDK surfaces in a hierarchical manner; red > green > yellow > blue. The walk to decision threshold for red, green, yellow, blue RDK surfaces, depicted as their respective colored curves. Adapted from “Feature integration

and object representations along the dorsal stream visual hierarchy”, by Perry, C. J. and Fallah, M. (2014), *Frontiers in Computational Neuroscience* 8 (84). p. 8.

(DOI:10.3389/fncom.2014.00084). © Perry and Fallah, 2014.

Finally, within a Bayesian framework, top-down visual association circuits can modulate visual processing by changing the weight of priors through learning or innate biases, thus resulting in different cognitive and behavioral outcomes, e.g., response inhibition mediated by prefrontal circuitry. The facilitatory effect of red on response inhibition (Blizzard et al., 2017, Ghasemian et al., 2021, Asare et al. in review-a), arising from learned or innate visual associations can be explained by a modification of the horse-race model of executive control, proposed by Logan and Cowan (1984) (Fig. 17). The authors suggest that response inhibition, and response execution are two independent processes competing to reach a decision threshold. If the delay (SSD) between the go and stop signal is large, the observer responds to the go-signal and executes the action, as they are unable to stop in time (gray curve, Fig. 17A). In contrast, if the SSD is small, the observer is able to stop in time, and withhold responding, therefore response inhibition, instead of execution, reaches threshold first (red and green curves, Fig. 17B). In consideration of the red-stopping bias observed in various SST studies, a red signal is able to reach threshold faster, compared to a green-stop signal, thus facilitating response inhibition faster than green (Fig. 17B). As mentioned previously, this advantage for red as an effective stop signal is likely established through visual associations (innate and learned), resulting in a stronger prior weighting for red in tasks involving response inhibition.

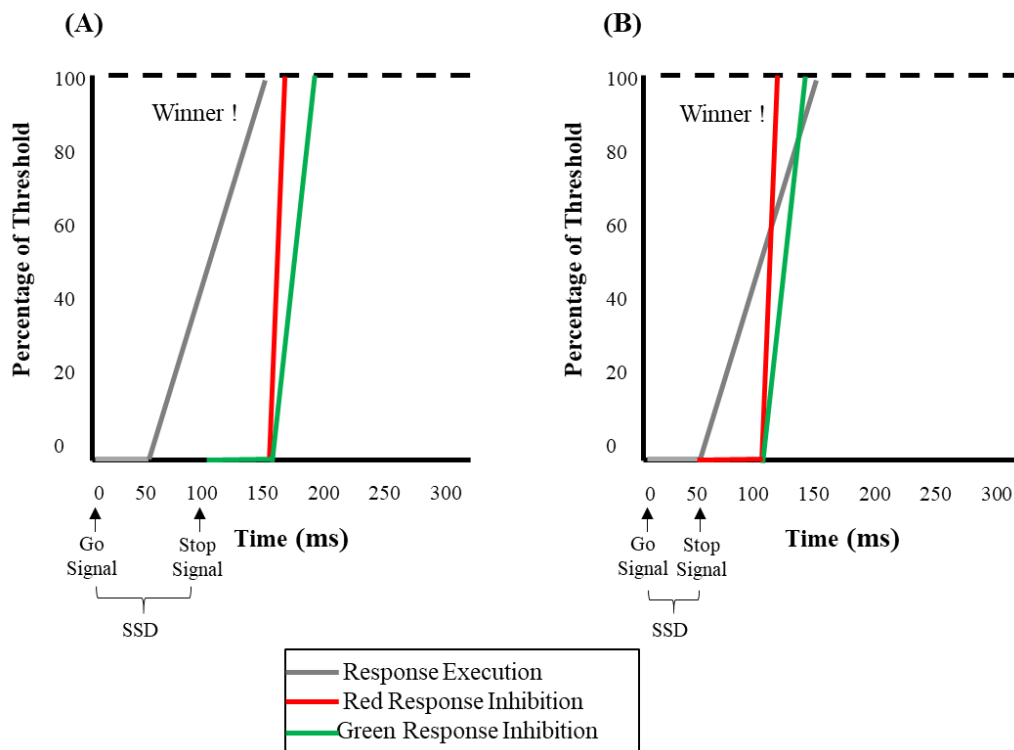


Figure 17. Race-horse model of response execution and response inhibition in SST task.

During a stop signal task, two independent processes, response execution and response inhibition, compete to reach a decision threshold. The process that reaches threshold first wins.

The gray line represents the time it takes for the execution of an action, whereas the red and green lines represent the time course for the inhibition of response for a red and green stop-signal, respectively. **(A)** Given a large delay between the onset of the go versus the stop signal (SSD), response execution reaches threshold first, therefore the action is executed. **(B)** For smaller SSDs, the participant is able to withhold their response in time, therefore response inhibition reaches threshold first. More specifically, behavioral studies have reported that red-stop signals, result in faster response inhibition compared to green-stop signals.

6.6 CONCLUDING REMARKS

Advances in the field of vision research have shown that the color of a signal can alter visual processing, affecting resultant cognitive and behavioral outcomes. In reviewing these studies, we have organized the findings into three underlying mechanisms: color opponency, attentional hierarchy, and visual associations. The hierarchical nature of the ventral and dorsal visual pathways allows for color-dependent modifications to occur at various stages of visual processing, depending on the mechanism at play. We have proposed how these three mechanisms are distributed across the visual processing stream, and also that the effects of color on cognitive and perceptual processes occur through Bayesian frameworks.

Therefore, it may be critical to consider the impact of aesthetically based color decisions on various aspects of psychological functioning, as color can influence our cognition and behavior. Furthermore, color modulation of cognitive and perceptual processes has significant implications for the development of human-computer interfaces and other technology. For example, previous work on neurodegenerative diseases (ND) has demonstrated that in people affected with NDs, executive functioning and cognition begin to deteriorate over time. Therefore, colors that bolster different cognitive, attentional, and other executive functions can be used to design appropriate visual inputs, living spaces, applications, and graphical interfaces for people with Alzheimer's and dementia, while avoiding colors that may weaken those processes. Given the influence of color on the human brain, as researchers, we must also carefully design and select appropriately colored stimuli for experimental research and interpret the results accordingly.

AUTHOR CONTRIBUTIONS

HS designed the theory, reviewed the literature, placed the findings into the theory framework and drafted the article. MF designed the theory, provided feedback on the framework, and revised the written draft.

FUNDING

This work was funded by a Vision: Science To Applications (Canada First Research Excellence Fund) Master's scholarship to HS, and an NSERC Discovery Grant (RGPIN 2016-05296) to MF.

CHAPTER 7

GENERAL DISCUSSION AND CONCLUSIONS

7.1 GENERAL DISCUSSION

Previous studies have reported that task-irrelevant color can influence high-level visual functions such as attentional selection (Tchernikov & Fallah, 2010), visual search (Lindsey et al. 2010; Fortier-Gauthier et al., 2013; Pomerleau et al., 2014) and response inhibition (Blizzard et al., 2017; Ghasemian et al., 2021), through driving differences in later stage decision making processes. In the first published research paper (Chapter 5), we investigated whether such color dependent modulations of visual processing can also be observed for low-level perceptual processes such as feature integration, using the flash-jump illusion. Our findings revealed that the color of the object modulates the integration of color and non-color features (i.e. motion), and thus, our perception of the flash-jump illusion. More specifically, red and blue flashes result in both more accurate and precise representations of the flashed object, compared to green and yellow, consistent with the predictions made by color opponency, thus implicating color opponent mechanisms in the color modulation of low-level processes. To our knowledge, this is the first report of object color modulating the integration of other features, as well as, evidence for the color-dependent modulation of low-level visual processes.

Given that prominent theories of motion induced position shifts (Nijhawan, 1994; Whitney & Murakami, 1998; Eagleman & Sejnowski, 2000; Schneider, 2018) are unable to fully account for and explain our current findings, we have interpreted the color-dependent modulation of the flash jump illusion in terms of a Bayesian framework, providing a new approach to understanding motion-based position shifts, as well as the integration of color and motion information. We

proposed that the color-dependent modulation of the flash jump effect is dependent on the representation of the flash being weighted differently by color, which is then integrated with motion information, giving rise to a posterior probability distribution corresponding to our perception of the illusion. This posterior probability function is differentially shifted forward based on flash color. In line with our current findings, a higher weighting is given to red and blue which likely arises due to weighted color opponent input where red and blue are the stronger, more advantaged colors from their respective opponent pairs. Therefore, red and blue flashes are less shifted forward than green and yellow.

This conceptual approach to color-dependent modulations is attractive because similar Bayesian frameworks can be applied to other visual processes and cognitive tasks as well to explain color differences. Future studies will be necessary to further test the empirical validity of this framework. Sundberg et al. (2006) report neural correlates of the flash-jump illusion in area V4, where, in response to the flashed stimuli, the receptive fields of V4 neurons were shifted along the direction of motion. However, the neural correlates for this Bayesian color modulation process are currently unknown. Given the previously observed retinotopic shifts in V4 neurons, it is expected that the color modulation would also be reflected within V4, with smaller retinotopic shifts for red and blue flashes. However, further neurophysiological and recording studies, testing the response of V4 neurons to all four colored flashes (i.e. red, green, yellow and blue) are required to confirm this prediction. Furthermore, it is important to note that even if the color modulation of the flash jump illusion is reflected in V4 neuronal responses, it does not necessarily confirm that the Bayesian process also occurs within V4. The Bayesian integration could occur outside of V4, perhaps, IT cortex or other higher level visual areas, which is then relayed back to V4 through feedback connections. Functional or virtual lesion studies may be

employed to elucidate the role of such other cortical areas. For example, persistence of color-modulated retinotopic shifts in V4 neurons after the application of TMS or cooling to the IT cortex would suggest that the Bayesian process occurs at the level of V4 or before it, while the absence of color-modulated retinotopic shifts in V4 suggests the involvement of higher order visual areas.

Furthermore, the current study is limited to four colors, corresponding to the color opponent system. Mixed colors, which are colors composed of two opponent colors may also be tested in future investigations to validate the color opponent weightings established in Chapter 5. We found that both red and blue have stronger Bayesian weights, resulting in more veridical, and less shifted representations of flash location. Therefore, based on these Bayesian weights, a color which is a mix of red and blue, such as purple, would also be less shifted. Similarly, a color which is a mix of a stronger (i.e. red) and a weaker color (i.e. yellow) such as orange would be more shifted compared to purple. Thus, the pattern of shifts for mixed colors, as an extension to our first study can further validate the opponent weights observed.

More generally, future experiments should also investigate the influence of object color on the integration of other object features such as shape, orientation etc., to determine whether the color modulation of feature integration is specific to the binding of motion information only, as demonstrated currently. Illusory conjunctions are errors in feature binding, where features of two different objects are mis combined into one object representation (Treisman & Schmidt, 1982). For example, color and shape features of a red circle and green square may be mis-combined and reported as a new object, a red square. Given that specific colors have been shown to modulate attention and attentional resources (Tchernikov & Fallah, 2010), perhaps this advantage is also

reflected in the integration of color and another feature such as shape, where certain colors reduce such illusory conjunctions.

As a result of our findings, in the second manuscript, we attempted to address unexplored questions related to the underlying neural mechanisms involved in color-dependent modulations. Although the effect of color on various aspects of psychological functioning such as attraction, motor performance, and cognitive performance has been reviewed in the past (Elliot & Maier, 2014; Elliot, 2015, 2019), there are large gaps in the existing literature. For example, much of the research in this field has focused on answering applied questions such as the link between color and consumer behavior (for a review see, Paul & Okan, 2011), food consumption (Shankar et al., 2009; for reviews, see Shankar, Levitan, & Spence, 2010; Spence et al., 2010), productivity (Kwallek, Lewis, & Robbins, 1988; Hatta et al., 2002; Kwallek, Soon, & Lewis, 2007; Küller, Mikellides, & Janssen, 2009, for a review, see, Savavibool, 2016), while only a small number of studies in comparison have investigated the effect of color on visual processes, attention and perception. Moreover, existing literature on color and psychological functioning has focused on providing evaluations of empirical advances, and recommendations for future research, however, possible underlying neural mechanisms or circuitry to explain such color modulations have not been adequately addressed. Therefore, to address these gaps, we reviewed different color effects reported for attentional and perceptual tasks to develop a theory of color-dependent modulations which describes three putative neural mechanisms and respective brain regions involved in color-dependent modulations of visual processing based on the level or stage that the visual process is conducted at (Chapter 6). Given that many aspects of visual perception follow a Bayesian framework, we also described how each color mechanism may get incorporated into a Bayesian

framework of perception to differentially assign color weights which modulate processes in the visual system at various stages.

Firstly, opponent color mechanisms (red vs green, blue vs yellow) arising from opponent circuitry in the LGN would allow for color-dependent modifications of early visual processes by advantaging one color from its competitive pair, while simultaneously disadvantaging the other. Therefore, our theory predicts that we would expect to find differential processing of colors within opponent pairs, but no differences between pairs as the opponent channels are independent of one another. We would expect to see significant differences between red and green signals, as well as blue and yellow signals, as corroborated by our behavioural experiment. As mentioned previously, current empirical evidence suggests that red signals are weighted higher than green (Fortier- Gauthier et al., 2013; Saini et al., 2021), and blue signals are weighted higher than yellow (Pomerleau et al., 2014, Saini et al., 2021), however, future studies are required to further validate these color opponency weightings by testing other low level visual tasks which may be modulated through color opponent mechanisms.

Next, the attentional color hierarchy (Tchernikov & Fallah, 2010), suggests a hierarchical structure of attentional advantage give to various colors. This mechanism predicts a significant difference between all colors, wherein red signals are weighted > green > yellow > blue. We propose that color selective neurons in area V4 likely give rise to this attentional hierarchy, modifying intermediate stages of visual processing. It should be noted that current evidence for color dependent modulations via attentional color hierarchy comes from various aspects of dorsal stream processes (Tchernikov & Fallah, 2010; Kehoe et al., 2018), future studies are needed to confirm the role of the attentional color hierarchy in modulating ventral stream processes.

Lastly, we theorized that visual associations which are implicit associations between repeated pairings of colors and specific messages based on learning, experience, or innate biases may also modulate later stages of the visual processing hierarchy through long-range, top-down signals from the prefrontal cortex (PFC). Current investigations have found strong support the association between red and stopping, which has been shown to differentially modulate various response inhibition tasks (Blizzard et al., 2017; Ghasemian et al., 2021). However, whether or not there are other color associations which modulate visual processing is unknown.

Furthermore, the interplay between evolutionary preserved color biases and learning/experience in the formation of strong color associations is not well understood. It may be fruitful to investigate the developmental course of color associations (i.e. from infancy to adulthood) to elucidate the role of evolution versus learning.

More generally, in the second manuscript, we have provided a theoretical framework for understanding and explaining the neural mechanisms which may underlie color dependent modulations. Future studies are required to validate the predictions and the neural correlates of each mechanism. Given that the proposed mechanisms predict different pattern of color effects for a given visual process, this allows for an effective way to empirically distinguish between them. Furthermore, we have theorized the involvement of specific brain regions for each mechanism based on the functional and structural organization of the visual system, however, future neuroimaging or neurorecording studies are required to confirm the exact neural correlates for each mechanism. Moreover, only a handful of studies have directly explored the link between color and visual processing, more studies employing various visual tasks are required to evaluate how ubiquitous these color modulations of visual processing are.

7.2 CONCLUSIONS

The manuscripts presented here have met their objectives outlined in Chapter 4 and have provided insight into how object color influences low-level visual processes, specifically, as well as visual processing in general. This thesis contributes to our understanding of inherent and automatic color dependent modulations and the mechanisms that may underlie such modulations. We demonstrated that color of the flash modulates its perceived location in the flash jump illusion, and thus the integration of color with motion information. We have also provided a novel interpretation of these results using a Bayesian framework to explain how the integration of color and motion information gives rise to the flash-jump illusion as well as its modulation based on the color of the flash. In addition, our theory of color-dependent modulations provides a general Bayesian framework for how color intrinsically modulates processing of information in the visual system through three mechanisms; color opponency, attentional hierarchy, and visual associations, as well as, outlining the predicted pattern of color effects and brain regions that may be involved for each mechanism.

Given the accumulating evidence for automatic and inherent color dependent modulations of psychological functioning, it may be critical for us to consider the impact of everyday color decisions such as the color of a dress, a room etc., as color can differentially influence our cognition and behavior. More importantly, seemingly irrelevant decisions regarding the color of experimental stimuli may have confounding effects as color is shown to modulate cognitive processes even when irrelevant to the experimental task. Finally, color research also has significant implications for the development of medical devices and technology, where specific colors which have been shown to reduce illusory shifts, or improve visual processing, executive and cognitive functions can be used to design graphical interfaces and applications for people who suffer with deficits in these domains.

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