THE IMPACT OF COLOR ON RESPONSE INHIBITION

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Abstract

Response inhibition is an important cognitive function that affects decision-making and action selection. Impairments in it occur in neurodegenerative diseases therefore, ways to support response inhibition are important for quality of life. One possibility is the use of color, as color has been shown to modulate inhibitory processes. The overall objective of this work was to determine the prefrontal networks underlying response inhibition that can be modulated through an automatic attentional process such as color. A series of three studies were performed whereby young adults performed a stop-signal task (SST) or a Go/No-go task (GNGT) with colored stimuli. In our first study, the SST, a reactive response inhibition task, was performed to determine whether the effect of color on response inhibition was due to color opponency, attentional color hierarchy, or visual associations. We found that while red stop signals produced faster response inhibition compared to green, blue and yellow stop signals did not differ from each other. This pattern of results was not consistent with color opponency or the attentional color hierarchy of red > green > yellow > blue. Therefore, red facilitating and green impairing response inhibition suggested that response inhibition was modulated by visual color associations where red means stop and green means go. In our second study, we tested if the color modulations between red and green extended beyond countermanding to more general inhibitory control by using a proactive response inhibition task, the GNGT. Indeed, participants were more successful on red in comparison to green No-go trials. Based on these results, a modified accumulator model and putative neural circuitry of color modulation response inhibition was proposed. In our third study, event-related potentials (ERPs) were recorded while participants performed a GNGT to test the putative underlying neural network. While the P300 was not modulated by color, we observed reduced N200 amplitudes and earlier N200 latencies

over the prefrontal areas proposed in study 2 in response to red No-go stimuli over green, yellow, and blue. The increased accuracy was argued to be an advantage conferred by learned and evolutionary associations to the colour red. The decreased N200 amplitudes suggested reduced conflict on No-go trials with red No-go stimuli compared to other colours. These findings bring us a step closer to mapping out the differential colour modulated neural circuitry involved in response inhibition and such research will help pave the way for efficient decision-making and staving off cognitive decline.

Dedication

I would like to dedicate this dissertation to my mother and father, Victoria Boateng and Otoabaa Asare-Baffour as well as my siblings Kofi, Anoah, and Ezekiel. Thank you for your continuous prayers, support, and encouragement.

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TABLE OF CONTENTS

List of Figures

List of Tables

CHAPTER 1: INTRODUCTION

According to Verbruggen & Logan (2008), "response inhibition is a hallmark of executive control referring to the suppression of inappropriate actions, which supports flexible and goal-directed behavior in environments". Response inhibition is also known in the literature as inhibitory control because it essentially helps one inhibit their natural tendencies or impulses in order to select a more appropriate response. For processing to be efficient, relevant information must be activated, and irrelevant information must be suppressed (Engle, Kane & Tuholski, 1999). Response inhibition tasks frequently involve 2-choice decision-making paradigms that sometimes utilizes colored stimuli. Color is an important feature for object discrimination and recognition (Swain & Ballard, 1991; Tanaka, Weiskopf, & Williams, 2001; Gao & Vasconcelos, 2007; Bramão et al., 2011; Hagen et al., 2014). Color is also integrated into object representation and can be used to guide visual processing to objects of interest through feature-based attention and attentional capture (Saenz, Buraĉas, & Boynton, 2003; Jolicoeur, Brisson, & Robitaille, 2008; Lennert et al., 2011; Ansorge & Becker, 2013; Khan, Van De Weijer, & Vanrell, 2009; Perry et al., 2012, 2014). As such, color presents a unique opportunity to investigate the mechanisms underlying response inhibition as the ability to suppress an inappropriate or undesired choice is an essential aspect of the decision-making process that has implications in the fields of health, sports, and technology.

CHAPTER 2: LITERATURE REVIEW

2.1 Response Inhibition Tasks

Questions concerning response inhibition that have been of interest are determining which factors or mechanisms manipulate response inhibition and how they do so at the neural level. In order to address these questions, a suitable paradigm to investigate response inhibition is needed. The earliest task to look at inhibition was the Stroop task (Stroop, 1935). In the task, subjects are presented with printed word colors (red, green, blue, and yellow) in either matched or unmatched ink. A subject automatically determines the semantic meaning of the word and then must consciously monitor itself and identify the color of ink in which the word is printed in instead; a process that is not automated. Stroop noted that participants took significantly longer to name the ink in which a word was printed instead of reading the word presented when both were unmatched. The interference that occurs was explained by how automatic reading is, where the brain instinctively determines the semantic meaning of the word (it reads the word "red" and thinks of the color "red"), and then must intentionally inhibit itself and identify instead the color of the word (where the ink is a color other than red). The fact that the network was trained more extensively with word stimuli than with colors meant that linguistic pathways had greater strengths than color ones. Thus, the strength of a pathway determines its speed of processing. In actuality, the Stroop effect is one of interference in the reaction time of a task however, recent inhibition research posits that individuals with a deficit in response inhibition (e.g., individuals with attention deficit disorder) performed worse on the task because they were not able to successfully stop (inhibit) the automated process of reading to name the ink (Lansbergen, Kenemans, &Van Engeland, 2007). While this task has been of great use, it is challenging to

modulate its' level of difficulty and as previously mentioned, it not only looks at inhibition, but at interference to the lingual pathway which sometimes runs the risk of confounding the inhibition literature.

In contrast, the Go/No-go task (GNGT), dependent on proactive response inhibition, selectively studies inhibitory control by measuring a participant's impulsivity and their capacity for sustained attention. In a Go/No-go test, one is required to perform an action given certain stimuli (e.g., press a button when a green stimulus is presented - Go) and inhibit that same action under a different set of stimuli (e.g., do not press that same button when a red stimulus is presented - No-go) (Donders, 1969; Logan, Cowan, & Davis, 1984; Verbruggen & Logan, 2008). Given that participants determine on each trial whether to respond or not, the task relies on proactive instead of reactive response inhibition (Aron, 2011). The task is very flexible in terms of modality and thereby enables a rigorous study of the cognitive processes underlying how motor activity is modulated. Nevertheless, this inhibitory task consists of Go trials where a participant is performing a motor action and Stop trials during which they are withholding a motor response. Behaviorally, this lack of motor activity during Stop trials presents a critical difference that sometimes needs to be accounted for. Therefore, an important component in designing an inhibition task is to ensure that prepotent motor activity is elicited on each trial, so that No-go trials can be accurately compared to Go trials to truly reflect inhibitory control.

The stop-signal task (SST) addresses the previously mentioned issue. It utilizes reactive response inhibition as it requires countermanding an already initiated response without any prior preparation (Aron et al., 2007; Chambers, Garavan, & Bellgrove, 2009; Chikazoe, 2010; Aron, 2011). This differs from proactive response inhibition (Cai, Oldenkamp, & Aron, 2011; Aron, 2011; Bloemendaal et al., 2016; Langford et al., 2016) which is based on inhibiting a response

based upon an initial perceptual decision-making process, such as in the go/No-go task. This task can be best understood as a more challenging version of a Go/No-go task. Introduced by Lappin and Eriksen in 1966, and further developed by Logan and Cowan (1984), the task demonstrates how once you have decided to initiate a movement, it is difficult to stop. In Go/No-go paradigms, there are stimuli you need to respond to, and others that you should not respond to. In the SST, the Go signal you need to respond to is always presented and therefore, response execution is always initiated. Therefore, that mental process can be studied when it has to be suppressed after a Stop signal is presented on select trials. In this task, the mechanisms of execution and inhibition are compared to a 'horse race' between Go and Stop processes that are believed to evolve independently over time. By varying the time between presentation of a Go-signal and Stop-signal (i.e.: the stop-signal delay (SSD)), one can manipulate whether the Stop process can be implemented sufficiently before the go-process (i.e.: whether inhibition will succeed or not) (See **Figure 1**). As such, an important contribution of this race model is that it provides a way to infer the time required for the Stop-process to catch up to the Go-process; the Stop-signal response time (SSRT) (See **Figure 1**). The SST is therefore a better reflection of real life because it allows one to quantitatively study at which point an initiated process cannot be stopped anymore.

Stop Signal Paradigm

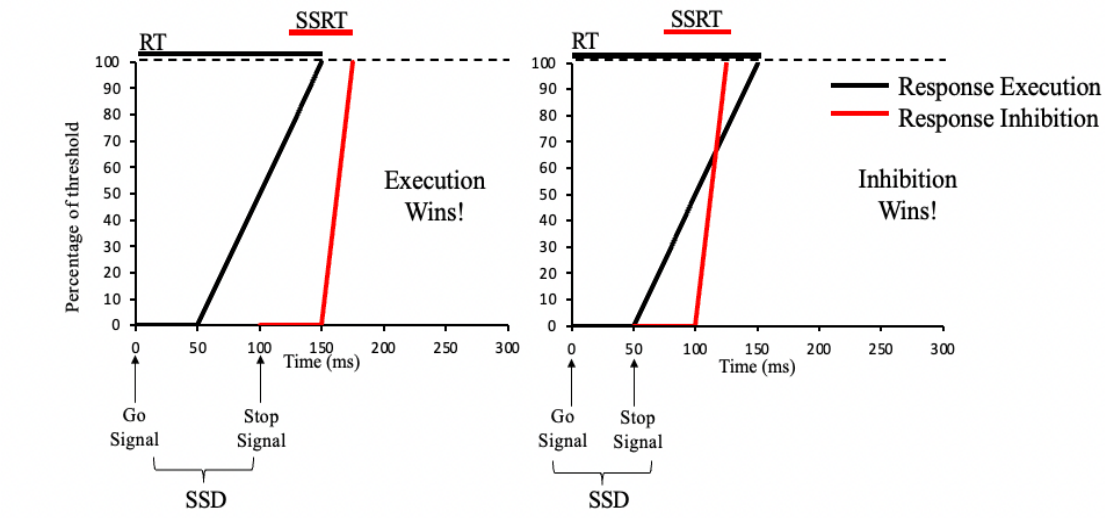

Figure 1. **Stop-Signal Paradigm: Race-horse Model.** A model of the cognitive process that occurs during the stop signal task termed 'race horse' to depict the competition between response execution (black) and response inhibition (red) processes. In the left diagram, a Stop-signal is presented after a long time delay (i.e.: SSD); therefore response execution is activated and wins over inhibition. In the right diagram, a Stop-signal is presented after a short time delay; therefore, response inhibition is activated and wins the race.

While the SST and the Go/No-go task are sometimes used interchangeably to study response inhibition, they assess and utilize different inhibitory processes. Because the SST initiates response execution on every trial, it relies on action cancellation and recruits sensory, motor, and prefrontal areas to countermand the developing response (Schachar et al., 2007; Raud et al., 2020). In contrast, the Go/No-go task requires identification of the item on each trial to determine whether or not to make a response, thereby relying on response execution or action restraint, without any parallel competing processes (Schachar et al., 2007; Raud et al., 2020).

2.2 Brain Structures associated with Response Inhibition

The precise localization of response inhibition within the prefrontal cortex (PFC) has proven to be controversial and difficult. The many variations of inhibition tasks spanning all sensory modalities have resulted in somewhat inconsistent results in mapping the regions of activation involved in the process. SST experiments have accounted for this by isolating the neurological Go processes from the Stop ones. Given that the Go processes are always activated in the SST task, they can be subtracted out of the Stop ones (Logan & Cowan, 1984; Enriquez-Geppert et al., 2010). Despite some observed inconsistencies, inhibition studies agree that there is frontal region activation involvement (Enriquez-Geppert et al., 2010; Aron, 2011; Schall et al., 2017; Verbruggen & Logan, 2017). This has prompted some investigators to consider the multiple domain hypothesis of response inhibition. The latter describes functional subdivisions in which activations within the frontal and subcortical regions govern different domains of response inhibition (Boehler et al., 2010). fMRI studies have greatly contributed to this hypothesis by helping identify the network of brain areas in the right-hemisphere responsible for response inhibition. This hypothesis posits that in response to a Stop stimulus, a signal from the right inferior and/or medial frontal cortex is sent to the basal ganglia to cancel the motor program triggered by the Go stimulus. This input enters the basal ganglia through the "hyperdirect" route of the subthalamic nucleus (STN), or the "indirect" route via the striatum (the caudate nucleus and the putamen). Then, interactions between the different parts of the basal ganglia and the associated STN give rise to a signal that is sent via the thalamus to the motor cortex, where the response is inhibited (Boehler et al., 2010) (see **Figure 2**).

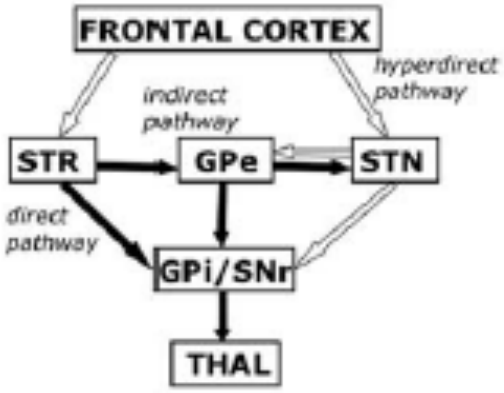

Figure 2. **Neural Pathways of Response Inhibition.** A model of the proposed three pathways of the multiple domain hypothesis going from the frontal cortex to the thalamus (direct, indirect, and hyperdirect). SNr, Substantia nigra; THAL, thalamus; STR, striatum, and ending in the thalamus before being redirected. White arrows are excitatory (Glutamatergic); black arrows are inhibitory (GABAergic). Figure taken from Aron & Poldrack (2006).

The claim of predominantly right hemispheric activations corresponding to response inhibition has been clarified in a study comparing both the GNGT and SST. Using fMRI, Rubia et al. (2001) were able to distinguish which brain regions were comparable and which ones differed among the two tasks. The researchers found that while selective inhibition in a Go/No-go task activates a bilateral, but more left hemispheric frontal and parietal network, withholding a planned motor response in a Stop task elicits a homologous right hemispheric network. This allowed them to conclude that the inferior frontal cortex seems to be specifically related to motor response inhibition, while dorsolateral, medial prefrontal, and parietal cortices mediate more general motor executive control functions such as motor attention, conflict monitoring, and response selection, necessary for inhibition task performance. So, the Go/No-go task with a lower load on inhibition elicits specific left hemispheric dorsolateral, medial prefrontal, and

parietal activations responsible for response selection. On the other hand, activations during the SST performance are more right hemispheric. Since then, numerous studies have pointed out a right-lateralized fronto-basal network at the core of the inhibitory control of motor action in SST (Aron and Poldrack, 2006; Verbruggen and Logan, 2008). In 2007, Chevrier, Noseworthy, & Schachar isolated error detection activity using trials in which a Stop-signal appeared, but the response was executed. These trials were modeled as Go-trials that were followed by error processing. The researchers found that response withdrawal activated the right inferior frontal gyrus and the basal ganglia while error detection, invoked by failed inhibition trials, activated the dorsal anterior cingulate cortex (dACC) and right middle frontal area. These findings supported the multiple domain hypothesis by confirming that there are distinct aspects of inhibition and performance monitoring which come into play at various phases of the SST (Chevrier, Noseworthy, & Schachar, 2007).

In a SST designed to relate performance to the degree of damage within specific prefrontal regions, Aron et al. (2003) studied patients with lesions to the right frontal lobe. They hypothesized that if the right prefrontal cortices were critical for response inhibition, then the extent of damage to the right inferior frontal gyrus (IFG), but not other areas would correlate with task performance. In their task, a left- or right-pointing arrow stimulus was displayed on a computer screen. The subjects responded with a left or right key press as quickly as possible (Go-signal) unless they heard a beep, in which case they tried to withhold a response (Stop-signal). SSRTs for patients with right frontal lesions were significantly slower than for controls. To test the specific hypothesis that the right IFG was critical for response inhibition, they correlated the damage to various regions of interest (ROIs) with SSRTs and found that indeed, the strength of correlation between SSRTs and right IFG was significantly greater than between

SSRTs and any other ROIs. These findings were specific to the right frontal lobe because patients with left frontal cortex lesions had significantly faster SSRTs that did not significantly correlate with performance. Their results demonstrate how a specific executive function, response inhibition, can be localized to a lateralized discrete region of the PFC (Aron et al., 2003). Once this was observed, Enriquez-Geppert et al. (2016) capitalized on the ease of increasing difficulty levels in the SST by having infrequent Stop trials with frequent Go responses. They observed that one endures a high conflict when going against an automated response such that the midcingulate cortex (MCC) and the dorsal anterior cingulate cortex (dACC) are more activated. The MCC in particular was said to detect the competition between the internal representations of withholding versus executing a response (Enriquez-Geppert et al., 2016). Their findings support previous claims that both structures are important for conflict detection (Botvinick, Cohen, & Carter, 2004; Braver et al., 2001). Following this detection of conflict, the pre-SMA has been identified as being important for preparation and inhibition of skeletomotor responses (Li et al., 2006). It's a cortical structure that has been implicated in volitional motor and cognitive control, as well as response planning and selection (Li et al., 2006). Therefore, we can begin to see a network form where once we detect conflict through the MCC or dACC, we get ready inhibit it using the pre-SMA. In 2006, Li et al. compared subjects who had long SSRTs to those who had shorter ones (i.e.: faster at inhibiting their responses). They demonstrated that shorter SSRTs correlated with greater activation in the anterior pre-SMA. Also, the effect size of its activity was positively correlated with the caudate (a structure of the basal ganglia). The authors concluded that these brain regions may represent the neural substrate of response inhibition independent of other cognitive functions (Li et al., 2006). The connection they made between the prefrontal and subcortical structures reiterates the previously

discussed multiple domain hypothesis of inhibition and paves the way for research focusing on the mechanistic network or response inhibition.

2.3 Color and Response Inhibition

Tchernikov & Fallah (2010) tested whether color could automatically bias selection. During a smooth pursuit task, they revealed that smooth pursuit was modulated by the color of the surface pursued. Even though the colors tested were equiluminant with each other, changing the color of the surface while maintaining the same velocity and luminance resulted in changes in pursuit velocity indicating that color modulates motion processing. In that same study, without a task demand to pursue, subjects presented with two superimposed surfaces equal in luminance and speed pursued one of the two superimposed surfaces showing that color differences alone drove target selection. Subjects showed a preference for pursuing red over other colors, a preference for green over yellow and blue, and a preference for yellow over blue. That same year, Lindsey *et al*. studied reaction times to targets of different desaturated colors (red, green, blue, and orange) placed in a visual display among white and saturated distractors (Lindsey et al., 2010). In their study, participants had to indicate the presence or absence of a target on every trial and the authors found faster RTs for desaturated red than desaturated orange and green, and slower RTs for desaturated blue. The previously mentioned studies support there being an attentional bias for some colors over others. Tchernikov and Fallah (2010) helped establish a color hierarchy of red>green>blue>yellow that had a hand in modulating motion processing and we wondered if the same could be observed for response inhibition mechanisms.

Blizzard *et al*. (2017) used a SST to study if this established color hierarchy could be extended to response inhibition. Participants performed the task using red and green colored

stimuli and the authors discovered that response inhibition but not execution was facilitated by red over green. However, their paradigm could not identify the mechanism accounting for the facilitation of red over green and thereby could not explain what happens to response inhibition when a color change signifying a stop signal appears. That is, could color be used to modulate response inhibition thereby providing an opportunity to map out the circuitry of this mental process?

2.4 The N200/P300 complex and Response inhibition

Electroencephalography (EEG) is a non-invasive neuroimaging method that records the electrical activity of the brain. Event-related potentials (ERPs) are measured brain responses that investigate voltage fluctuations time locked to an event, such as the onset of a stimulus or a button press resulting from specific sensory, cognitive, or motor events.

There is not yet an undisputable ERP signature of the response inhibition process; however, EEG investigations of the SST usually reveal a well-known N200/P300 complex. The N200 (N2) event-related potential (ERP) component is characterized by a frontal central negative potential with a latency of 200-300ms post stimulus presentation (Falkenstein, Hoorman, & Hohnsbein, 1999; Gajewski, Stoerig, & Falkenstein, 2008). Reliably, an augmented No-go N2 is observed compared to the Go N2 and is often interpreted as reflecting the inhibition required in stop-trials (Kok et al., 2004; Enriquez-Geppert et al., 2010; Huster et al., 2010; Huster et al., 2013). The increased N2 amplitude in No-go vs Go trials may reflect the activation of the response inhibition process as well as the inactivation of response execution (Géczy et al., 1999; Baumeister et al., 2014). Additionally, varying response frequencies can enhance the N2 amplitude. Nieuwenhuis et al. (2003) reported an enhanced Go N2 when presenting rare go-trials

(20 % chance of presentation) in the context of frequent No-go trials. These observations indicated that the N2 might reflect conflict caused by competition between the frequently and infrequently required responses in the context of conflict-monitoring and the overall early processes in response inhibition (Nieuwenhuis et al., 2003; Randall & Smith, 2011).

The P300 (P3) ERP component is characterized by a positive frontal central polarity and latency of 300-600 ms post stimulus onset. As with the N2, amplitude differences have been found in response to Go versus No-go trials and varying response frequencies (Dimoska, Johnstone, & Barry, 2006; Kok et al., 2004; Ramautar, Kok, & Ridderinkhof, 2004). The frontocentral P3 is the most common ERP index of successful response inhibition with many studies having shown increased P3 amplitudes for successful versus failed stop trials in healthy individuals (Wessel & Aron, 2013; Huster et al., 2013). The component's latency range has led to suggestions that it reflects late-stage/ finalization of response inhibition processes (Band & van Boxtel, 1999; Donders & Van Boxtel, 2004; Tian, Liang, & Yao, 2014). In a study by Smith and colleagues (2007), P3 amplitudes increased when participants were required to inhibit a planned response or change their response suggesting that the P3 component indexed inhibitory load. In support of this, the component has been thought to reflect memory-updating processes as it has been proposed to reflect consciously maintained working memory traces (Näätänen, 1990; Watter, Geffen, & Geffen, 2001; Scharinger et al., 2017). Despite evidence for the relation between successful response inhibition and the P300, it is disputed whether it is a direct reflection of the response inhibition process. Some have argued that the P300 peaks too late relative to SSRTs and therefore, rather than reflecting response inhibition, the P300 indicates performance evaluation (Dimoska et al., 2003; Huster et al., 2013). Another argument against the P300 being predictive of response inhibition lies in it not being exclusive to the SST and other

inhibition tasks. Notably, the P3 is commonly observed following unexpected or rare events (i.e.: novel and oddball tasks) and P300-like potentials have also been associated with decision-making and information processing (Wessel & Aron, 2015). Nevertheless, when a response inhibition process occurs, there remains a clear-cut temporally precise neural marker in the form of the P300 (Wessel & Aron, 2015).

ERPs have been successful in replicating the fronto-basal-thalamo network that has been previously described in the multiple domain hypothesis using a SST but not a Go/No-go task (Manuel, Bernasconi, & Spierer, 2013). Therefore, the prefrontal activation patterns engendered by the reactive SST remains to be replicated and supported in the proactive Go/No-go task.

2. 5 Color and the N200/P300 complex

Not many studies have looked at the interaction of color and ERPs however, the N200 and color have been previously studied as they pertain to attention. Pomerleau et al. (2014) used ERPs to study the deployment of attention to colors (red, green, blue, orange). They isolated lateralised components (the posterior contralateral positivity; Ppc, the N2 posterior contralateral; N2pc, and the temporal and contralateral positivity; Ptc) due to their link to visual attention and found that even when equiluminant, attention was deployed to red followed by blue more quickly than other colors. As previously noted in other studies, the uniqueness of red was also observed in their experiments, as it was always first in guiding visual attention over other colors. Generally, red targets tended to produce a larger Ppc, an earlier N2pc, and a larger Ptc relative to targets in other colors. Blue targets also produced an earlier N2pc relative to yellow and green and the authors expressed caution when using both red and blue in EEG experiments even when they are isoluminant. Blue and red learned color associations have been further studied recently

in the context of Go/No-go tasks. Kubo et al., 2021 provided participants with blue and red Go/No-go stimuli with three different Go probabilities (30, 50, and 70%). Their findings revealed slower RTs with red compared to blue Go stimuli especially with lower Go probabilities. Furthermore, the amplitudes of the N200 and P300 components were larger on red compared to blue Go/No-go trials and were also larger with lower Go probability (Kubo et al., 2021). Together, these findings demonstrate an advantage of red over other colors that can be studied using ERP components N200 and P300. Nevertheless, the behavioral implications of this advantage and its impact on response inhibition need to be further explored.

2.6 Research Objectives

We proposed three studies to investigate the effect of color on response inhibition. The first was behavioural and investigated if the color modulations of reactive response inhibition (SST) were a result of color opponency, color hierarchy, or learned associations. In the second study, we hypothesized that the color differences we observed in the first study would generalize to proactive response inhibition (2-choice discrimination Go/No-Go task) if they were an inherent part of inhibitory control rather than just countermanding. Based on the results, we proposed the underlying neural circuitry and modified accumulator models that mediated the effects of color on response inhibition. Lastly, in the third study, we used EEG to map out the proposed neural circuitry and investigate how inhibition-related components (N200 and P300) were differentially modulated by color in response inhibition.

CHAPTER 3: STUDY 1
ROLE OF COLOR IN RESPONSE INHIBITION
Manuscript to be submitted to Journal of Vision (JOV)

Abstract

Recently, color has been shown to affect executive functions. In one such study, red and green stimuli modulated response inhibition, but not response execution, in the stop signal task. In this study, we performed a series of experiments using the stop signal task to determine whether the effect of color on response inhibition was due to color opponency, attentional color hierarchy, or visual associations. We found that while red stop signals produced faster response inhibition compared to green, blue and yellow stop signals did not differ from each other. This pattern of results was not consistent with color opponency where differences in response inhibition should have occurred for both color opponent pairs. When all four colors' effects on response inhibition were compared red was the fastest, blue and yellow were neutral, and green was the slowest. This pattern is also not consistent with the attentional color hierarchy of red > green > yellow > blue. Therefore, red facilitating response inhibition, green impairing response inhibition, and the other two colors falling in between suggests that response inhibition is modulated by visual color associations where red means stop and green means go.

Introduction

Color is an important feature for object discrimination and recognition (Swain & Ballard, 1991; Tanaka, Weiskopf, & Williams, 2001; Gao & Vasconcelos, 2007; Bramão et al., 2011; Hagen et al., 2014) such as when determining the ripeness of a piece of fruit. As color is integrated into object representations, it can also be used to guide visual processing to objects of interest through feature-based attention and attentional capture (Saenz, Buraĉas, & Boynton, 2003; Jolicoeur, Brisson, & Robitaille, 2008; Lennert et al., 2011; Ansorge & Becker, 2013; Khan, Van De Weijer, & Vanrell, 2009; Perry et al., 2012, 2014). In fact, studies have shown that individual isoluminant colors have different attentional strengths in guiding eye movements (Bauer, Jolicoeur, & Cowan 1996a; Bauer, Jolicoeur, & Cowan 1996b; Tchernikov & Fallah, 2010; Kehoe, Rahimi, Fallah, 2018). Other studies have shown an advantage for red in visual search using EEG, where attention was deployed to red more quickly than to other colors, as measured on the N2PC component (Lindsey et al., 2010; Fortier-Gauthier, Dell'acqua, & Jolicoeur, 2013; Pomerleau et al., 2014).

To determine if the aforementioned color modulation of attention extended to other executive functions, Blizzard et al. (2017) used the stop signal task (SST) to study the effects of color on response execution and inhibition. In the SST, participants respond to a simple discrimination (go-signal) as quickly as they can, while on a subset of trials a stop-signal occurs, indicating they must inhibit that response. Response execution and inhibition have been shown to be independent processes that race to reach a threshold (Logan & Cowan, 1984; Hanes, Patterson, & Schall, 1998; Kalanthroff, Goldfarb, & Henik, 2013; Gulberti, Arndt, & Colonius, 2014). Using this paradigm, Blizzard et al. (2017) found that when the stop signal was a color change on the target, red stop signals were processed faster than green ones, but in a separate

experiment, when the go-signal required discriminating between red and green, there was no effect of color. Thus, response inhibition, but not execution, was facilitated by red over green changes in the same object file. While these prior studies determined that isoluminant colors modulate perceptual and cognitive processes, they have not elucidated the underlying mechanism. In this study, we built upon the results of Blizzard et al. (2017) to determine which of three potential mechanisms: color opponency, color hierarchy, or color associations, drives color modulations of response inhibition, a key executive function.

Color opponency, based on early-stage color processing, uses three opposing color pairs: red/green, blue/yellow and achromatic (Hering, 1964). While color opponent theory by itself does not indicate which color in a given pair would have greater weight in attention or response inhibition, it may be based on cone proportions. Red (L) cones outnumber green (M) cones by about 1.6-2 to 1 in the average eye while blue (S) cones constitute about 4-10% of the total number of cones (Curcio & Allen, 1990; Roorda & Williams, 1999; Lennie, 2000). Thus, the advantage for red over green may be due to their relative cone proportions feeding into color opponency in early visual processing. If color opponency does underlie the red-green differences found in perceptual and cognitive processes to date, then response inhibition should show similar effects for the concomitant color pair: yellow and blue. In the opponent system, yellow arises from a combination of red and green (L & M) cone input resulting in a higher proportion of yellow compared to blue input. As such, we would expect yellow to facilitate response inhibition over blue. If no difference between yellow and blue is found for response inhibition, then another mechanism must be at play.

The second potential mechanism, the intrinsic color hierarchy, was first shown to affect smooth pursuit eye movements (Tchernikov & Fallah, 2010). After a saccade to two

superimposed surfaces moving in opposite directions that only differed in isoluminant colors, participants were found to automatically follow one of the two superimposed surfaces such that there was a color preference for pursuing red over the other colors, green over yellow and blue, and yellow over blue. Furthermore, the speed of pursuit was dependent on the distance between the two surface colors in CIE xyY color space. Their results demonstrated that an intrinsic color hierarchy guided smooth pursuit target selection and that the color hierarchy derived from a color space representation. Concurrently, a separate visual search study showed a similar color hierarchy (Lindsey et al., 2010), where the reaction times were faster for red than orange and green, and slowest for blue. These studies describe a hierarchical bias for red followed by other colors, ending with blue. If the intrinsic color hierarchy drives response inhibition, then in testing these colors in the stop signal task, stop signal reaction times should be fastest for red, then green, yellow, and slowest for blue.

The third possibility is that a visual association for the color red may have emerged from evolutionary predispositions that contributed to adaptation and survival (Mollon, 1989; Osorio & Borovyeb, 1996; Dominy & Lucas, 2001). We evolved in an environment where red is a danger signal, from some red berries warning of toxicity to red as the color of fresh blood leading to a physiological stress response. Green on the other hand, found in plants and trees is associated with food, growth, and a healthy environment. It is likely that these unconscious associations have made way into our everyday lives where traffic lights turn red to stop cars and green to get cars moving. Similarly, in education settings, red marks on assessments signify errors. Thus, our environment is filled with warnings in red and safety in green, which may strengthen through experience these effects of color on executive functions. If associations underlie the effects of color seen previously, then red (stop) will facilitate response inhibition, green (go) will slow

response inhibition and importantly, the other colors without task-relevant associations will not modulate response inhibition.

Present Study

We used the color-dependent stop signal task (Blizzard et al, 2017) to determine whether the effects of color on response inhibition were due to color opponency, color hierarchy, or color associations. While all three potential mechanisms support red facilitating response inhibition over green, it is the effects of yellow and blue that distinguish between them. We first replicated the original results of red facilitating response inhibition compared to green, but with the stop signal color change on a separate object dissociating response inhibition from response execution. We then tested if color-mediated response inhibition was due to color opponency by comparing yellow versus blue stop signals. In a second experiment all four colors were tested together to see if the color hierarchy (red > green > yellow > blue) mediates response inhibition or if color associations drove the effects (red facilitate, yellow and blue neutral, green impede). The results of these experiments will determine the underlying mechanism for color modulation of response inhibition, providing a foundation for how color affects executive functions more generally.

Materials and Methods

Participants

York University students (ages: 18-33 years) participated in the experiments for partial course credit. All participants were right-handed and had normal or corrected-to-normal acuity and normal color vision (Ishihara, 2006). Forty participants performed Experiment 1A (29

women; M = 19.73, SD = 3.01), 20 performed Experiment 1B (16 women; M =18.91, SD = 2.88), and 40 performed Experiment 2 (28 women; M = 19.58, SD = 3.62). All experiments were approved by York University's Human Participants Review Committee and were performed in accordance with the Declaration of Helsinki (2003).

Equipment

Participants sat 57 cm away from a 17'' CRT monitor (Dell M991, refresh rate = 60 Hz, resolution = 1280 × 1024) with their head stabilized by a headrest (UHCO Tech). Experimental control was maintained by Presentation (Neurobehavioral Systems). Responses were made using left and right arrow keys on a computer keyboard with the right hand.

Stimuli and Procedure

Experiment 1A. In this experiment, we tested whether red and green visual stop-signals would affect response inhibition when on a separate object than the target. Participants were seated in a dark room in front of a black screen. A trial consisted of the appearance of a white (CIE X = 23.11, Y = 24.30, Z = 33.74) right or left arrow at the centre of the screen and a 113 × 113 pixels white box placed above or below (counterbalanced across trials). Participants were instructed to respond as quickly and accurately as possible using the corresponding right or left keyboard arrow (go-trial). On a subset of trials, the white box changed to an isoluminant red (CIE X = 52.64, Y = 28.27, Z = 2.27) or green (CIE X = 13.13, Y = 27.86, Z = 4.67) color, which was the signal to withhold their response (stop-trial).

The experiment consisted of 34 blocks with 6 go-trials and 3 stop-trials for each stop color (red and green) per block for a grand total of 612 trials. Trial type and go-signal color were

pseudo randomly interleaved within each block. Participants received visual feedback for errors on arrow discrimination, responses on stop-trials, and failures to respond within a 750 ms time window on go-trials. The delay between the go- and stop signals (stop-signal delay, SSD) began at 50 ms and then varied using 2 simultaneous staircases, one for each color. In the first stage of the staircase, the SSD would increase by 50 ms, if a participant successfully inhibited their response on a stop-trial or decrease by 50 ms if they failed to inhibit their response. After a double reversal, the step size decreased for the next stage to 20 ms, 10 ms, and 5 ms, to provide a more accurate measure of the SSD. The experiment ended after all stages were completed or at the end of 34 blocks. **Figure 3A** shows the time course of both go- and stop-trials in the SST task with a spatially separated color change to red or green. The entire session lasted around 20 minutes.

Experiment 1B. In this experiment, we tested whether blue and yellow visual stop-signals would affect response inhibition. This experiment was identical to the first one except the isoluminant color change of the stop box was to isoluminant yellow (CIE $X = 34.82$, $Y = 28.36$, $Z = 3.28$) or blue (CIE $X = 33.52$, $Y = 27.46$, $Z = 141.8$).

Experiment 2. In this experiment, we directly compare all four colors from the prior experiments. This experiment was identical to the first two, but the color change occurred on the target arrow (see **Figure 3B**) and the number of trials per block doubled due to having 4 colors and 4 simultaneous staircases. The entire session lasted around 40 minutes.

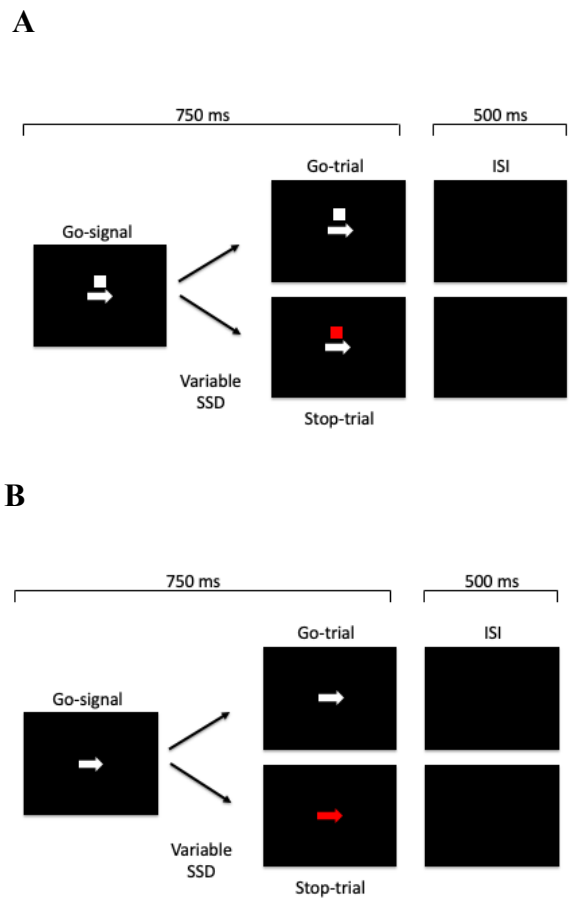

Figure 3. **Stop-Signal Task A.** Participants reported the direction of a white Go signal arrow when the color of the box placed above or below remained white. On a subset of trials, this box changed from white to either red/green (Exp. 1A) or yellow/blue (Exp. 1B), which signaled participants to withhold their response. **B.** In Experiment 2, the stop signal color change occurred on the target (arrow) and could be any of the four colors: red, green, yellow or blue (pseudorandomly interleaved).

Data Analysis

Participant response times in any given condition that fell outside of 2.5 standard deviations were removed from further analysis. Mean Go signal RTs were calculated as the

average response time on go-trials. Participants' overall mean SSD was then subtracted from the mean Go signal RT to compute the SSRT. All statistical analyses were done using IBM SPSS statistics for Macintosh, Version 26.0. Paired samples t-tests were used to compare accuracies, error RTs and SSRTs in Experiments 1A and 1B and a repeated measures ANOVAs with stop-signal color as the independent variable was conducted separately for response accuracies, error RTs, and SSRTs in Experiment 2.

Results

One participant was excluded in Experiment 2 due to reactions times being above 2.5 standard deviations. **Table 1** shows the mean accuracies, error RTs, SSDs, and computed SSRTs split by stop signal color in Experiments 1A, 1B, and 2. **Table 2** shows the mean accuracies and RTs for the Go signal in each experiment. Paired samples t-tests were performed to analyze mean accuracies, error RTs, and SSRTs between red and green stop signals in Experiment 1A and between yellow and blue stop signals in Experiment 1B. Repeated-measures ANOVAs were conducted with stop-signal color as the within-subjects factor for Experiment 2.

Table 1

Mean and standard deviations of SST variables split by stop signal colors.

	Stop signal color	Accuracy (% *M* (*SD*))	Error RTs (*M* (*SD*))	SSDs (*M* (*SD*))	SSRTs (*M* (*SD*))
Experiment 1A	Red	89.25 *(6.99)*	533.50 (*57.72)*	269.75 *(72.66)*	225.53 *(41.30)*
	Green	90.65 *(6.07*)	538.35 *(52.89)*	249.13 *(54.54)*	250.10 *(29.53)*
Experiment 1B	Yellow	88.80 *(5.76)*	545.50 *(51.66)*	349.61 *(75.94)*	204.25 *(39.84)*
	Blue	90.45 *(6.38)*	544.70 *(53.15)*	338.94 *(74.13)*	213.96 *(47.54)*
Experiment 2	Red	90.40 *(4.48)*	550.73 *(35.39)*	347.56 *(53.80)*	203.16 *(28.64)*
	Yellow	90.60 *(4.54)*	550.03 *(35.18)*	342.19 *(60.87)*	208.73 *(36.13)*
	Blue	90.88 *(4.77)*	547.53 *(32.93)*	334.38 *(56.60)*	213.68 *(34.76)*
	Green	90.60 *(3.64)*	550.07 *(33.20)*	328.00 *(57.69)*	222.25 *(40.91)*

Table 2

Mean and standard deviations of Go signal RTs.

	Go signal color	Accuracy (% *M* (*SD*))	RTs (*M* (*SD*))
Experiment 1A	White	93.05 *(5.62)*	512.*20 (44.34)*
Experiment 1B	White	89.21 *(5.92)*	552.29 *(41.85)*
Experiment 2	White	90.74 *(3.91)*	544.02 *(36.48)*

Experiment 1A

In Experiment 1A, the accuracy on Go signal (white) trials was (*M* (*SD*) = 93.05 (*5.62*)) and the mean RT for the Go signal trials (white) was *M* (*SD*) = 512.20 *(44.34)* (see **Table 2**). The accuracy on red stop signal trials (*M* (*SD*) = 89.25 *(6.99)*) was not significantly different than that on green stop signal trials (*M* (*SD*) = 90.65 (*6.07*)), *t* (19) = -2.05, *p* = .054, *d* = -.46 (see **Table 1**). The mean error RT on red stop signal trials (*M* (*SD*) = 533.50 (*57.72)*) was not significantly different than that on green stop signal trials *(M* (*SD*) = 538.35 *(52.89)); t* (19) = -3.16, *p* = .76, *d* = - .71.

The mean SSRT for red stop signal trials (*M* (*SD*) = 225.53 *(41.30))* was significantly faster than for green stop signal trials (*M* (*SD*) = 250.10 *(29.53)), t* (19) = -2.68, *p* = .015, *d* = -.60, CI_{95} [-1.07, -.12]). **Figure 4** shows the ~25ms difference between red and green mean SSRTs.

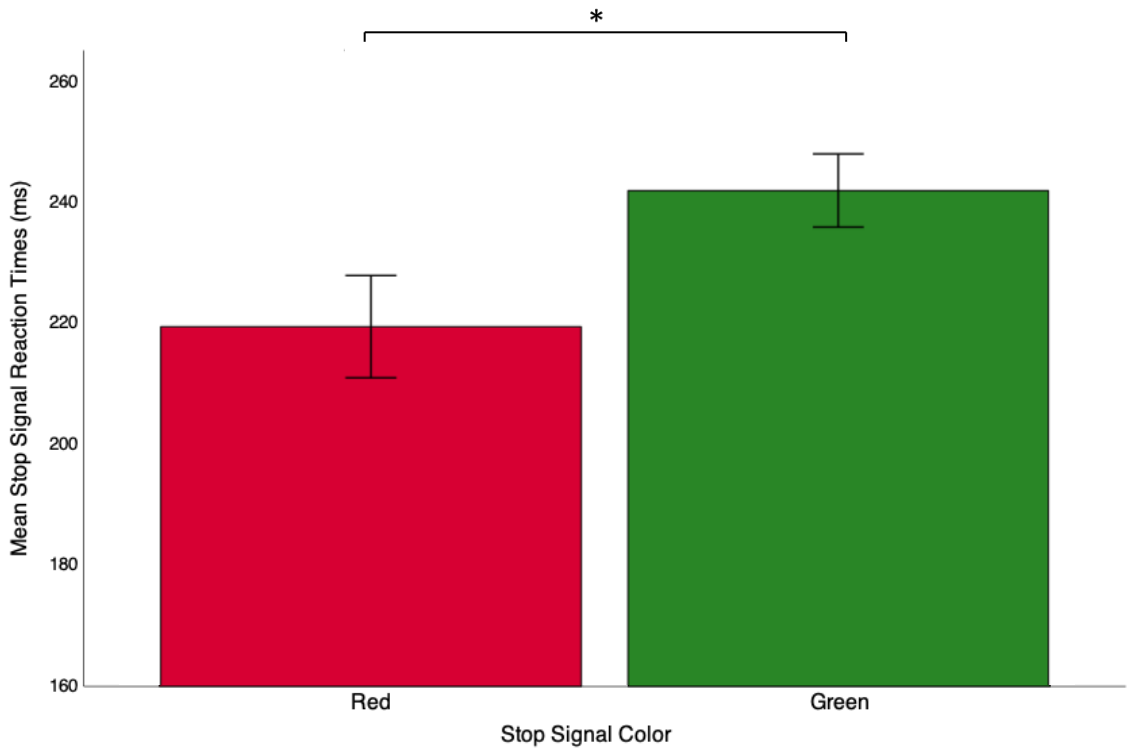

Figure 4. Stop Signal Reaction Times in Experiment 1A. Mean SSRTs (ms) plotted as a function of stop signal color. Error bars represent standard error of the means. *$p < 0.05$.

Experiment 1B

In Experiment 1B, the accuracy on Go signal trials was (*M* (*SD*) = 89.21 (*5.92*)) and the mean RT for the Go signal trials (white) was *M* (*SD*) = 552.29 (*41.85*) (see **Table 2**). The accuracy on yellow stop signal trials (*M* (*SD*) = 88.80 (*5.76*)) was not significantly different than

that on blue stop signal trials (*M* (*SD*) = 90.45 (*6.38*)), *t* (19) = 1.70, *p* = .08, *d* = -.42 (see **Table 1**). The mean error RT on yellow stop signal trials (*M* (*SD*) = 544.50 *(51.66))* was not significantly different than that on blue stop signal trials *(M* (*SD*) = 544.70 *(53.15)); t* (19) = 2.38, *p* = .82, *d* = .053.

The mean SSRT for yellow stop signal trials (*M* (*SD*) = 204.25 *(39.84)*) was not significantly different than the mean SSRT for blue stop signals (*M* (*SD*) = 213.58 (*48.81*)), *t* (18) = -.99, *p* = .34, *d* = -.22, CI_{95} [-.66, .23] (see **Figure 5**).

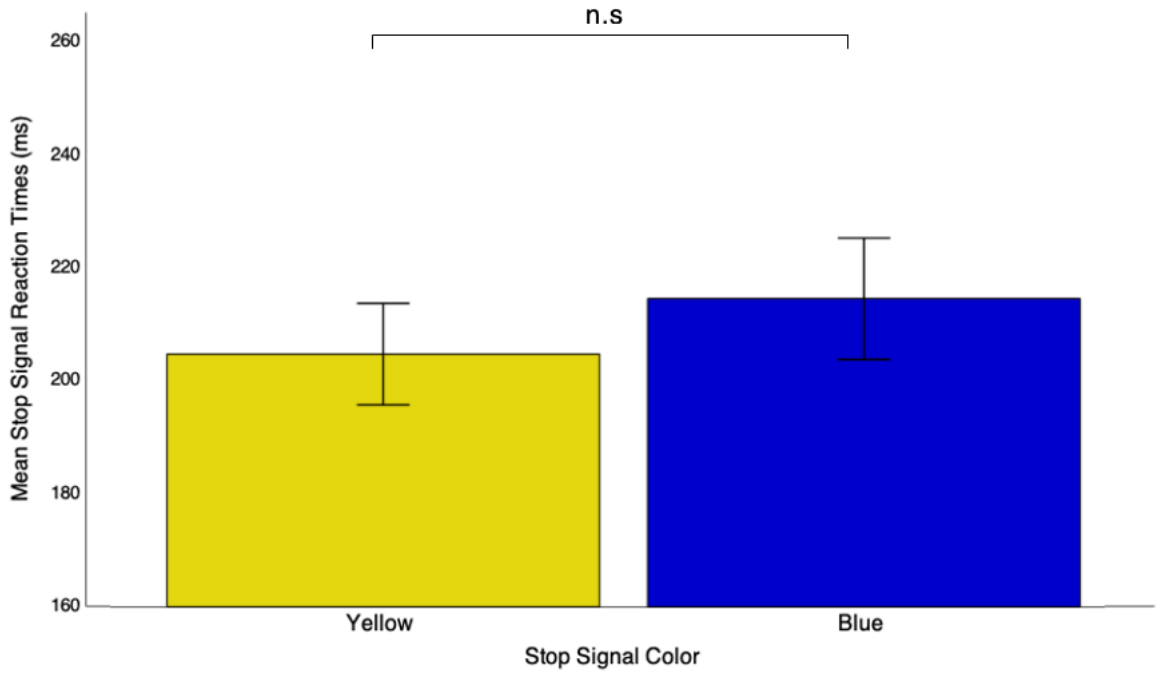

Figure 5. **Stop Signal Reaction Times in Experiment 1B.** Mean SSRTs (ms) plotted as a function of stop signal color. Error bars represent standard error of the means. n.s is non-significant.

Meta-analysis

An independent samples t-test was run to compare the mean aggregate accuracy of Go responses (i.e., errors constituted Go signal response omissions or incorrect Go signal button response) between experiments. A significant difference in accuracy was found between Experiments 1A (*M* (*SD*) = 93.05 (*5.62*)) and 1B (*M* (*SD*) = 89.21 (*5.92*)), t (38) = 2.94, p = .004, d = .81, such that participants in Experiment 1A were more accurate than those in 1B. There was also a significant difference in RTs between the experiments, t (38) = -4.11, $p < .001$, d = -.73, such that RTs in Experiment 1A (*M* (*SD*) = 512.20 (*44.34*)) were significantly faster than those in Experiment 1B (*M* (*SD*) = 552.29 (*41.85*)). The color pairs tested separately could not be directly compared due to these differences in performance, Therefore, a second experiment combining all four colors within subjects was conducted.

Experiment 2

A second experiment using all four colors (red, green, blue, and yellow) as stop signals was conducted to test if the color hierarchy of red> green> blue>yellow underlies color modulation of response inhibition as measured by the stop signal reaction time (SSRT). The mean accuracy and mean RT on Go signal trials were *M* (*SD*) = 90.74 (*3.91*) and *M* (*SD*) =544.02 (*36.48*) respectively (see **Table 2**). A repeated-measures ANOVA was conducted with stop-signal color as the within-subjects factor which revealed no significant effect of stop-signal color on accuracy, *F (3,117*) = .40, p = .75, η^2 = .01 or error RTs, *F (3,117*) = .97, p = .41, η^2 = .024. However, there was a significant main effect of stop-signal color on SSRTs, *F (3,117*) = 5.29, p = .002, η^2 = .119. Bonferroni adjusted post-hoc pairwise comparison analyses were then

performed to compare the mean SSRTs of different stop signal colors between themselves (see **Figure 6**). Green stop signal SSRTs (*M* (*SD*) = 222.25 (*39.34*)) were significantly slower (~19 ms) than red stop signal SSRTs (*M* (*SD*) = 203.16 *(32.48)*), $p = .006$. No other significant color pair differences were observed.

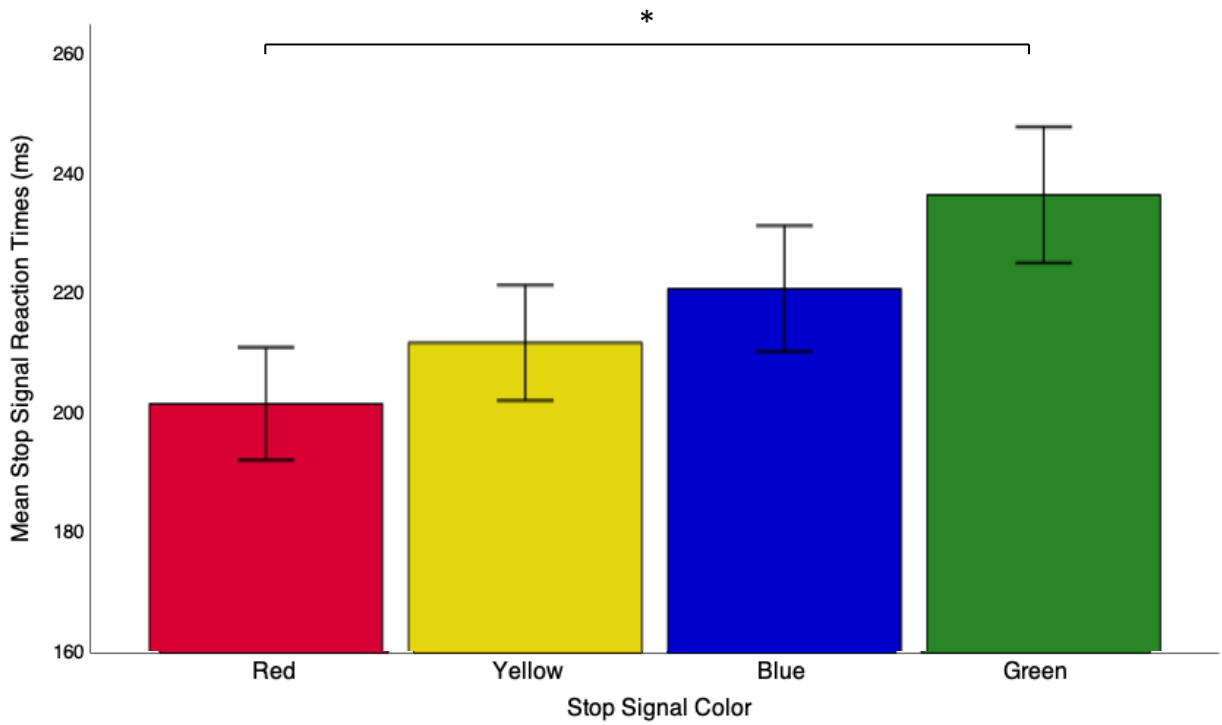

Figure 6. **Stop Signal Reaction Times in Experiment 2.** Mean SSRTs (ms) plotted as a function of stop signal color. Error bars represent standard error of the means. *$p < 0.05$.

Discussion

When red and green stop signals occurred on a separate object than the target, red facilitated response inhibition while green, relative to red, slowed it. This result extended the previous study (Blizzard et al., 2017) by determining that the effect of color was not dependent on a color change within the target's object file. As response execution and inhibition are

competing processes in the race-horse model, it was possible that the red stop-signal color change on the target object provided a link whereby it slowed response execution which would then appear as speeded response inhibition. By splitting the processes, the color change on the separate object no longer directly competed in the object file with the discrimination of the arrow direction of the target. As the results for red and green with spatially separate objects mirrors that for the stop signal appearing on the target object, it is parsimonious to expect that both results were due to the differential effects of red and green on response inhibition, independent of response execution. Looking at how the race horse model is modulated by color, we propose that red stimuli engage response inhibition first thereby facilitating it before green stimuli engage response inhibition (see **Figure 7**).

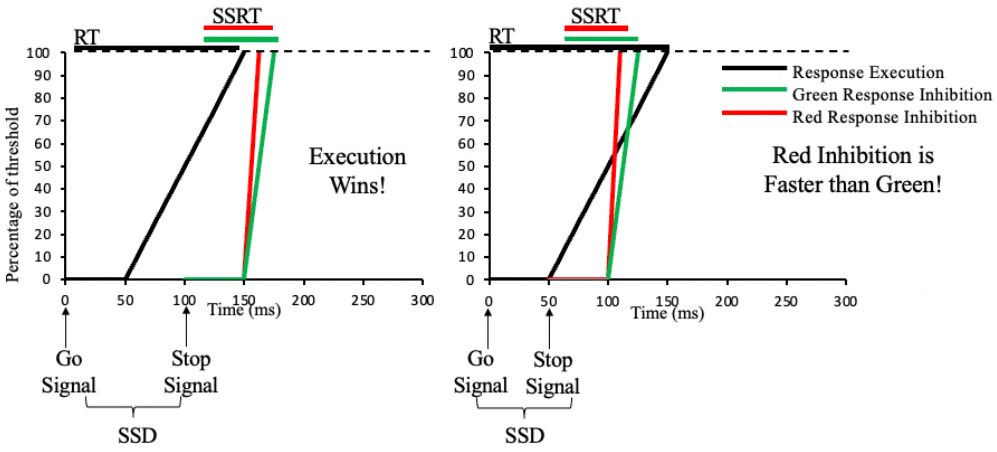

Figure 7. **Stop-Signal Paradigm with Red and Green: Race-horse Model.** A model of the cognitive process that occurs during the stop signal task termed 'race horse' to depict the competition between response execution (black) and response inhibition (red and green) processes. In the left diagram, a Stop-signal is presented after a long time delay (i.e.: SSD); therefore response execution is activated and wins over inhibition whether it is red or green. In the right diagram, a Stop-signal is presented after a short time delay; therefore, red response inhibition is activated before green response inhibition and wins the race.

To test the color opponency hypothesis, we compared yellow and blue stop signals. Due to the relatively very low prevalence of blue cones, the a priori expectation would be for a larger yellow advantage over blue effect than was seen for red vs green. As there were no differences between the SSRTs, color opponency was not supported as the underlying mechanism. Thus, the significant advantage for red over green was not simply due to a difference in cone proportions feeding into opponent cells as there was no advantage for yellow over blue. Taken together, color opponency is not the mechanism underlying color modulation of response inhibition.

To determine if the color hierarchy drives color modulation of response inhibition, the relative ordering of all four colors' SSRTs is needed. When we compared the two experiments, we found that the reaction times were faster, and accuracies were higher for Experiment 1A than for 1B. As such, we could not make a direct comparison between their stop signal reaction times. The difference in performance in the two experiments may be a result of the arousal theory of color (Walter, Apter, & Svebak, 1982; Buechner & Maier, 2016) which states that the color red leads to a heightened state of arousal. Thus, the participants in Experiment 1A may have been more alert than those in Experiment 1B, which would confound a direct comparison of the four colors effects on response inhibition. Therefore, we ran an additional experiment comparing all four colored stop signals simultaneously which resulted in similar accuracies and reaction times across the colors, supporting an equal state of alertness and performance. Green SSRTs were slowest, followed by blue and yellow which did not differ from each other, and then red which produced the fastest SSRTs. This ordering did not match the attentional color hierarchy (Tchernikov & Fallah, 2010) which predicted red having the fastest SSRTs followed by green,

then yellow and finally blue with the slowest, suggesting that it also is not the mechanism underlying color modulation of response inhibition.

Color hierarchy effects being found in pursuit target selection but not in response inhibition may be due to the differing cognitive processes in the two tasks. When making a saccade to a moving object, the oculomotor system automatically initiates smooth pursuit of that object, even without a task demand to follow it. When making a saccade to two surfaces that are equal in all respects other than direction, no pursuit occurs, but if there is a difference in contrast, the higher contract surface is pursued (Fallah & Reynolds, 2012). In the Tchernikov and Fallah (2010) study, when a saccade was made to two superimposed surfaces moving in opposite directions that differed in isoluminant color, pursuit automatically followed the surface higher in the color hierarchy, treating it similarly to having a higher contrast. Thus, the color hierarchy may be limited to driving bottom-up target selection mechanisms. This is very different than in the current study, where task-dependent colored stop signals modulated response inhibition, an executive function mediated by prefrontal cortex. The stage of cortical processing necessary to perform a task therefore likely plays a role in which color mechanism may affect it.

Color Associations

With no evidence supporting color opponency or the color hierarchy, the effects of red and green on response inhibition likely depend on innate or learned color associations. While our study does not address the age-old debate of nature versus nurture, there is evidence suggesting that the enhanced and non-constrained effect of red is innate and evolutionary. Recently, Ghasemian et al. (2021) used a color-dependent stop signal task to study response inhibition in macaque monkeys. They observed the same advantage of red over green in the monkeys as was

seen in human (Blizzard et al, 2017). Given that these monkeys were not exposed to the experience-dependant learning that humans are, they suggest that these effects must be innate, developed at an earlier point in the evolution of man and monkey. The innate advantage of red for response inhibition could be a result of conditions where red is associated to blood, poisonous fruits, and dangerous animals. It would be particularly favourable for survival to have red and green modulated inhibitory circuits to prevent or allow certain behaviors and these inherent circuits would have been prioritized by evolutionary pressure. We use red and green in our man-made environment to reflect stop and go, which may be an outcome of their innate relationships to response inhibition. That usage would then lead to further reinforcement by experience-dependant learning, resulting in the effects found in this study.

Related Color Effects

Prior studies have looked at the effects of colour on alertness and arousal in other contexts. For example, blue light has been shown to be associated with increased heart rate and wakefulness (Brainard et al., 2001; Thapan, Arendt, & Skene, 2001; Caiochen et al., 2005). In some cases, it's used as light therapy for individuals with seasonal affective disorder to elevate mood (Strong et al., 2009; Gordjin & Meesters, 2012). On the other hand, increased exposure to blue light greatly reduces melatonin which consequently has negative repercussions for sleep in the evening or at nighttime (Caiochen et al., 2005; Souman et al., 2018). But red can produce similar increases in alertness. However, the mechanism is different from that for blue light since red light does not affect melatonin levels (Figueiro et al., 2009; Sahin & Figueiro, 2013). The effect of red light on arousal may instead rely on bottom-up attentional modulation (as per Tchernikov & Fallah, 2012; Bauer, Jolicoeur, & Cowan 1996a; Bauer, Jolicoeur, & Cowan

1996b, Jolicoeur et al., 2006). As blue light affects arousal through a separate mechanism from red light, it is not surprising that no effect of blue was seen on response inhibition.

In another related study, Payen et al. (2011) observed that seeing red as opposed to blue or gray prior to a strength test inhibited force development, without facilitating force production, consistent with our findings on response inhibition. This suggests that red has a general effect on response inhibition, rather than a task specific effect for the SST. While red speeds up response inhibition and inhibits force development, Elliot and Aarts (2011) demonstrated that viewing red amplified physical output in terms of speed and strength for a currently underway motor action. Taken together, red signals, with an innate association to danger, inhibits upcoming actions, while also enhancing ongoing motor responses likely through fight or flight-based sympathetic nervous system activation. Since there have not been complimentary studies looking at the effects of green on motor output, it is unknown if the association of green with go generalizes beyond slowing response inhibition in the stop signal task.

Neurophysiological studies have also demonstrated that under certain conditions (e.g.: negative priming tasks), brain areas in the prefrontal cortex such as the anterior cingulate cortex and pre-supplementary motor area use suppression to exert top-down influence on decision-making (Houghton & Tipper, 1984; Aron, 2007; Botvinick et al., 1999; Khan, Van De Weijer, & Vanrell, 2009; Duque et al., 2013). Therefore, red colored stimuli may be acting on these processes to facilitate inhibition and to promote the efficiency of decision-making mechanisms. Other top-down influences of color include red colored interior design enhancing workplace performance (Kwallek, Soon, & Lewis, 2007; Küller, Mikellides, & Janssesn, 2009) and the link between red and attraction (Guéguen, 2012; Pazda, Elliot, & Greitmeyer, 2012; Elliot et al., 2013).

In summary, red facilitates response inhibition while green, relative to red, impairs it. Red and green work in a push-pull manner that is innate and conserved through evolution. This has likely led to their usages in everyday life from traffic lights to electronics. Red is clearly special in its modulatory effects, but more work is required to how generalizable the effects of green on response inhibition are. Our study shows that this facilitation is not due to color opponency or color hierarchy, but instead is likely due to innate color associations that have led to red meaning stop and green meaning go in our everyday lives. While further research is needed to see how generalizable this red-green push-pull modulation is for other executive functions, these findings provide insight in how to develop age-friendly graphical interfaces to better accommodate reduced response inhibition in children (Johnstone et al., 2007; Robinson et al., 2009) and older adults (Kane et al., 1994; Tamm, Menon, & Reiss, 2002).

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CHAPTER 4: STUDY 2
RED AND GREEN SIGNALS MODULATE ERRORS OF RESPONSE INHIBITION IN A GO/NO GO TASK

Abstract

Recent studies have shown that red and green modulate a number of cognitive functions. In the stop signal task, response inhibition was modulated by an innate visual association of red with stop and green with go. But in that task, an upcoming action has to be countermanded, which is a specific instantiation of reactive response inhibition. If color modulations are inherently part of inhibitory control, they should generalize to proactive response inhibition paradigms as well. To test this, we investigated the effects of red and green on a 2-choice left/right arrow discrimination go/no-go task. First, we found that red and green go trial accuracy and reaction times (response execution) did not differ from each other but differed from white no-go trials. In a second experiment which associated the colors as no-go signals instead, performance on red no-go trials was higher than on green no-go trials. Overall, color did not modulate arrow discrimination or response execution, but did affect no-go performance. Red enhances and green impairs proactive, as well as reactive, response inhibition. Based on these results, we propose a model of underlying neural circuitry and modifications of an accumulator model, to incorporate the effect of color on proactive response inhibition.

Introduction

Decision-making plays a central role in everyday life. Response inhibition, the ability to suppress an inappropriate or undesired choice, is an essential aspect of the decision-making process. As impairments in response inhibition are seen in several neurodegenerative disorders (Migliaccio et al., 2020) such as Alzheimer's disease (Bélanger, Belleville, & Gauthier, 2010; Medina et al., 2021) and Parkinson's (Zhang et al., 2016; Palermo et al., 2017), ways to optimize its functioning is of particular interest for improving quality of life for those patients.

Based on prior research that has shown color affects target selection (Tchernikov & Fallah, 2010), decision-making (Perry & Fallah, 2012; Perry, Tahiri, & Fallah, 2014; Perry & Fallah, 2014), and attentional deployment (Pomerleau, et al. 2013), Blizzard *et al*. (2017) investigated whether color affected response execution and response inhibition in a stop-signal task (SST). In the SST, a go signal is presented on every trial but on a subset of trials, after a variable delay, a stop-signal is presented indicating that the participant needs to inhibit their response. The variable time delay between the presentations of the go- and stop-signal can be manipulated in a staircase design (Logan & Cowan, 1984) to determine the stop signal reaction time: the time needed for the response inhibition process to complete before the response is made. In this racehorse model, the response execution and response inhibition processes "race" against each other with the one completing first determining the behavioral outcome (Logan & Cowan, 1984; Verbruggen & Logan, 2009). The results of the Blizzard *et al.* study (2017) showed that red stop signals sped up response inhibition more than green did in the race against response execution. More recently, a follow-up stop-signal study conducted with the four colors of the color opponency system (Asare et al., *in preparation*) observed that red enhanced and green hindered response inhibition, while blue and yellow fell in between and did not differ from

each other. These results determined that with blue and yellow having a neutral effect, red sped up while green in fact slowed stop signal reaction times. Thus, the effects of color on response inhibition were consistent with the association of red meaning stop and green meaning go in our everyday lives. Whether this is a learned or innate association has recently been investigated in an SST task performed by macaque monkeys (Ghasemian et al., 2021). The authors hypothesized that if color modulated cognitive functions in macaques, it would be evidence for innate neural circuitry rather than experience-dependent learning. The macaques performed a stop-signal task with red, green, and blue colored stimuli as stop-signals and produced shorter stop-signal reaction times with red stimuli compared to green (Ghasemian et al., 2021) replicating Blizzard et al's (2017) results from human participants. These results demonstrated that the effects of red and green on response inhibition are innate and conserved phylogenetically.

The SST utilizes reactive response inhibition as it requires countermanding an already initiated response without any prior preparation (Aron et al., 2007; Chambers, Garavan, & Bellgrove, 2009; Chikazoe, 2010; Aron, 2011). This differs from proactive response inhibition (Cai, Oldenkamp, & Aron, 2011; Aron, 2011; Bloemendaal et al., 2016; Langford et al., 2016) which is based on inhibiting a response based upon an initial perceptual decision-making process, such as in the go/no-go task. It is possible that the color modulation found previously (Blizzard et al, 2017; Ghasemian et al, 2021) may be specific to reactive response inhibition found in the SST task. If the visual associations of red and green evolved as part of an alertness/arousal response (Elliot et al., 2007; Soldat, Sinclair, and Mark, 1997), it is possible that they would be integrated specifically into reactive inhibition, rather than generalizing across both types of response inhibition. Similarly, it may be that the effects of red and green found previously are due to specific aspects of the SST task itself, such as change detection, varying

difficulty level, speed accuracy trade-off, competitive execution and inhibition processes, and higher cognitive load.

A commonly used paradigm dependent on proactive response inhibition is using the go/no-go task (GNGT) (Donders, 1969; Logan, Cowan, & Davis, 1984; Verbruggen & Logan, 2008). In this task, a single item is discriminated on each trial which will determine whether a response is made or not. Unlike the SST, the go and no-go signals are presented on different trials, removing the requirement for change detection and race-horse competition, resulting in lower cognitive load and a constant level of difficulty. Given that participants determine on each trial whether to respond or not, the task relies on proactive instead of reactive response inhibition (Aron, 2011).

While the SST and the GNGT are sometimes used interchangeably to study response inhibition, they assess and utilize different inhibitory processes. Because the SST initiates response execution on every trial, it relies on action cancellation and recruits sensory, motor, and prefrontal areas to countermand the developing response (Schachar et al., 2007; Raud et al., 2020). In contrast, the GNGT requires identification of the item on each trial to determine whether or not to make a response, thereby relying on response execution or action restraint, without any parallel competing processes (Schachar et al., 2007; Raud et al., 2020).

Two-choice discrimination tasks have primarily been used to assess accuracy and response time in selection-based scenarios (Gomez, Ratcliff, & Perea, 2007). However, Middlebrooks & Schall (2014) investigated whether discrimination mechanisms shared resources with response inhibition mechanisms. They unified a 2-choice discrimination task where participants had to decide whether a stimulus contained more cyan or more magenta by making a visual saccade to the right or left with a stop-signal task. If discrimination and response

inhibition mechanisms overlap or share a common resource (Kahneman, 1973; Navon & Gopher, 1979), interactions between choice difficulty and stopping efficiency would be present. In contrast, the reaction times for stopping did not change with respect to the difficulty of the choosing task. As such, they concluded that the mechanisms for choosing and stopping are functionally independent for a saccade response (Middlebrooks & Schall, 2014). More recently, the same authors performed neural recordings of prefrontal neurons during the same task whereby countermanding was successful with varying decision-making difficulty. They found that prefrontal neurons contributed to both choosing and stopping concurrently and subsequent computational modelling supported a unification of both processes. The authors posited that either the neurons signalled perceptual decision-making and are then unaffected by action cancellation or that there's a unification of both processes whereby they take place concurrently (Middlebrooks et al., 2020). It remains unclear if the mechanisms are functionally independent or not in a manual response task.

To see if not only response inhibition but decision-making would be modulated by the inherent stop and go associations for red and green, we adopted a paradigm akin to Middlebrooks & Schall (2014) that incorporates both decision-making (2-choice discrimination task) and response inhibition (GNGT), but with a manual instead of a saccadic response. In the first experiment, participants were asked to report the direction of a right or left arrow (discrimination) when it was green or red (go). On trials where the arrow displayed was white instead of colored, they needed to withhold their response (no-go). In a second experiment, participants complete the reversed task where they were asked to report the direction of the arrow when it was white (go) and withhold their response when the arrow was green or red (no-go). Having noted the differences between the SST and GNGT, our aim was to determine if the

color association modulations observed in the higher cognitive load and reactive SST (Blizzard et al. 2017; Asare et al., *in preparation*) generalize to response inhibition in the lower cognitive load and proactive GNGT. One aspect of the GNGT is that a go trial has a shorter reaction time when it follows a go trial than a no-go trial (Fadeev et al., 2020; Erika-Florence et al., 2014; Liebrand et al., 2018). If we find that color modulates the *strength* of the no-go signal, then these trial-over-trial effects should be further modulated by that strength, resulting in differences in white go signal trial reaction times based on the color of the previous no-go trial. If no such modulation of trial history effects is found in spite of color effects on no-go trials, then it suggests that the color modulations affect the speed rather than the strength of response inhibition.

Present Study

To see if not only response inhibition but decision-making would be modulated by the inherent stop and Go associations for red and green, we adopted a paradigm akin to Middlebrooks & Schall (2014) that incorporates both decision-making (2-choice discrimination task) and response inhibition (Go/No-go Task), but with a manual instead of a saccadic response. In the first experiment, participants were asked to report the direction of a right or left arrow (discrimination) when it was green or red (Go). On trials where the arrow displayed was white instead of colored, they needed to withhold their response (No-go). In a second experiment, participants completed the reversed task where they were asked to report the direction of the arrow when it was white (Go) and withhold their response when the arrow was green or red (No-go). Having noted the differences between the SST and Go/No-go Task, our aim was to determine if the color association modulations observed in the higher cognitive load and reactive

SST (Blizzard et al. 2017; Asare et al., *in preparation*) would generalize to response inhibition in the lower cognitive load and proactive Go/No-go Task. One aspect of the Go/No-go Task is that a Go trial has a shorter reaction time when it follows a Go trial than a No-go trial (Fadeev et al., 2020; Erika-Florence et al., 2014; Liebrand et al., 2018). If we find that color modulates the *strength* of the No-go signal, then these trial-over-trial effects should be further modulated by that strength, resulting in differences in white Go signal trial reaction times based on the color of the previous No-go trial. If no such modulation of trial history effects is found in spite of color effects on No-go trials, then it suggests that the color modulations affect the speed rather than the strength of response inhibition.

Materials and Methods

Participants

All participants were right-handed and had normal or corrected-to-normal visual acuity and normal color vision as per Ishihara's Test for color blindness (Ishihara, 2006). Twenty-four York University students participated in experiment 1 (19 women; age: 18 to 26; $M = 19.42$, $SD = 1.84$) and 24 participated in experiment 2 (16 women; age: 18 to 26; $M = 20.25$, $SD = 2.23$) for partial course credit. In accordance with the Declaration of Helsinki (2003), all participants gave written informed consent. The experiments were approved by York University's Human Participants Review Committee.

Equipment

Participants sat 57 cm away from a 17'' CRT monitor (Dell M991, refresh rate = 60 Hz, resolution = 1280 × 1024) with their head stabilized by a headrest (UHCO Tech). Experimental

control was maintained by Presentation software (Neurobehavioral Systems). For all experiments, responses were made using left and right arrow keys on a computer keyboard with the right index finger.

Stimuli and Procedure

Experiment 1. On each Go trial, an isoluminant green CIE $X = 13.13$, $Y = 27.86$, $Z = 4.67$) or red (CIE $X = 52.64$, $Y = 28.27$, $Z = 2.27$) left or right arrow appeared for 300ms at the center of a black screen (0.20 cd/m^2). Participants were required to report the direction of the arrow as fast as possible within 750ms. On No-go trials, a white (CIE $X = 23.11$, $Y = 24.30$, $Z = 33.74$) arrow was presented which indicated to participants to not make a response. The interstimulus interval was a randomized time between 500 and 1000 ms to control for practice effects (see **Figure 8A**).

There was a total of 12 blocks with each block consisting of 75 Go trials and 25 No-go trials pseudorandomly interleaved. Participants received auditory feedback for errors on arrow discrimination, responses on stop-trials, and failures to respond within the 750 ms time window on go-trials. After every block, each participant received visual feedback on his or her accuracy and reaction time to encourage high performance. The entire session lasted around 40 minutes.

Experiment 2. The task was the same as in experiment 1, but with the Go and No-go trial stimuli switched. When a white arrow was presented, participants were required to respond as fast as possible using the right or left arrow key (go-trial). When the arrow presented was green or red (No-go trials), participants were required to not make a response (see **Figure 8B**).

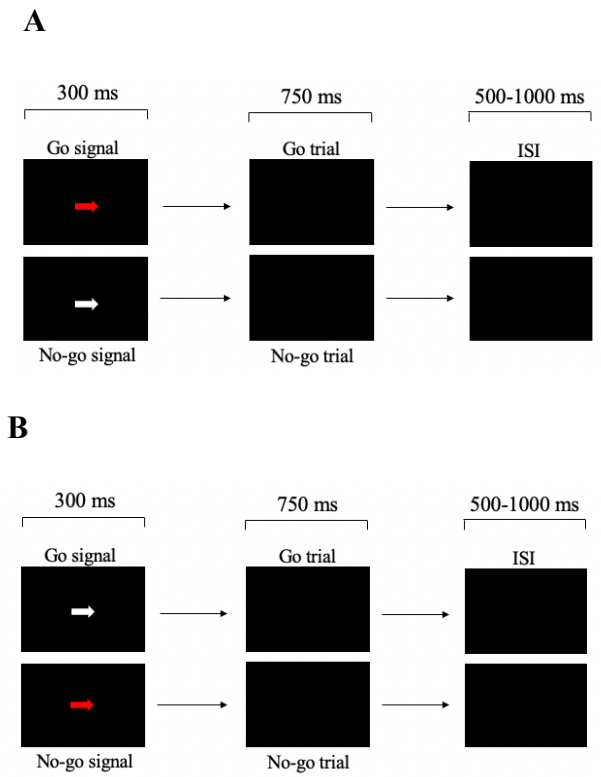

Figure 8. 2-Choice Discrimination Go/No-go Task. A. In experiment 1, participants responded to the direction of a green or red arrow (go trials). On a subset of trials, a white arrow was presented (No-go trials), which signaled participants to not make a response. **B.** In experiment 2, participants responded to the direction of a white arrow (go trials). On a subset of trials, the arrow presented was green or red (No-go trials), which signaled participants to not make a response.

Data Analysis

Participant response times in any given condition that fell outside of 2.5 standard deviations were removed from further analysis. Error rate was computed for Go trials as the number of unsuccessful Go trials/ total number of Go trials. For No-go trials, it was computed as number of unsuccessful No-go trials/ total number of No-go trials for each color separately.

Reaction times for successful Go trials and unsuccessful No-go trials were also computed. All statistical analyses were done using IBM SPSS statistics for Macintosh, Version 27.0.

Results

Table 3 shows the mean error rate (%) and mean RTs (ms) for the go and no-go colors in experiments 1 and 2. Mean error rates were not significantly different between left (M = 3.18, SD = *1.91*) and right arrows (M = 3.90, SD = *1.97*); t *(23)* = 1.57, p = .13. RTs were also not significantly different between left (M = 379.91, SD = *24.12*) and right arrows (M = 378.44, SD = *30.55*); t *(23)* = -.88, p = .39, therefore "left" and "right" responses were combined for the subsequent analyses.

Experiment 1

In experiment 1, the go trial mean errors were not normally distributed (Shapiro-Wilk's test), so non-parametric tests were used. A Wilcoxon signed rank test showed no significant difference in mean errors between green (M = 4.00, SD = 2.41) and red (M = 4.38, SD = 2.44) go trials (Z = - 1.026, p = .31). Additionally, mean errors on white no-go trials (M = 6.28, SD = 5.78) were not significantly different than mean errors on red and green go trials; (Z = -1.20, p = .23) and (Z = - 1.74, p = .08) respectively (see **Figure 9**). Bonferroni-corrected paired samples t-tests revealed that green go RTs (M = 382.71, SD = 50.86) were not significantly different than red go RTs (M = 386.04, SD = 52.05); (t *(23)* = -2.11, p = .138) (see **Figure 10)**, but RTs on green and red go trials were each significantly slower than RTs on white no-go error trials (M = 348.78, SD = 47.18); t *(22)* = 5.00, p < .001 and t *(22)* = 5.03, p < .001 respectively.

Experiment 2

In experiment 2, the Shapiro-Wilk's test of normality was violated for no-go trial mean errors, therefore a Wilcoxon signed rank test was conducted to analyze the mean error rates. Participants made significantly more errors on green (M = 3.27, SD = *3.01*) compared to red no-go trials (M = 1.85, SD = 2.27), (Z = - 2.72, p = .007). Mean errors on white go trials (M = 4.25, SD = 2.17) were not significantly different than mean errors on green no-go trials; (Z = - 1.93, p = .054) but were significantly different than errors on red no-go trials (Z = -3.40, p < .001) (see **Figure 9**). Bonferroni-corrected paired samples t-tests showed no significant difference in RTs (see **Figure 10**) between green (M = 347.43, SD = 27.69) and red (M = 345.06, SD = 50.91) no-go error trials (t *(15)* = .29, p = .24), but RTs on green no-go error trials were significantly faster than RTs on white go error trials (M = 379.13, SD = 35.31; t *(20)* = -4.00, p < .001) while red no-go error-trials were not (t *(16)* = -2.09, p = .16).

Table 3

Accuracy, error rates, and RTs of Go/No-go task.

Experiment 1	Go Color	Error Rate (M (*SD*))	RT (M (*SD*))
	Green	4.00 (*2.41*)	382.71(*50.86*)
	Red	4.38 (*2.44*)	386.04(*52.05*)
	No-go color	Error Rate (M *(SD)*)	RT (M (*SD)*)
	White	6.28 (*5.78*)	348.78 (*47.18*)

Experiment 2	Go Color	Error Rate (M *(SD)*)	RT (M *(SD)*)
	White	4.25 *(2.17)*	379.13 (*35.31*)
	No-go Color	Error Rate (M *(SD)*)	RT (M *(SD)*)
	Green	3.27 (*3.01*)	347.43 (*27.69*)
	Red	1.85 *(2.27)*	345.06 (*50.91*)

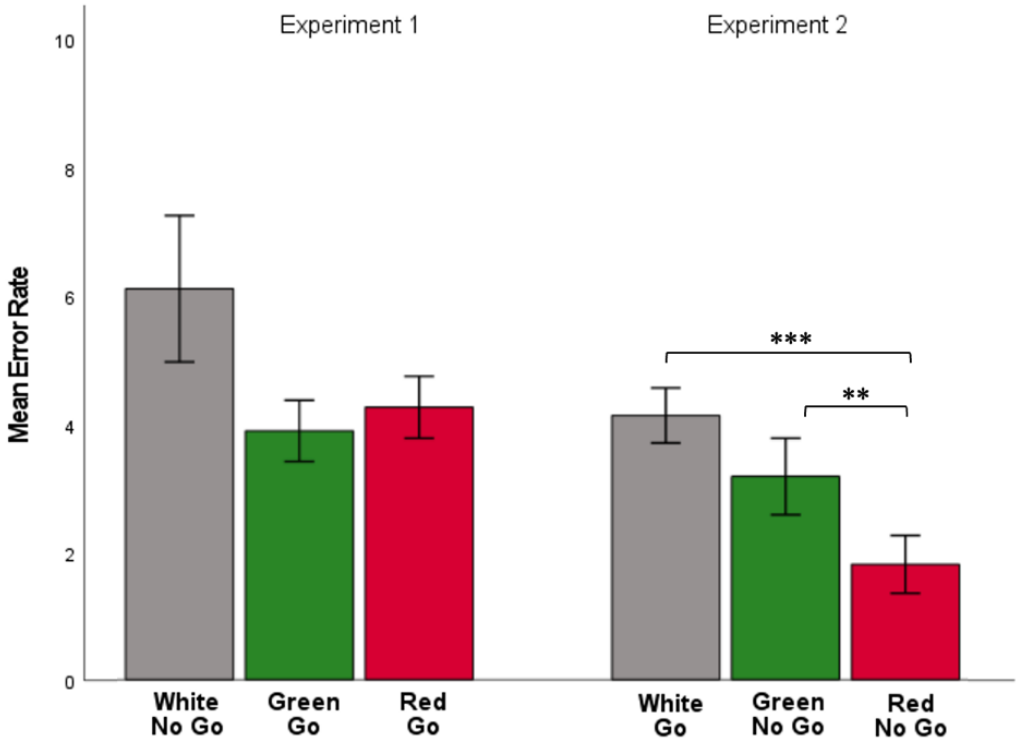

Figure 9. Error Rates across Colors in Go/No-go Experiments 1 and 2. In experiment 1, there are no significant differences between mean error rates. In experiment 2, mean error rates are greater for white go signals compared to red no-go signals and greater for green compared to red no-go signals. Error bars represent standard error of the means. ** $p < 0.01$. *** $p < 0.001$.

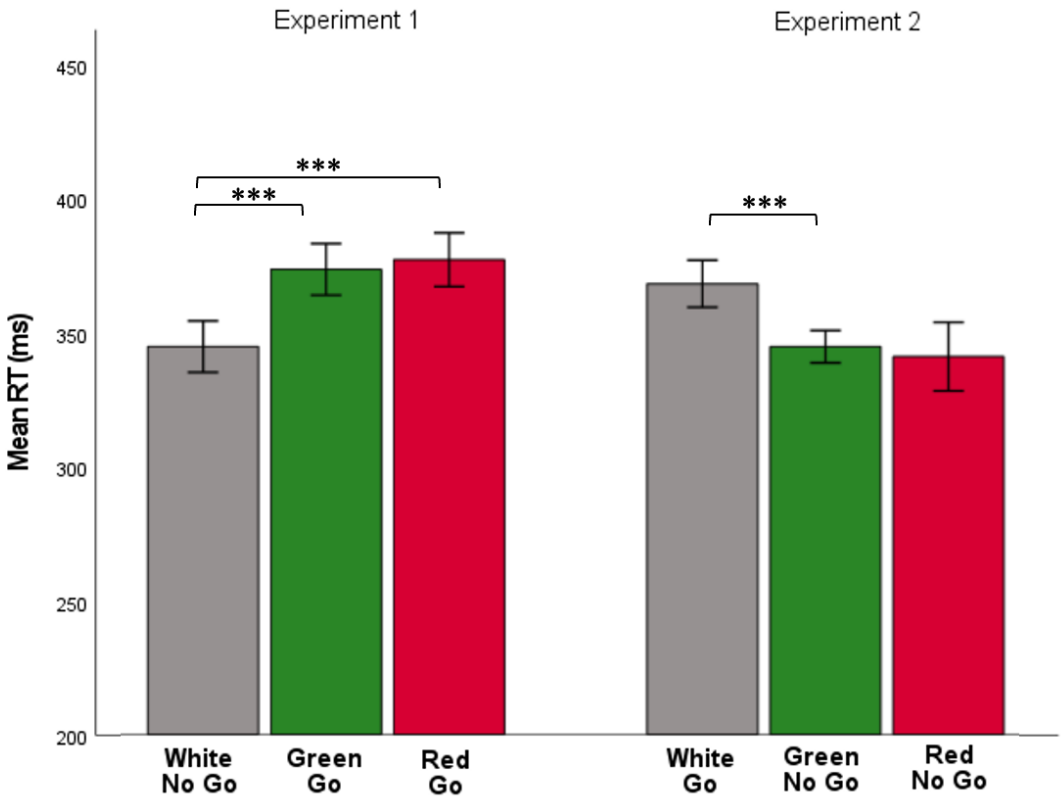

Figure 10. Reaction Times across Colors in Go/No-go Experiments 1 and 2. In experiment 1, mean RTs are faster for white no-go signals compared to red and green go signals and faster for green compared to red go signals. In experiment 2, mean RTs are slower for white go signals compared to green and red no-go signals. Error bars represent standard error of the means. *** $p < 0.001$.

Meta-Analysis of Color across both Experiments

A meta-analysis was conducted across both experiments to investigate the effect of colors across go and no-go signals. A 3 (Color: white, green, red) × 2 (Signal Type: colored go signals, colored no-go signals) repeated-measures ANOVA revealed a significant main effect of color (*F*

(2, 92) = 8.94, p <.001, η^2 = .16) such that Bonferroni-corrected pairwise comparisons revealed significant differences between white and green error rates (p = .037) and between white and red error rates (p = .003) but not between green and red error rates (p = .19) (see **Figure 9**).

A significant between-subjects effect of signal type (F (1, 46) = 6.07, p = .018, η^2 = .12) was also found such that error rates were greater in experiment 1 (colored go/white no-go) compared to experiment 2 (white go/colored no-go). The interaction between colors and their signal type was not statistically significant (F (2, 92) = 1.53, p = .22, η^2 = .032) for error rates (see **Figure 11**).

For reaction times, the was no main effect of color (F (2, 74) = .14, p =.87, η^2 = .004) nor between-subjects effect of signal type (F (1, 37) = 1.23, p = .28, η^2 = .032). However, the interaction between them was significant (F (2, 74) = 15.79, p < .001, η^2 = .30), due to white signals producing faster RTs on go trials and slower RTs on no-go trials than red and green (see **Figure 12**).

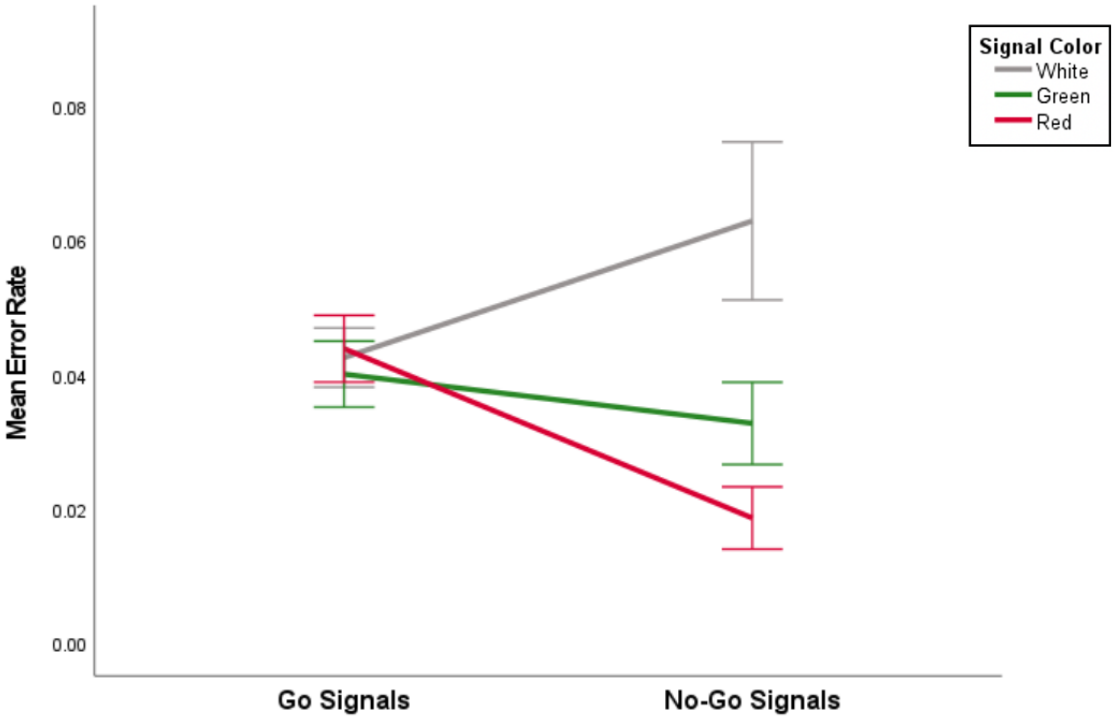

Figure 11. **Error Rates across Signal Type in Experiments 1 and 2.** Mean error rates for white, green, and red in Go/No-go experiments 1 and 2. Error bars represent standard error of the means.

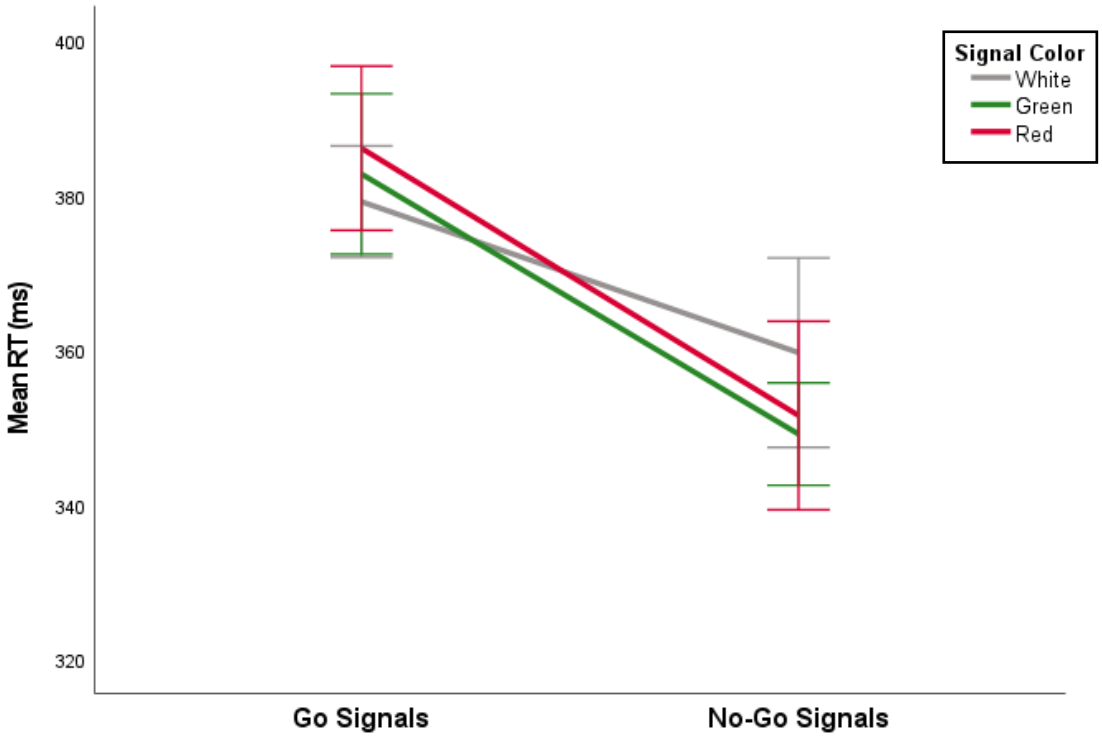

Figure 12. **Reaction Times across Signal Type in Experiments 1 and 2.** Significant interaction between color and signal type (i.e.: colored go signals vs colored no-go signals) for white, green, and red in Go/No-go experiments 1 and 2. Error bars represent standard error of the means.

Trial History

In experiment 1, we tested whether the color of a go signal which did not affect go error rates or reaction times, primed inhibitory control on subsequent no-go trials and found no significant difference ($t\ (23)$ = .60, p = .56) in the error rates on white no-go trials following green (M = 7.48, SD = 6.87) versus red (M = 7.09, SD = 5.98) go trials. We also found no significant difference ($t\ (23)$ = -1.32, p = .20) between white no-go error RTs following green (M

= 314.67, *SD* = 21.87) versus red (*M* = 320.87, *SD* = 22.27) go signals. In experiment 2, we tested whether color modulation of response inhibition would carry over to the subsequent white go trial. A paired samples t-test comparing the error rates of go responses after successful red no-go trials (*M* = 3.67, *SD* = 2.75) versus after successful green no-go trials (*M* = 4.07, *SD* = 3.07) was not statistically significant (*t (23)* = -.87, *p* = .39). There was also no significant difference between the RTs of go responses following green (*M* = 387.95, *SD* = 40.38) and red (*M* = 387.51, *SD* = 43.58) no-go trials (*t (23)* = .23, *p* = .82).

Discussion

This study assessed if the innate color associations of green and red found in reactive inhibition (SST) generalized to proactive response inhibition (Go/No-go task). In the first experiment, green and red arrows were presented as go signals and white arrows were presented as no-go signals. The color of the arrow did not affect its discrimination performance or response execution reaction times, consistent with prior studies using the SST (Blizzard et al., 2017; Asare et al., *in preparation*). In the second experiment, white arrows were presented as go signals while green or red arrows denoted no-go signals. We found lower error rates for red compared to green no-go stimuli. Therefore, red enhances and green impairs proactive response inhibition as well as reactive response inhibition, which suggests that the effects of red and green generalize to all types of response inhibition. Taken together, discrimination decision-making, response execution, and response inhibition can be considered functionally separate processes, where only response inhibition is affected by color.

Combining the results from the two experiments allows for comparing colors (white, green, red) across both go and no-go signals. No-go error rates were lowest for red, then green

followed by white stimuli. Therefore, red facilitates response inhibition more than green, yet white, which activates both red and green cones, has a weaker effect on response inhibition than red or green alone. This may be due to competition between red and green, which are opponent colors, counteracting each other's effects rather than an additive process. Alternatively, it may be due to categorical colors and their semantic meanings, (Adams & Osgood, 1973; Kay & McDaniel, 1978; Lin et al., 2013) with white lacking any such meanings and thus having the weakest effect which explains its lack of perceptual saliency.

Prior studies have suggested that red produces an alertness or arousal response, (Crowley, 1993; Elliot & Aarts, 2011; Labrecque, Patrick, & Milne, 2013). If that is the case, the effects of red may just be due to a higher level of arousal rather than a direct effect on response inhibition. Such an increase in arousal should carry over from that trial to the next, as it takes time to diminish. To test this hypothesis, we investigated whether red and green go signals (Exp. 1), if they produced nonspecific increases in arousal, would modulate response inhibition produced by a white no-go signal on the following trial. We found no such effects which suggests that the innate effects of red and green directly modulate response inhibition. Next, we investigated whether the color effects were due to modulating the speed or the strength of response inhibition. If red no-go signals (Exp. 2) produced stronger response inhibition than green no-go signals, then the reaction times of go trials should be slower if they followed red no-go trials than green ones. However, if red no-go signals instead sped up completion of the response inhibition process over green no-go signals, then there should not be any effect on the subsequent trial. There was no evidence of any difference in reaction times of go trials that followed red versus green no-go trials. Therefore, it is likely that red and green affect the speed of response inhibition, but not its strength. Taken together, red and green directly modulate the

speed by which the response inhibition process completes. Future studies would need to determine if the color effects on response inhibition are specific to manual responses or are effector-independent and present for gaze responses as well.

Neural Circuitry

Action selection has been shown to be dependent on inferior frontal cortex (Aron, Robbins, and Poldrack, 2004; 2014). More specifically the inferior frontal gyrus and the inferior frontal junction are involved in top-down suppression of actions (Aron & Poldrack, 2006; Sharp et al., 2010; Cai and Leung, 2011; Levy and Wagner, 2011). Action selection is multi-faceted and would include both the selection of a specific action as well as the inhibition of alternative actions, e.g.: proactive response inhibition, (Rowe, Hughes, & Nimmo-Smith., 2010; Zhang, Hughes, & Rowe, 2012). Stopping, however, relies on inhibition of an action currently in preparation, e.g.: reactive response inhibition, (Aron & Poldrack, 2006). So, while there is functional independence between action selection and stopping, both processes are still mechanistically similar (Boucher et al., 2007; Logan et al., 2015; Middlebrooks et al., 2020). Therefore, areas common to both action selection and stopping are likely candidates as mediating the effects of red and green on both types of response inhibition. A meta-analysis conducted by Rae et al. (2014) investigated the overlap between action selection and stopping. While action selection also recruits the left pre-SMA, left premotor cortex, and bilateral middle frontal gyrus, stopping differentially recruits the left inferior frontal gyrus (pars triangularis) and bilateral anterior insula. Both action selection and stopping recruit the pre-supplementary motor area (pre-SMA) and inferior frontal gyri. Therefore, this fronto-parietal network is the likely recipient of the red and green input that modulates response inhibition. However, these two areas do not

inhibit responses directly, they are part of a larger motor control network that runs through subcortical areas to the spinal cord (see **Figure 13**). Output from the prefrontal portion of the network feeds into subcortical areas through the direct, indirect, and hyperdirect pathways to the basal ganglia (prefrontal loops, e.g.: Boehler et al., 2010). The direct pathway facilitates behavioral execution by disinhibiting thalamic control of motor output (Albin, Young, & Penny, 1989). As there has been no evidence supporting the effects of red and green on response execution, this pathway is likely not modulated by color. The indirect pathway results in inhibition of thalamic motor output. Thus, this pathway could mediate proactive response inhibition, and based on the results of this study, would be modulated by red and green. The hyperdirect pathway is a faster pathway to the subthalamic nucleus (STN) that bypasses the striatum which results in reactive response inhibition (e.g., Jahfari et al., 2011) and therefore would also likely be modulated by red and green colors. Future neuroimaging or neurophysiology studies will be needed to test this theoretical neural circuitry (see **Figure 13**).

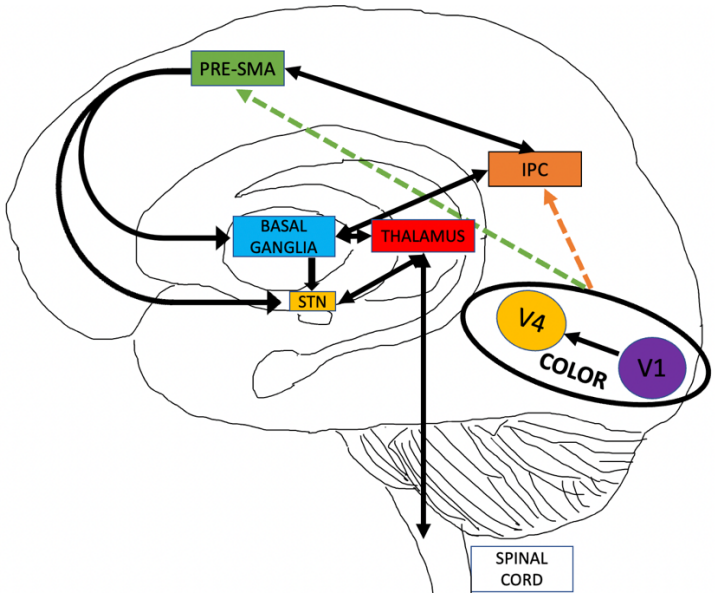

Figure 13. **Theoretical neural circuitry of color information.** Theoretical neural circuitry of color information (V1 to V4) being sent to the inferior parietal cortex (IPC) and the pre-supplementary motor area (pre-SMA) then to the basal ganglia, subthalamic nucleus (STN), thalamus and spinal cord through the indirect pathway and to the subthalamic nucleus (STN), thalamus and spinal cord through the hyperdirect pathway.

Putative Mechanism

In both experiments, color information is processed until a decision is made about whether it is a go or no-go trial. Accumulator models (Vickers, 1970; Smith & Vickers, 1980; Hanes & Schall, 1996; Ratcliff, Cherian, & Segraves, 2003) represent this as the accumulation of information until a decision threshold is reached (see **Figure 14**). As color had no effect on response execution in go trials, that information accumulation would be independent of whether the stimulus was red (Exp 1), green (Exp 1), or white (Exp 2). However, color did affect performance on no-go trials, which could arise from one of two mechanisms within the accumulator model (Purcell & Palmieri, 2017). The first potential mechanism is if color

modulated the slope of information accumulation such that red no-go stimuli were processed faster than green and green no-go stimuli were processed faster than white (see Figure 7a). Information would accumulate until either a decision (threshold) is reached, or in a speeded task like this, the individual makes a response without full information. In the latter case, the error rates produced are dependent on how far away the accumulated information is relative to the threshold at the time the response is made. **Figure 14A** is a depiction of this model based on the behavioral results of these experiments: red stop signals result in a faster slope and at the time of the decision, will produce less errors than green with its slower slope. The slope for white stop signals is slower yet, producing the highest error rates of the three. The second potential mechanism is based on the color of the stop signal affecting the height of the decision threshold. As red facilitated proactive response inhibition, the threshold for red-dependent response inhibition would be lower than that for green, which would be lower yet than that for white, (see **Figure 14B**). Thus, red no-go stimuli are more likely to reach threshold by the time the speeded decision needs to be made, resulting in lower error rates than green stimuli, with white having the highest threshold and error rate of the three colors. If the task was not speeded, participants could delay their decision until fully certain, i.e.: for both potential mechanisms and any of the colors, the threshold would be reached, and no response would be made. Future neurophysiology studies could determine whether red and green modulate the rate of information accumulation or the thresholds.

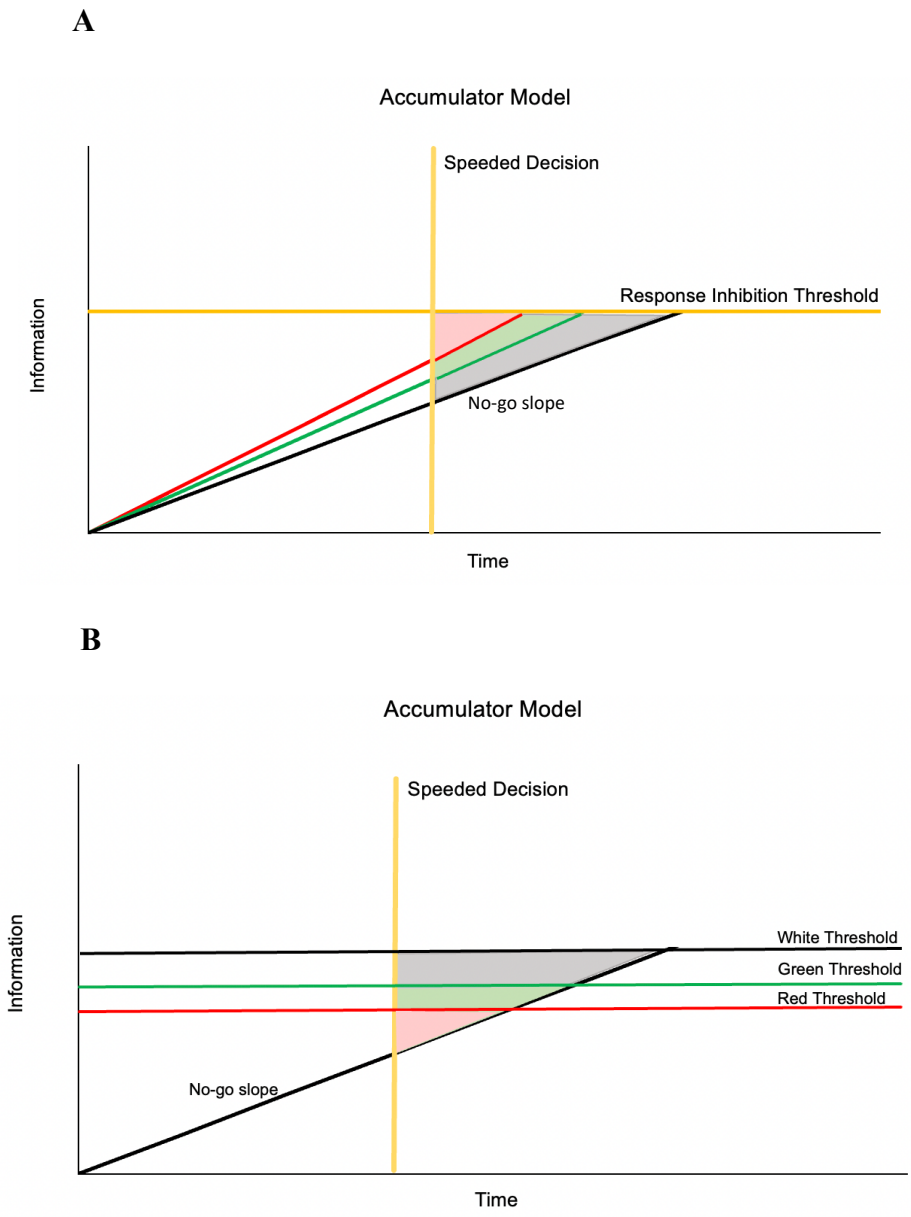

Figure 14. Accumulator model of proactive response inhibition. A. Based on the results of Experiments 1 & 2, if color modulates the rate of information accumulation towards the response inhibition threshold, red will produce less errors than green which will produce less errors than white. Shaded regions represent proportion of errors. **B.** Alternatively, color could affect the threshold in the model, providing the same results where red produces less errors than green which produces less errors than white. Shaded regions again represent proportion of errors.

Conclusion

In this study we investigated the effects of color on proactive response inhibition and found that red facilitates response inhibition compared to green, consistent with the effects of red and green on reactive response inhibition. Therefore, the innate color associations of red and green (Ghasemian et al., 2021) are integrated into both proactive and reactive inhibitory circuitry. This integration could potentially be through prefrontal cortex activation feeding into basal ganglia loops, which would support the effects of red and green on both forms of response inhibition being automatic, inherent, and evolutionarily conserved.

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CHAPTER 5: STUDY 3

THE N2 COMPONENT REFLECTS COLOR MODULATION OF RESPONSE INHIBITION IN A GO/NO-GO TASK

Abstract

Red colored stimuli have been shown to facilitate response inhibition over green. To further investigate color modulated response inhibition and its underlying network, event-related potentials (ERPs) were recorded while participants performed a Go/No-go task. We hypothesized that the N200 and P300 which reflect response inhibition would be modulated by the color of the no-go stimuli. Accuracy was highest for red no-go stimuli, followed by green and yellow, then blue. Robust effects were found for the P100 whereby red attenuated its amplitude compared to green, yellow, and blue in the posterior regions of the brain. This suggests that the cost of attention was lesser for red compared to other colors. The N200 reflected the more efficient inhibition for red with reduced amplitudes and earlier latencies compared to the other colors. The modulation of the N200 occurred over the frontal and frontal central regions, suggesting the involvement of the pre-SMA. The P300 was not modulated by color, suggesting that color did not affect inhibitory load. These findings bring us a step closer to mapping out the differential colour modulated neural circuitry involved in response inhibition.

Introduction

Recent studies have shown that red and green colors modulate response inhibition (Blizzard et al., 2017; Asare et al., *in preparation*; Asare, Jordan, & Fallah, *in preparation*). Red stimuli facilitate stopping while green impairs it, compared to other colors such as yellow, and blue. This modulation has been observed in the stop-signal task (SST); a reactive response inhibition task whereby motor responses are initiated on every trial, and individuals must employ action cancellation to countermand their responses on a subset of trials when a stop signal occurs after a variable delay (Verbruggen & Logan, 2008). The effects of red and green on inhibitory control have also been found in proactive response inhibition via the Go/No-go task (GNGT) whereby participants are presented with either a go or a no-go stimulus in respective trials and must respond accordingly (Gomez, et al., 2007). In this task, the trial stimulus determines if a response is to be made or not. Therefore, individuals are said to rely on action restraint to inhibit their responses (Schachar et al., 2007; Raud et al., 2019).

Response inhibition has not been clearly tied to a specific ERP (event-related potential) component in EEG (electroencephalography) studies, although a number have implicated the N200/P300 complex (Simson et al., 1977; De Jong et al., 1990; Luck & Kappenman, 2011). Since color modulates response inhibition, we can use it to identify the electrophysiological correlates of response inhibition and its underlying neural circuitry. This will provide further insight on inhibitory control networks and how neurodegenerative diseases impact them.

Color and the N200/P300 complex

There is evidence for an automatic attentional color hierarchy (Tchernikov & Fallah, 2014; Perry & Fallah, 2014; Kehoe, Rahimi & Fallah, 2018). Electrophysiological correlates of

color modulating attention have also been found. The color hierarchy has received additional support from a neuroimaging study, wherein Pomerleau et al. (2014) used ERPs to study the deployment of attention to colors (red, green, blue, orange). Lateralised components including the posterior contralateral positivity (Ppc), the N200, and the temporal contralateral positivity (Ptc) showed automatic color attentional modulation. Red targets produced a larger Ppc, earlier N200, and a larger Ptc. Blue targets also produced an earlier N200 relative to yellow and green. Blue and red color associations have been further studied recently in the context of Go/No-go tasks. Kubo et al., 2021 used blue and red Go/No-go stimuli with three different Go probabilities (30, 50, and 70%). Slower responses were made with red compared to blue Go signals especially with lower probabilities. Furthermore, the amplitudes of the N200 and P300 components in the frontal and central regions of the brain were larger on red compared to blue go trials and moreso with lower Go probability (Kubo et al., 2021). Together, these findings demonstrate that the advantage of red over other colors in an intrinsic attentional color hierarchy (Tchernikov & Fallah, 2014) is reflected in the N200 and P300 components in posterior regions of the brain. Therefore, it is likely that color modulation of response inhibition will be found in fronto-central components reflecting response inhibition.

Response inhibition and the N200/P300 complex

The N200 (N2) event-related potential (ERP) component is characterized by a frontal central negative potential with a latency of 200-300ms post stimulus presentation (Falkenstein et al., 1999; Gajewski, Stoerig, & Falkenstein 2008). Reliably, an augmented no-go N200 is observed compared to the go N200 and is suggested to potentially reflect the inhibition required in stop-trials (Kok et al., 2004; Enriquez-Geppert et al., 2010; Huster et al., 2010; Huster et al.,

2013). There are three options as to how the N200 might do so. The increased N200 amplitude in no-go vs go trials may reflect the activation of the response inhibition process or the inactivation of response execution (Géczy et al., 1999; Baumeister et al., 2014). However, the likelihood of a go trial also modulates the N200, as Nieuwenhuis et al. (2003) reported an enhanced N200 when presenting rare go-trials (20% chance of presentation) in the context of much more common no-go trials. These observations indicated that the N200 might then reflect conflict caused by competition between the frequently and infrequently required responses in the context of conflict-monitoring (Nieuwenhuis et al., 2003; Randall & Smith, 2011).

The P300 (P3) ERP component follows the N200 and is characterized by a frontal central negative polarity with a latency of 300-600 ms post stimulus onset. As with the N200, amplitude differences have been found in response to go versus no-go trials and varying trial type proportions (Dimoska et al., 2006; Kok et al., 2004; Ramautar, Kok, & Ridderinkhof, 2004). The frontocentral P300 is the most common ERP index of successful response inhibition with many studies (see Huster et al., 2013's review) having shown increased P300 amplitudes for successful versus failed stop trials. The component's latency range suggests that it reflects the late-stage response inhibition process (Band & van Boxtel, 1999; Donders & van Boxtel, 2004; Tian, Liang, & Yao, 2014). Consistent with this idea, Smith and colleagues (2008) found that P300 amplitudes increased when participants were required to inhibit a planned response or change their response suggesting that the P300 component indexed inhibitory load. Not surprisingly, there are conflicting views on whether the P300 is a direct reflection of response inhibition. While the P300 is related to response inhibition in these tasks, it is also found in a range of other tasks. Notably, the P300 is commonly observed following unexpected or rare events (i.e.: novel and oddball tasks) and P300-like potentials have also been associated with decision-making and

information processing (Wessel & Aron, 2015). The P300 has also been thought to reflect memory-updating processes as it has been associated with consciously maintained working memory traces (Näätänen, 1990; Watter, Geffen, & Geffen, 2001; Scharinger et al., 2017). Even when it is associated with response inhibition, some have argued that due to its late latency it reflects performance evaluation rather than response inhibition, (Dimoska et al., 2003; Huster et al., 2013).

In this study, we used EEG to elucidate the prefrontal networks involved in response inhibition that can be modulated by colour in a go/no-go task. Based on prior studies (Blizzard et al., 2017; Asare et al., *in preparation*; Asare, Jordan, & Fallah, *in preparation*), red facilitates and green impairs response inhibition. We hypothesize that color modulation of response inhibition will be reflected in the N200 (response inhibition) and P300 (inhibitory load) ERPs with reduced amplitude and latency shifts for red No-go trials in comparison to green, yellow, and blue. This study will therefore determine if and how color modulation of response inhibition is reflected in the N200 and P300 components which would determine which component(s) is/are responsible for the activation of response inhibition, the inactivation of response execution, and/or conflict monitoring.

Materials and Methods

Participants

Thirty-six participants (25 women) from York University, aged 18 to 36 years (M = 20.57, SD = 3.53), were included in the experiment. All participants were right-handed and had either normal or corrected-to-normal vision and successfully passed Ishihara's Test for color blindness (Ishihara, 2006). All participants received a partial course credit for their participation and in accordance with the Declaration of Helsinki (2003), gave written informed consent prior

to participation. All experiments were approved by York University's Human Participants Review Committee.

Equipment

Participants sat 57 cm away from a 21'' CRT monitor (ViewSonic G225f, 60-50 Hz, resolution = 1280 × 1024), and made responses using the "0" key on a numeric keypad with the right index finger. Experimental control was maintained by Presentation (Neurobehavioral Systems).

EEG data was recorded using a NeuroScan SynAmps system at a sampling rate of 256 Hz, using a 64-channel Quik-Cap Hydro Net cap, fitted according to the international 10-20 system. Vertical electrooculograms (EOGs; electrical activity that measures eye blinks) were recorded by placing an electrode above and below the right eye. Electrode impedance was kept below 5kΩ for all electrodes. The ground electrode was located between Cz and Fz, and all electrodes were referenced to Cz.

Stimuli and Procedure

In this experiment, participants were seated in dark room in front of a black screen displaying a fixation cross at the center. They were required to respond as fast as possible using the "0" key on a numeric keypad when a black and white (CIE $X = 10.84$, $Y = 11.74$, $Z = 16.49$) checkerboard was presented (go-trial). When a black and colored (red (CIE $X = 21.23$, $Y = 11.51$, $Z = 2.07$), green (CIE $X = 5.69$, $Y = 11.46$, $Z = 2.50$), yellow (CIE $X = 10.89$, $Y = 11.53$, $Z = 2.66$), or blue (CIE $X = 14.80$, $Y = 11.74$, $Z = 16.49$) checkerboard was presented instead (no-go

trials), they withheld their response. The four colors were selected to be photometrically isoluminant.

Participants completed 12 blocks (70 go trials/30 no-go trials per block). The no-go trials were equally distributed between all four color conditions across the session. The stimuli were presented on the screen for 300ms followed by an inter-trial stimulus interval between 500-1000ms. Participants received auditory feedback for errors consisting of responses on no-go trials, and failures to respond within the 450ms time window after stimulus presentation on go trials (see **Figure 15**). The entire session lasted around 30 minutes.

Data Analysis

Behavioral

Accuracy was computed for white checkerboard go trials, and for no-go trials split by color. Reaction times were computed for correct go-trials, and for successful no-go trials, again split by color. All statistical analyses were done using IBM SPSS statistics for Macintosh, Version 27.0.

Electrophysiological

EEG data was preprocessed using custom routines in MATLAB 2014a (TheMathWorks, Natick, MA) and the EEGLAB toolbox (Version 19; Delorme & Makeig, 2004). The data was visually inspected for bad channels and epochs with atypical artifact activity (e.g., from gross movement or spurious muscle activity). Such data was removed and the remaining data was re-referenced to a common average. The continuous time series was then filtered using symmetric two-way least squares finite impulse response (FIR) filters (0.1Hz high-pass). Then, the data was

epoched with respect to the go or no-go stimulus, beginning at 200 ms before stimulus onset and extending to 1000 ms post-stimulus onset. Moving window peak-to-peak artifact detection removed all eye-blink and other muscle or electrodes related artifacts and only participants with 50% or more trials remaining were included in all the analyses. Finally, a low-pass 30Hz (FIR) filter was applied to the data and the ERP was computed for each trial. Thus, successful go and no-go trials were included in each participant's grand average ERP waveforms and further analyzed. Mean amplitudes between 75 and 150 ms for the N100 and P100, between 175 and 325 ms for the N200, and between 325 and 425ms for the P300 were computed, and latencies were taken from the peak amplitude for each component. These were computed at all electrode sites except for the EOGs and mastoids.

Analyses of the ERP data were conducted using IBM SPSS statistics version 26. All repeated-measures ANOVAs were conducted between the 4 no-go colors for the relevant electrode regions listed (Frontal (FP1, FPz, FP2, AF3, AF4, F1, Fz, F2, F3, F4, F5, F6, F7, F8); Frontal Central (FC1, FCZ, FC2, FC3, FC4, FC5, FC6); Central (C1, CZ, C2, C3, C4, C5, C6); Central Parietal (CP1, CPZ, CP2, CP3, CP4, CP5, CP6); Parietal Occipital (PO3, POZ, PO4, PO7, PO8); and Occipital (O1, OZ, O2, CB1, CB2). The no-go data was additionally subjected to a condition comparing the left vs. right hemispheres. For regions in which a main effect of color was observed, we then conducted a repeated-measures ANOVA for each electrode individually. When an electrode specifically showed a main effect of color, Bonferroni-corrected pairwise comparisons were conducted.

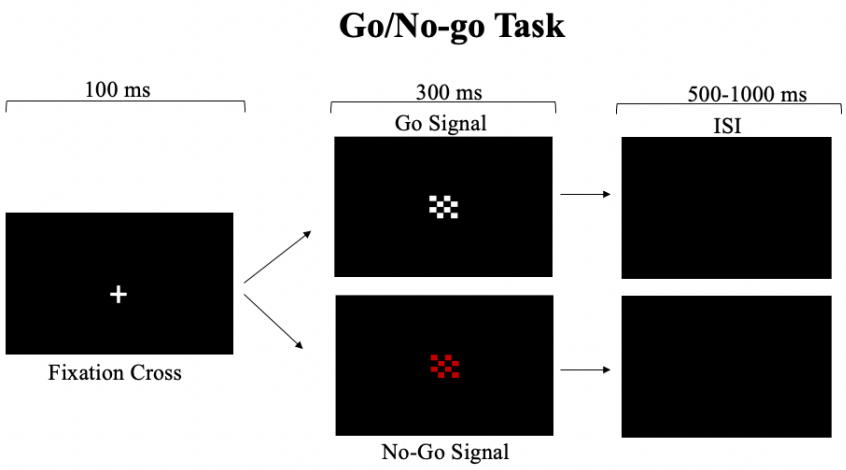

Figure 15. Go/No-go Task. For the Go/No-go task, participants responded to a black and white checkerboard using the key "0" on a numeric keypad. On a subset of trials, the checkerboard presented was black and either red, green, blue, or yellow (isoluminant with each other, equal proportions, pseudorandomly interleaved), which signaled participants to not respond.

Results

Behavioral

One participant was excluded for having less than 40% accuracy on the red, green, blue and yellow no-go colors. **Table 4** shows the accuracies (%) and mean RTs (ms) for the remaining participants. Paired samples t-tests were performed between go and no-go trial accuracies and RTs. As expected, significantly less errors were made on go trials (M = 5.18, SD = 3.65) compared to no-go trials (M = 34.76, SD = 10.94), $t(35)$ = -15.91, p <.001. Similarly, RTs were significantly slower on go trials (M = 271.65, SD = 12.66) compared to response errors on no-go trials (M = 251.63, SD = 12.82), $t(35)$ = 20.71, p <.001. Further analyses were crucially focused on differences between the colors on no-go accuracies and reaction times.

A repeated-measures ANOVA was conducted to investigate the effect of no-go color on RTs and accuracy. There was a main effect of color on mean no-go accuracies (F (3, 105) = 35.49, $p < .001$, $\eta^2 = .50$). Post-hoc Bonferroni-corrected pairwise comparisons (see **Figure 16**) showed that participants made less errors on red no-go trials ($M = 26.26$, $SD = 10.19$) compared to green ($M = 36.03$, $SD = 12.92$), $p < .001$; yellow ($M = 36.43$, $SD = 13.32$), $p < .001$; and blue ($M = 40.32$, $SD = 11.83$), $p < .001$ no-go trials. Participants also made less errors on green ($M = 36.03$, $SD = 12.92$) compared to blue ($M = 40.32$, $SD = 11.83$), $p < .001$ no-go trials. There were no significant differences between green and yellow or yellow and blue comparisons. In contrast to the accuracy results, there was no significant effect of color on reaction times (F (3, 105) = 1.09, $p = .36$, $\eta^2 = .03$).

Table 4

Mean and standard deviations of Go/No-go Task variables.

Signal	Color	% Error (M *(SD)*)	RTs (M *(SD)*)
Go	White	5.18 *(3.65)*	271.65 *(12.66)*
No-go	Red	26.26 *(10.19)*	250.15 *(14.17)*
	Green	36.03 *(12.92)*	252.03 *(15.49)*
	Yellow	36.43 *(13.32)*	252.23 *(13.17)*
	Blue	40.32 *(11.83)*	252.11 *(11.86)*

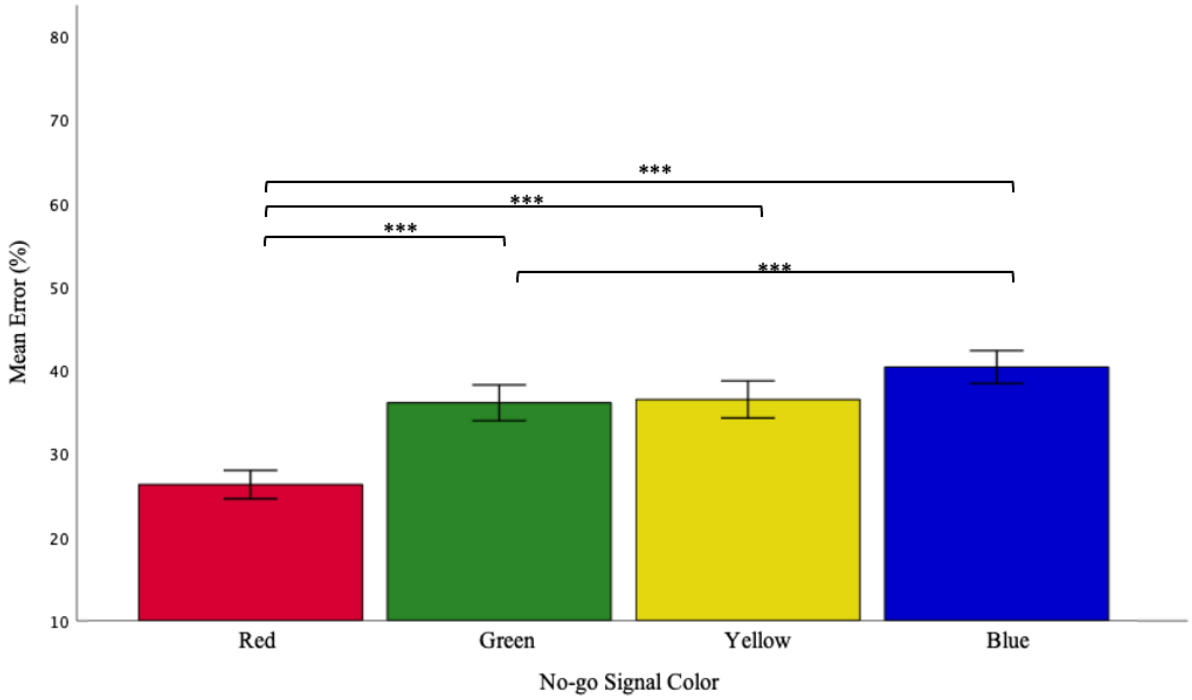

Figure 16. Errors in the Go/No-go Experiment. Mean errors for the No-go colors in the Go/No-go task**.** Error bars represent standard error of the means. *** $p < .001$.

Electrophysiological

All participants included in the behavioral analysis were included in the EEG analysis as none had more than 50% of their EEG recording rejected due to artifacts. See **Table 5** for a summary of robust and significant results.

Amplitudes. Repeated-measures ANOVAs were conducted to see if there were any main effects of color on specific scalp regions, hemispheres and electrodes. For the N100 and P100, there was a main effect of color on the mean amplitudes between 75 ms and 150 ms in the frontal central (F (3, 105) = 2.80, p =.043, partial η^2 = .074) and central (F (3, 105) = 2.96, p =.036, partial η^2 = .078) regions for the N100 and in the parietal occipital (F (3, 105) = 7.95, p <.001, partial η^2 = .19) and occipital (F (3, 105) = 10.55, p <.001, partial η^2 = .23) regions for the P100.

The effect of color was also significant for the interaction of the frontal central (F (3,105) = 2.92, p =.038, partial η^2 = 0.77), central (F (3,105) = 3.82, p =.012, partial η2 = .098), parietal occipital (F (3, 105) = 6.79, p <.001, partial η^2 = .16) and occipital regions (F (3, 105) = 9.29, p <.001, partial η^2 = .21) regions with hemispheric segmentation. In the frontal central and central regions, no individual electrodes showed a significant main effect of color demonstrating that the effect of color on the N100 was weak and diffuse, potentially reliant on electrode differences.

However, the effect of color on the P100 was robust. In the parietal occipital region, the individual electrodes that showed a significant main effect of color were POZ (F (3,105) = 9.38, p <.001, partial η^2 = .21), PO3 (F (3,105) = 7.35, p <.001, partial η^2 = .17), PO4 (F (3,105) = 8.45, p <.001, partial η^2 = .20), and PO7 (F (3,105) = 3.25, p =.025, partial η^2 = .085). Bonferroni corrected pairwise comparisons showed that at POZ, the mean red no-go amplitude (M = .51, SD=1.62) was significantly smaller than the mean green (M = 1.18, SD= 1.60) (p < .001), yellow (M = 1.10, SD=1.49) (p = .009), and blue (M = 1.09, SD= 1.52) (p = .001) no-go amplitudes. At PO3, the mean red no-go amplitude (M = 1.22, SD=1.61) was significantly lower than the mean green (M = 1.88, SD= 1.66) (p = .003), yellow (M = 1.72, SD=1.73) (p = .048), and blue (M = 1.81, SD= 1.82) (p = .012) no-go amplitudes. At PO4, the mean red no-go amplitude (M = 1.11, SD=1.67) was significantly lower than the mean green (M = 1.74, SD= 1.79) (p = .010), yellow (M = 1.80, SD=1.54) (p = .002), and blue (M = 1.77, SD= 1.65) (p = .001) no-go amplitudes. At PO7, the mean red no-go amplitude (M = 1.67, SD=1.61) was significantly lower than the mean green (M = 2.12, SD= 1.70) (p = .040) no-go amplitudes. Thus, unlike the N100, the early component P100 showed an effect of color with red consistently producing a smaller amplitude than green, yellow and blue in the parietal occipital region (see **Figure 17**).

In the occipital region, the individual electrodes that showed a significant main effect of color on the P100 were O1 (F (3,105) = 8.70, p <.001, partial η2 = .20), OZ (F (3,105) = 12.85, p <.001, partial η^2 = .27), O2 (F (3,105) = 10.79, p <.001, partial η^2 = .24), CB1 (F (3,105) = 12.85, p =.003, partial η^2 = .13), and CB2 (F (3,105) = 7.78, p <.001, partial η^2 = .18). Bonferroni corrected pairwise comparisons showed that at O1, the mean red no-go amplitude (M = 1.26, SD=1.67) was significantly lower than the mean green (M = 2.00, SD= 1.74) (p < .001), yellow (M = 1.88, SD=1.82) (p = .002), and blue (M = 1.77, SD= 1.77) (p = .023) no-go amplitudes. At OZ, the mean red no-go amplitude (M = 1.11, SD=1.67) was significantly lower than the mean green (M = 1.74, SD= 1.79) (p = .010), yellow (M = 1.80, SD=1.54) (p = .002), and blue (M = 1.77, SD= 1.65) (p = .001) no-go amplitudes. At O2, the mean red no-go amplitude (M = 1.07, SD=1.73) was significantly lower than the mean green (M = 1.75, SD= 1.83) (p = .003), yellow (M = 1.89, SD=1.61) (p < .001), and blue (M = 1.81, SD= 1.64) (p < .001) no-go amplitudes. At CB1, the mean red no-go amplitude (M = .98, SD=1.55) was significantly lower than the mean green (M = 1.64, SD= 1.48) (p = .001), and yellow (M = 1.56, SD=1.71) (p = .002) no-go amplitudes. At CB2, the mean red no-go amplitude (M = .87, SD=1.61) was significantly lower than the mean green (M = 1.45, SD= 1.64) (p = .008), yellow (M = 1.71, SD=1.53) (p < .001), and blue (M = 1.43, SD= 1.51) (p = .013) no-go amplitudes. In the occipital region, as in the parietal occipital, red no-go amplitudes are significantly lower than green, yellow, and blue P100 amplitudes. So, once more, while there is relatively no effect of color on the N100 electrodes, the effect of color on the P100 is quite robust (see **Figure 17**).

For the N200, there was a main effect of color on the mean amplitudes between 175ms and 325ms in the frontal central (F (3, 105) = 7.00, p <.001, partial η^2=.167) and central regions (F (3, 105) = 5.66, p <.001, partial η^2=.139). These effects of color were also respectively

significant for the interactions of the frontal central (F (3,105) = 6.49, p <.001, partial η^2=.156) and central; (F (3,105) = 5.81, p =.001, partial η^2=.142) regions with hemispheric segmentation. In the frontal central region, the individual electrodes that showed a significant main effect of color were FC5 (F (3,105) = 5.19, p =.002, partial η^2 = .13), FC3 (F (3,105) = 8.34, p <.001, partial η^2 = .19), FC1 (F (3,105) = 5.10, p =.002, partial η2 = .127), FC2 (F (3,105) = 3.32, p =.023, partial η^2 = .087), and FCZ (F (3,105) = 6.19, p =.001, partial η^2 = .150) demonstrating that the effect was more prominent in the left compared to the right hemisphere. Bonferroni corrected pairwise comparisons showed that at FC5, the mean red no-go amplitude (M = -.007, SD=1.13) was significantly lower than the mean green (M = -.59, SD= 1.17) (p < .001) and blue (M =-.58, SD=1.081) (p = .004) no-go amplitudes. At FC3, the mean red no-go amplitude (M =.081, SD=1.21) was significantly lower than the mean green (M = -.65, SD= 1.42) (p < .001), yellow (M = -.52, SD= 1.29) (p = *.014)*, blue (M = -.57, SD=1.13) (p < .001) no-go amplitudes. At FC1, the mean red no-go amplitude (M = -.25, SD = 1.35) was significantly lower than the mean green (M = -.82, SD = 1.55) (p = .010), yellow (M = -.817, SD = 1.52) (p = *.033)*, blue (M = -.77, SD =1.47) (p = .005) no-go amplitudes. At FCZ, the mean red no-go amplitude (M = -.65, SD =1.72) was significantly lower than the mean green (M = -1.36, SD = 1.78) (p = .007), yellow (M = -1.39, SD = 1.80) (p = *.013)*, blue (M = -1.32, SD =1.91) (p = .002) no-go amplitudes. At FC2, the mean red no-go amplitude (M = -.66, SD =1.35) was significantly lower than the mean yellow *(M* = -1.23, SD = 1.31) (p = *.021)* no-go amplitudes only. In the frontal central region, red no-go amplitudes were smaller than green, yellow, and blue amplitudes. This color modulation was stronger in the left than the right hemisphere. Therefore, not only is the effect of color on the frontal central N200 robust but it is also left lateralized (see **Figure 17**).

In the central region, the significant main effect of color was observed at C5 (F (3,105) =

3.16, p =.028, partial η^2 = .083), C3 (F (3,105) = 4.27, p =.007, partial η^2 = .109), C1 (F (3,105) = 7.56, p <.001, partial η^2 = .18) and CZ (F (3,105) = 3.11, p =.03, partial η^2 = .082) demonstrating once again that the effect of color was more prominent in the left hemisphere. At C5, the mean red no-go amplitude (M =.35, SD =.89) was significantly lower than the mean blue (M = -.016, SD = .89) (p = .029) no-go amplitudes. At C3, the mean red no-go amplitude (M =.51, SD =.89) was significantly lower than the mean yellow (M =.11, SD =1.04) (p = *.006)* and blue (M =.13, SD =1.02) (p = .021) no-go amplitudes. At C1, the mean red no-go amplitude (M =.51, SD =1.07) was significantly lower than the mean green (M = .078, SD = 1.12) (p = .025), yellow (M = -1.50, SD = 1.38) (p = *.003)*, blue (M =.51, SD = 1.07) (p = .001) no-go amplitudes. Our findings for the central N200 replicate those for the frontal central N200 in that red, again, had a left lateralized smaller amplitude compared to green, yellow and blue (see **Figure 17**).

For the P300, we observed no significant effect of color on the mean amplitudes between 325 and 425ms so no further analyses were conducted. This suggests that there is no inhibitory load difference between colors in our task.

Latencies. For the N100, there was no significant effect of color on peak latencies. For the P100, there was a main effect of color on the peak latencies between 75 ms and 150 ms in the parietal occipital (F (3, 105) = 6.33, p =.001, partial η^2 = .15) and occipital (F (3, 105) = 7.57, p <.001, partial η^2 = .18) regions. Consistent with the amplitude modulations, this main effect of color was again significant for the interactions of the parietal occipital (F (3, 105) = 5.62, p =.001, partial η^2 = .14) and occipital (F (3, 105) = 7.45, p <.001, partial η^2 = .18) regions with hemispheric segmentation. In the parietal occipital region, the individual electrodes that showed a significant main effect of color were PO3 (F (3,105) = 3.50, p = .018, partial η^2 = .091) and PO4 (F (3,105) = 3.67, p =.015, partial $\eta 2$ = .095). Bonferroni corrected pairwise comparisons

showed that at PO4, the peak latency of green (M = 111.00, SD=15.62) was significantly earlier than blue (M = 117.81, SD= 15.62) (p = .021). Within the parietal occipital, red P100 amplitudes were smaller than other colors, but latency differences between red and other colors were not observed except for green peaking earlier than blue suggesting an interplay between the color modulations and their effect on latency in this region (see **Figure 18**).

In the occipital region, the electrodes that showed a significant main effect of color were O1 (F (3,105) = 3.16, p = .028, partial η^2 = .083), OZ (F (3,105) = 4.10, p =.009, partial η^2 = .11), O2 (F (3,105) = 5.37, p = .002, partial η^2 = .13) and CB1 (F (3,105) = 4.22, p =.007, partial η^2 = .11). Bonferroni corrected pairwise comparisons showed that at O1, the peak latency of red (M = 108.64, SD=18.85) was significantly earlier than yellow (M = 115.28, SD=15.93) (p = .019). At O2, the peak latency of red (M = 107.17, SD=17.02) was significantly earlier than blue (M = 115.72, SD=15.99) (p = .014). At CB1, the peak latency of red (M = 105.81, SD=17.75) was significantly earlier than yellow (M = 113.03, SD=16.18) (p = .005). In the occipital region, red peaked earlier than yellow and blue which is consistent with the amplitude differences observed between those same colors (see **Figure 18**). However, red was not significantly earlier than green and this might be explained by the smallest mean error difference occurring between red and green.

For the N200 latencies, there was a main effect of color on the peak latencies between 175ms and 325ms in the frontal (F (3,105) = 3.55, p =.017, partial η^2 = .092), frontal central (F (3,105) =12.73, p <.001, partial η^2 = .27), central (F (3,105) = 9.062, p <.001, partial η^2 = .21), and central parietal (F (3,105) =3.02, p =.033, partial η^2 = .079) regions. The main effect of color was also significant for the interactions of the frontal (F (3,105) =3.33, p =.022, partial η^2 = .088), frontal central (F (3,105) =10.71, p <.001, partial η^2 = .234), and central (F (3,105) = 7.28,

p <.001, partial η^2 = .17) regions with hemispheric segmentation. In the frontal region, the electrodes that showed a significant main effect of color were AF3 (F (3,105) =3.49, p = .018, partial η^2 = .091), F1 (F (3,105) = 4.03, p = .009, partial η^2 = .10), FZ (F (3,105) =3.22, p =.026, partial η^2 = .084), F2 (F (3,105) = 3.67, p = .015, partial η^2 = .095), and F7 (F (3,105) = 2.83, p =.042, partial η2 = .075). Bonferroni corrected pairwise comparisons showed that at AF3, the peak latency of red (M = 272.75, SD = 36.28) was significantly earlier than blue (M = 290.78, SD = 30.54) (p = .004). At F1, the peak latency of red (M = 261.56, SD = 25.38) was significantly earlier than blue (M = 272.78, SD = 22.44) (p = .01). Lastly, at F2, the peak latency of red (M = 257.11, SD = 26.30) was significantly earlier than blue (M = 267.417, SD = 20.23) (p = .041). In the frontal regions, red N200 peaked consistently earlier than blue and this was left lateralized (see **Figure 17**). This is consistent with the red N200 amplitude being left lateralized and significantly smaller than blue as well. Yellow and green fell in between red and blue N200 latencies, such that there were no significant differences between each and red.

In the frontal central region, the individual electrodes that showed a significant main effect of color were FC1 (F (3,105) =12.83, p < .001, partial η^2 = .27), FCZ (F (3,105) =18.61, p < .001, partial η^2 = .35), FC2 (F (3,105) =9.22, p < .001, partial η^2 = .21), FC3 (F (3,105) = 6.052, p < .001, partial η^2 = .147), and FC4 (F (3,105) =11.47, p <.001, partial η^2 = .25). At FC1, the peak latency of red (M = 244.08, SD = 19.21) was significantly earlier than green (M = 252.75, SD = 16.20) (p = .014), yellow (M = 255.17, SD = 18.76) (p = .003), and blue (M = 272.78, SD = 22.44) (p < .001). At FCZ, the peak latency of red (M = 241.67, SD = 16.94) was significantly earlier than green (M = 250.06, SD = 15.25) (p < .001), yellow (M = 252.17, SD = 16.03) (p < .001), and blue (M = 256.83, SD = 18.58) (p < .001). At FC2, the peak latency of red (M = 245.36, SD = 17.55) was significantly earlier than yellow (M = 253.25, SD = 14.57) (p =

.007) and blue (M = 257.61, SD = 19.59) (p = .001). Lastly, at FC4, the peak latency of red (M = 245.81, SD = 19.73) was significantly earlier than green (M = 252.19, SD = 17.39) (p = .030), yellow (M = 254.53, SD = 17.94) (p < .001), and blue (M = 259.67, SD = 21.95) (p = .001). In the frontal central regions, red N200 peaked consistently earlier than all other colors (see **Figure 18**). Unlike in the frontal region, in addition to being earlier than blue, red is also earlier than yellow and green. These pattern differences between the frontal and frontal central regions suggest that color modulation of latency is primarily localized to the frontal central regions.

In the central region, the individual electrodes that showed a significant main effect of color were C1 (F (3,105) = 7.14, p < .001, partial η^2 = .169), CZ (F (3,105) = 11.49, p < .001, partial η^2 = .315), C2 (F (3,105) = 5.33, p =.002, partial η^2 = .132), C4 (F (3,105) = 4.29, p = .007, partial η^2 = .108), and C5 (F (3,105) = 3.092, p =.030, partial η^2 = .081). At C1, the peak latency of red (M = 233.08, SD = 18.49) was significantly earlier than yellow (M = 242.61, SD = 18.67) (p = .001), and blue (M = 246.78, SD = 14.89) (p < .001). At CZ, the peak latency of red (M = 233.92, SD = 16.11) was significantly earlier than green (M = 242.83, SD = 16.31) (p < .001), yellow (M = 243.75, SD = 14.12) (p < .001), and blue (M = 246.14, SD = 19.22) (p < .001). At C2, the peak latency of red (M = 236.28, SD = 19.65) was significantly earlier than blue (M = 247.67, SD = 17.59) (p = .003). At C4, the peak latency of red (M = 231.19, SD = 24.17) was significantly earlier than blue (M = 246.44, SD = 17.77) (p = .001). At C5, the peak latency of red (M = 234.06, SD = 38.20) was significantly earlier than green (M = 254.22, SD = 37.69) (p = .022). In the central region, N200 latencies are once again lateralized to the left with red N200 latencies peaking earlier than blue (see **Figure 18**). While red at times peaks earlier then green or yellow, that depends on individual electrodes, suggesting it is not a robust effect.

Once again, color modulation of N200 latencies is consistent with the modulation of the amplitudes.

In the central parietal region, the electrodes that showed a significant main effect of color were CPZ (F (3,105) = 5.30, p =.002, partial η^2 = .13), CP2 (F (3,105) = 3.58, p =.016, partial η^2 = .093), and CP6 (F (3,105) =2.76, p =.046, partial η^2 = .073). At CPZ, the peak latency of red (M = 223.50, SD = 22.34) was significantly earlier than green (M = 231.61, SD = 21.130) (p = .002), yellow (M = 230.53, SD = 19.89) (p = .018), and blue (M = 232.64, SD = 19.095) (p = .042). At CP2, the peak latency of red (M = 215.36, SD = 21.08) was significantly earlier than green (M = 227.28, SD = 24.89) (p = .003), and yellow (M = 226.42, SD = 22.33) (p = .001). The robustness of red N200 latencies being earlier than other colors decreases as we move away from the frontal central regions with red being earlier than other colors at few electrode sites and with the effect of lateralization no longer being maintained.

Unlike the P300 amplitude results, there was a main effect of color on the peak P300 latencies between 325 ms and 425 ms in the frontal central (F (3,105) = 3.015, p = .033, partial η^2 =.079) region alone. Bonferroni corrected pairwise comparisons showed that only at FC2 (F (3,105) = 3.58, p = .016, partial η^2 = .093) was the peak latency of red (M = 357.81, SD = 24.37) significantly earlier than that of green (M = 369.72, SD = 26.63) (p = .001). Therefore, red shows an earlier P300 latency shift compared to green in a single electrode location within the frontal central region where we have peak color modulations of red on response inhibition.

Table 5

Significant main effects of No-go colors on electrophysiology amplitude and latency measures in the Go/No-go task.

		Amplitudes		Latencies	
Potential	Brain Region	Electrode	No-go colors	Electrode	No-go colors
P100	Parietal occipital	POZ	Red & Green Red & Yellow Red & Blue	----------	----------
		PO3	Red & Green Red & Yellow Red & Blue	PO3	----------
		PO4	Red & Green Red & Yellow Red & Blue	PO4	Green & Blue
		PO7	Red & Green	----------	----------
	Occipital	O1	Red & Green Red & Yellow Red & Blue	O1	Red & Yellow
		OZ	Red & Green Red & Yellow Red & Blue	OZ	----------
		O2	Red & Green Red & Yellow Red & Blue	O2	Red & Blue
		CB1	Red & Green Red & Yellow	CB1	Red & Yellow
		CB2	Red & Green Red & Yellow Red & Blue	----------	----------
N200	Frontal	----------	----------	AF3	Red & Blue
		----------	----------	F1	Red & Blue
		----------	----------	FZ	----------
		----------	----------	F2	Red & Blue
		----------	----------	F7	Red & Blue
	Frontal Central	FC1	Red & Green Red & Yellow Red & Blue	FC1	Red & Green Red & Yellow Red & Blue
		FCZ	Red & Green Red & Yellow Red & Blue	FCZ	Red & Green Red & Yellow Red & Blue
		FC2	Red & Yellow	FC2	Red & Yellow Red & Blue
		FC3	Red & Green	FC3	Red & Yellow

		Red & Yellow Red & Blue		Red & Blue
	----------	----------	FC4	Red & Green Red & Yellow Red & Blue
	FC5	Red & Green Red & Blue	----------	----------
Central	C1	Red & Green Red & Yellow Red & Blue	C1	Red & Yellow Red & Blue
	CZ	----------	CZ	Red & Green Red & Yellow Red & Blue
	----------	----------	C2	Red & Blue
	C3	Red & Yellow Red & Blue	----------	----------
	----------	----------	C4	Red & Blue
	C5	----------	C5	Red & Green

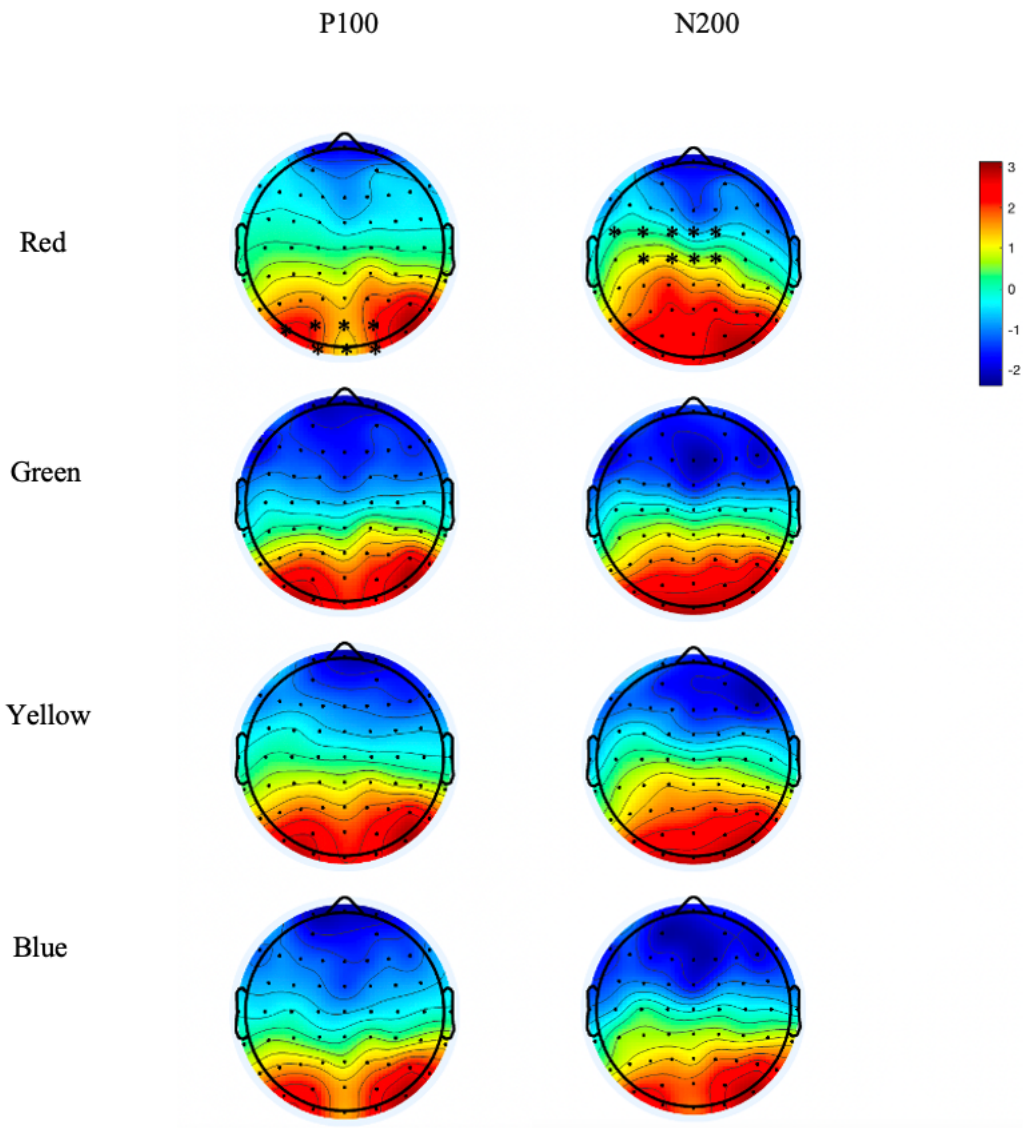

Figure 17. Scalp Maps of the P100 and N20 No-go Colors. Scalp maps of the P100 (75-150ms) and N200 (175-325 ms) No-go colors in the Go/No-go task**.** *p <.05 denotes significant amplitude differences between red and other colors.

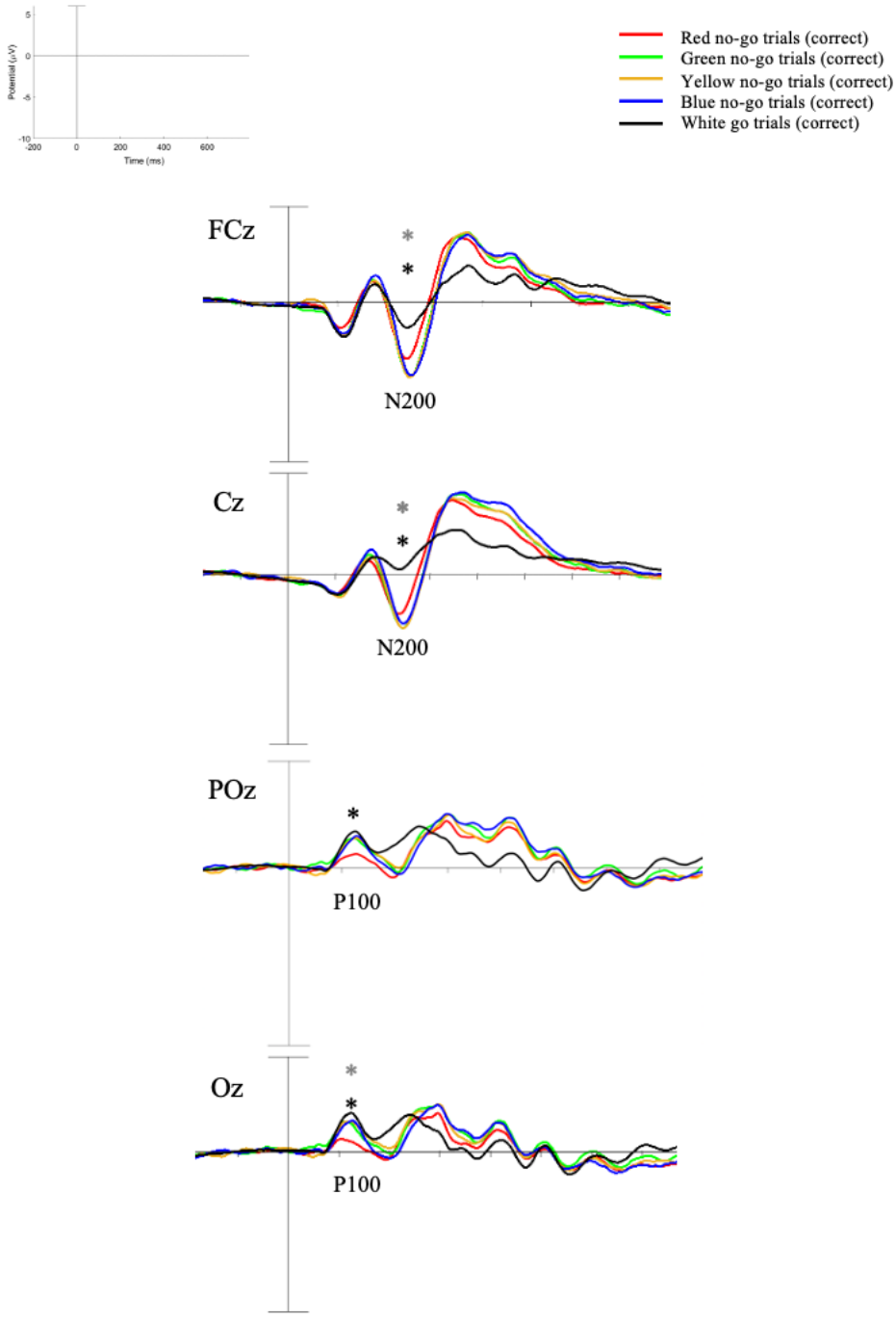

Figure 18. Go/No-go grand average event-related potential waveforms. Go (black) and No-go (red, green, blue, and yellow) grand average event-related potential waveforms along the midline. Significant amplitude (*) and latency (*) color differences denoted at the FPz, Cz, Pz, and Oz electrode site. *$p < .05$

Discussion

The current study used EEG to investigate the ERP components responsible for colour modulations of response inhibition. Behaviourally, red no-go stimuli were responded to with the greatest accuracy, while blue no-go stimuli were responded to with the least accuracy. The accuracy with which participants responded to green and yellow no-go stop signals were not significantly different from one another and fell between the red and blue no-go accuracies. We then investigated how this pattern of behavioral results was reflected in four components potentially arising from response inhibition: the N100, P100, N200, and P300.

Amplitude and Latency

No consistent effect of color on the N100 was found, that is, in the frontal central and central regions where there was a main effect of color, no individual electrodes showed significant color modulations on the amplitudes or latencies of the N100. The visual N100 is commonly distributed over the frontal central regions of the brain and increases the more attention is deployed to a target or location (Haider, Spong, & Lindsey, 1964; Easer, Harder, & White, 1969; Voorhis & Hillyard, 1977) and thereby reflects the benefit of attention (Luck et al., 1994). The very weak and diffuse color modulations of the N100 are likely due to having a single item on the display to process, thus not needing to rely on attentional selection.

The effect of color on the P100 was robust as red consistently had a smaller amplitude than green, yellow, and blue in the parietal occipital and occipital regions. Within the parietal occipital region, P100 latency differences between red and the other colors were not observed but green was found to peak earlier than blue consistent at least with blue having the weakest behavioral effect on response inhibition. In the occipital region, red peaked earlier than yellow

and blue, consistent with the behavioral results. While the P100 amplitude increases with attention similar to the N100 amplitude, it is distributed more posteriorly (Haider, Spong, & Lindsey, 1964; Easer, Harder, & White, 1969; Mangun & Hillyard, 1991; Voorhis & Hillyard, 1977). Additionally, Luck et al. (1994) specify that the P100 reflects the cost of attention because it is decreased when one stops paying attention or shifts their attention away from a target (Mangun & Hillyard, 1991; Voorhis & Hillyard, 1977; Luck et al., 1994). In this study, red attenuated the P100 amplitude compared to green, yellow, and blue in the parietal occipital and occipital regions. Latency differences were not found between red and the other colors, but blue did have a later latency than green. In the occipital region, red peaked earlier than yellow and blue however, red was not significantly earlier than green, which might be explained by the mean error difference between red and green being the smallest. These observations are in line with our behavioral findings of there being less errors made on red no-go trials compared to all other colors and could be explained as the cost of attention being less for red than other colors.

The effect of color on the N200 was also robust but unlike the P100 it was left lateralized. In the frontal central and central region, red no-go amplitudes were smaller than green, yellow and blue and this color modulation was greater in the left compared to the right hemisphere. However, these effects did not extend into the central parietal region. The effect of color on the N200 latencies showed that red consistently peaked earlier than blue and this color modulation was left lateralized in the frontal region as well. In the frontal central regions, red N200 latency was earlier than green, yellow and blue. In the central region, N200 latencies were also lateralized to the left and red N200 latencies were again earlier than blue. Some individual electrodes also showed red peaking significantly earlier than green and yellow. In the central parietal region, the earlier timing of red N200 latencies than other colors decreased as we moved

posteriorly from the frontal central regions resulting in color effects at few electrode sites and the loss of left lateralization. It is likely that for the N200, red compared to other colors reduces inhibition load. Our N200 findings are consistent with a more general observation that enhanced inhibitory control is reflected by a greater N200 amplitude and/or later N200 latency (Falkenstein, Hoormann, & Hohnsbein, 1999; Moreno et al., 2014). Reduced N200 for red, rather than green, no-go stimuli would occur if red needs less inhibitory control due to its inherent association with stopping. The earlier N200 onset may also reflect the advantage for red in response inhibition as the no-go N200 latency has been found to be delayed with greater task difficulty (Gajewski & Falkenstein, 2012).

For the P300, we observed no significant effect of color on amplitude. There was a red P300 latency shift earlier than green, but only on the FC2 electrode. As such, the effect of color on the P300 was not readily evident. Research on the P300 has typically found it to be a correlate of successful response inhibition. In a study that investigated fronto-central P300 onset using a SST, Wessel & Aron (2015) found that P300 onset latencies occurred significantly earlier on successful stop trials. The lack of significant findings in this study however might be explained by the P300 denoting inhibitory load instead of conflict. As previously noted, the P300 component has been linked to the working memory needed to support cognitive load (Näätänen, 1990; Watter, Geffen, & Geffen, 2001; Scharinger et al., 2017). Accordingly, our study did not manipulate task loads and the different no-go colours can therefore be thought to have comparable inhibitory loads.

N200/P300 comparison with behavioral results

The N200/P300 complex was investigated as they arise from successful no-go trials. In the frontal regions, red no-go N200 amplitudes were smaller than the other colors and this color modulation was left lateralized. Accordingly, red N200 latencies were consistently earlier than blue and this was left lateralized as well. Red N200 latencies were not significantly faster than yellow or green likely because those two colors fell between red and blue N200 latencies. However, this is consistent with the attentional color hierarchy found in the behavioral results where red no-go errors were the fewest followed green and yellow, then blue. In the frontal central regions however, red N200 was consistently earlier than all other colors suggesting that latency differences peak in this region.

In the central region, N200 latencies are left lateralized and red N200 latencies were again earlier than blue. Some individual electrodes showed earlier red latencies than green or yellow. Once again, these findings are consistent with those of red N200 amplitudes being lateralized and smaller compared to green, yellow and blue. The persistent left lateralization in our observations might be explained by the inclusion of only right-handed individuals in our experiment. Previous studies have shown that handedness can affect the N200 (Shi, Wang, & Yang, 2005; Chikara, Komarov, & Ko, 2018) which would explain the left lateralization observed for the component.

Evolutionarily Conserved and Learned Associations of Colour

Behaviourally, the order of no-go signal accuracies in our study follows the colour hierarchy for automatic target selection identified by Tchernikov & Fallah (2010) with red as the most effective, followed by green, yellow, and then blue as the least effective color for stopping. Our findings also replicate those previously observed in Go/No-go task (Asare et al., *in*

preparation) in which participants were more accurate at inhibiting their responses to red no-go stimuli compared to green no-go stimuli. This hierarchical colour processing may be explained by evolutionarily conserved and learned colour associations. Ecologically, red often signals danger; it is the colour of blood and fire, and for humans and some primate species, red facial colouration is often associated with anger and aggression (Setchell & Wickings, 2005). In contrast, green is the color of healthy vegetation, signalling water and the potential for food. Non-human primates also demonstrate the same faster stopping with red stimuli, followed by green, then blue which supports the contribution of evolution to colour hierarchy (Ghasemian et al., 2015). This inherent advantage of red for response inhibition, likely produced our association of red with stopping which led to the use of red in sirens, stop lights, stop signs, and other systems that warn of danger. Such usage reinforces the visual association through learning. Similarly, green is a positive signal that impairs stopping, which led to its use as a signal for (turn) on, something running, good, safe, etc. “Green means go” is reinforced by its usage in our environment like in traffic lights and early childhood educative games, songs, and various children's media (Suskauer et al., 2008). The learned association to green being weaker than red may explain why, in this study, participants' accuracies with green fall in-between that of red and blue.

Although the color modulations in this study match the attentional color hierarchy identified by Tchernikov and Fallah (2010), they differ from the results of a study by Asare et al., (in press) in which participants performed a stop signal task where the stop signal was a change from white to either red, blue, green, or yellow. Their results revealed that participants' red stop-signal reaction times (SSRTs) were the fastest, followed by yellow and blue, which had no significant differences between them, and green RTs were the slowest. The differences in the

pattern of color responses can be explained by taking into account the differences in task demands of the SST and GNGT. Both paradigms involve response execution and inhibition. However, the SST stop signal is displayed with a variable time delay after the initial presentation of the go-stimulus, while in the GNGT, each trial either begins with the go-stimulus or stop-signal (Aron, 2011). In the SST, since the stop-signal is presented after the onset of the go-stimulus, the response is already underway. Therefore, the inhibition process reflects the countermanding of an upcoming response. This inconsistent mapping of stimuli to task goals prevents automatic processing from developing and the task is said to be reactive. Meanwhile, stopping in GNG trials involves discriminating between go and no-go signals, rather than countermanding a response (De Jong et al., 1990). The consistent mapping of stimuli to behaviors allows for automaticity to develop throughout the course of the experiment with the go-stimulus initiating the automatic go response and the stop-stimulus initiating the automatic inhibition process (Schneider & Shiffrin, 1977), which is dependent upon proactive response inhibition. In addition, the SST requires a greater cognitive load and reflects top-down, controlled inhibition while the GNGT reflects automatic, bottom-up inhibition demanding less cognitive resources (Verbruggen & Logan, 2008). Hence, the effects of the preferential frontal processing of red stimuli and the stronger learned and evolutionary associations of red compared to green, is observed in the automatic responses reflected in the GNGT as well as the SST. But the effects of the green-go association are only reflected in the SST because the task has greater top-down demands than the GNGT.

Brain Regions involved in Response Inhibition

Various studies have yielded overlapping results that support the involvement of frontal brain regions in response inhibition. When stopping relies on inhibition of an action currently in preparation like reactive response inhibition, (Aron & Poldrack, 2004) it recruits the left inferior frontal gyrus (pars triangularis), bilateral anterior insula, the pre-supplementary motor area (pre-SMA), and inferior frontal gyri (Rae et al., 2014). When proactive response inhibition is activated in a Go/No-go task, source localization of the N200 revealed selective activation of the (rostral) ACC and pre-supplementary motor area (pre-SMA) (Gonzalez-Rosa et al., 2013). The ACC is primarily associated with conflict monitoring (Donkers & Van Boxtel, 2004), which is not relevant to this study as both colors are no-go signals and thus do not produce conflict. Therefore, it is likely that color modulation of pre-SMA activity is driving the amplitude and latency shifts in the N200 component. This reflects response inhibition, supported by fMRI (Braver et al., 2001), cortical stimulation mapping (Ikeda, 1999), and direct activation, which inhibits ongoing motor activities (Ikeda et al., 1993). Therefore, the pre-SMA is likely part of the fronto-parietal response inhibition network modulated by red and green input. We have previously suggested (Asare et al., *in preparation)* that color modulation of response inhibition is mediated by output from prefrontal cortex feeding into subcortical areas through the indirect, and hyperdirect pathways to the basal ganglia (prefrontal loops, e.g.: Boehler et al., 2010). The indirect pathway mediates proactive response inhibition through inhibition of thalamic motor output and could be modulated by color input to prefrontal cortex. The hyperdirect pathway mediates reactive response inhibition (e.g., Jahfari et al., 2011) could also be modulated by color (Asare et al*., in preparation*).

Conclusion

The current study tested young adults on a Go/No-go task while recording EEG. It was observed that behaviorally red facilitates response inhibition compared to other colors. Similarly, we found the same effects of color on the P100 and N200 signifying that red requires less inhibitory control than other colors. However, the P300 was not modulated, which suggests that color does not affect inhibitory load. Future studies could test this paradigm in older and cognitively impaired adults to determine how their concomitant impairment in response inhibition could be mitigated through the use of the color red and how that would be reflected in their fronto-parietal networks. This would contribute to understanding how response inhibition changes with age and with cognitive decline. Further investigation of such networks would then allow for the development of focused treatments and improvements to help enhance and potentially reverse decline and better the lives of those suffering from dementia.

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CHAPTER 6: GENERAL DISCUSSION

By investigating the role of color in response inhibition, the aim of this research project was to gain an understanding of the networks underlying this executive function and how an attentional feature such as color could facilitate or hinder it. Following findings of red over green facilitating response inhibition (Blizzard et al., 2017), three studies were conducted to shed light on how color modulates inhibition.

6.1 Summary of Findings

In study 1, we investigated if the underlying mechanism of color modulating reactive response inhibition was color opponency, color hierarchy, or visual associations and found that it was the latter. Our association of red meaning stop, and green meaning go is more than just a semantic shortcut, it actually impacts how efficiently we stop. In Study 2, we tested whether the findings from study 1 were specific to countermanding, that is, was it specific to reactive response inhibition which has its own network of areas, or were our observed color modulations more broadly affecting inhibitory control? We found that indeed, the facilitation effects of red over green extended to proactive response inhibition. As such, we suggested a network of areas and pathways of how color information proceeds from V4 in the visual cortex to the prefrontal cortices to influence inhibitory control through subcortical loops. We also proposed a modified accumulator model of how color modulations would produce accuracy differences by modulating the speed at which information accumulates to reach the inhibitory decision. Lastly, in Study 3, we conducted an EEG study to test if the network identified in Study 2 was involved as hypothesized. That is, would ERP components N200 and P300 be modulated by color such that they would reflect our behavioral results? Indeed, we found that the red N200 had a smaller

amplitude and earlier latency compared to other colors while the P300 was minimally modulated by color. As such, red compared to other colors reduces the need for other top-down resources required to stop and did so earlier in the brain compared to other colors. The inhibitory load of the GNGT was not modulated by color but there was a cost of attentional resources as denoted by robust P100 effects. These findings therefore supported our proposed network of color information recruiting fronto-parietal structures (i.e.: the pre-SMA and IPC) and using the indirect and hyperdirect pathways to the basal ganglia to modulate inhibitory control.

6.2 A Model for Response Inhibition

Looking at the red/green racehorse model and the GNG accumulator models, we observe that the change in slopes of information could be modulated by color resulting in earlier and more accurate stopping with red compared to green in both proactive and reactive response inhibition (see **Figure 19**). Response inhibition thresholds shifting based on color is less likely because though it could explain the GNGT results, it does not extend to the SST. As the brain is parsimonious and tends to reuse the same circuitry in multiple areas, it is likely that color modulates the rate of information accumulation in inhibitory control.

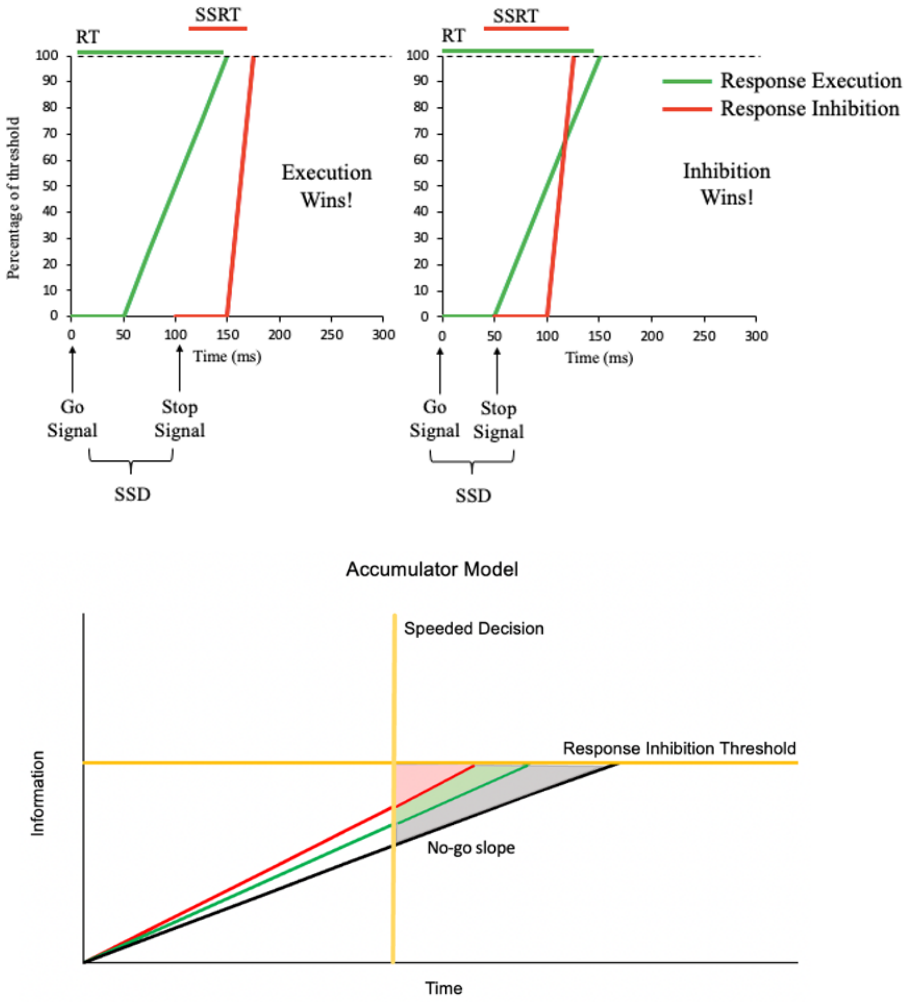

Figure 19. SST and GNGT Response Inhibition Models. SST (Reactive response inhibition) and GNGT (Proactive response inhibition) models describing how the slopes of information are modulated by color and result in earlier and more accurate stopping with red compared to green.

6.3 The Related Color Effects of Red

What is it about red that is so different than other colors? We have mentioned how evolutionarily red often signals danger; it is the colour of blood, fire, and poison berries and frogs, and for humans and some primate species, red facial colouration is often associated with anger and aggression (Setchell & Wickings, 2005). Additionally, there is reinforcement learning

of the association of red with stopping due to its use in sirens, stop lights, stop signs, and other systems that warn of danger. According to a study by Elliot et al. (2007), red may also be associated with the psychological danger of failure. This learned association of red and failure in achievement contexts may have developed through the education system as red ink is often used to mark incorrect answers. In the Elliot et al., 2007 study, red was found to negatively impact performance in achievement contexts, showcasing the effect of colour on behavior. As previously noted, Payen et al. (2011) observed that seeing red as opposed to blue or gray prior to a strength test inhibited force development consistent with our findings on response inhibition. Elliot and Aarts (2011) demonstrated that viewing red amplified physical output in terms of speed and strength for a currently underway motor action. Taken together, red signals, with an innate association to danger, inhibits upcoming actions, while also enhancing ongoing motor responses likely through fight or flight-based sympathetic nervous system activation. Since there have not been complimentary studies looking at the effects of green on motor output, it is unknown if the association of green with Go generalizes beyond slowing response inhibition in the stop signal task.

6.4 Limitations and Future Research

Our first study showed that only red/green colors affected reactive response inhibition, and visual associations. The same was assumed for proactive response inhibition, but it was possible that the underlying mechanism of it depended on color hierarchy and opponency. Our third study assessed this assumption and found that it was more color hierarchy than just red/green visual associations, but also, that red was primary, likely due to the evolutionarily conserved red visual association. Future studies should see if proactive inhibition follows the

same color hierarchy-based ordering we found in study 3, rather than the red vs green facilitation with yellow and blue as neutral modulators observed in study 1.

Additionally, as noted, there is a gap in the literature pertaining to green, its evolutionary and learned associations. Using the paradigms employed in this research project, this gap could be narrowed and corroborate the proposed models and networks of response inhibition and execution. A potential limitation of our third study is that it investigated general effects of colours on the N200 and P300 ERP components. Further research is required to explore N200 and P300 subcomponents, along with other related components to allow for a better understanding of the specific effects of colours on the inhibition process reflected in ERP components. No imaging techniques were used to localize the observed ERP activity to particular brain regions; thus, the aforementioned brain regions were identified based on prior research that produced N200 and P300 ERPs with different response inhibition tasks. Since no other studies have used neuroimaging methods to investigate the effects of colours on response inhibition using a Go/No-Go paradigm, there exists the possibility that the resultant imaging results could provide broader networks than that of preexisting research. The effects of colour on inhibitory control can be extended beyond response inhibition. One such possibility is to explore interference suppression, using the Eriksen flanker task. Using a flanker task/Go/No-go hybrid, Bridges et al., (2012) observed slight differences in brain activation in response to different types of inhibition, namely response inhibition and interference suppression. Lastly, the current research project tested healthy young adults response inhibition tasks. Research studies affirm that this is an executive function that declines with age and dementia as older adults have more difficulty maintaining enough focus to complete a complex task that involves irrelevant information (Mayr, 2001). Future research should test current paradigms on healthy older adults

and those with dementia and such results could be compared with those of the present study. This would contribute to understanding how response inhibition changes with age and cognitive decline. The findings would help elucidate the response inhibition related neural circuitry affected by such processes. Identification of the neural circuitry affected by dementia may allow for the development of more focused treatments and improvements to everyday items that will help enhance the lives of those suffering from dementia.

6.5 Conclusion

Red colored stimuli compared to other colors facilitate response inhibition. The mechanism by which this facilitation occurs seems to depend on an innate visual association of red meaning stop. Thus, red compared to green, yellow, and blue facilitates more efficient inhibition. We expect our findings to allow for targeted interventions to support response inhibition through design and training programs and that this will help facilitate the development of new technologies, diagnostic tools, and everyday items. Additionally, these projects will advance work relevant to graphical user interfaces, to big data visualization, and to designing technology for aging individuals. Moreover, it will be relevant for aging and patient populations wherein executive functions are impacted (e.g.: dementia, Alzheimer's, Parkinson's) if we aim to use red liberally to facilitate response inhibition and thereby support those with dementia and other cognitive impairments that target response inhibition to remain in their homes longer and keep up their quality of life.

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