RESEARCH ARTICLE



Oculomotor system can differentially process red and green colors during saccade programming in the presence of a competing distractor

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Abstract

Selective attention filters irrelevant information entering our brain to allow for fine-tuning of the relevant information processing. In the visual domain, shifts of attention are most often followed by a saccadic eye movement to objects and places of high relevance. Recent studies have shown that the stimulus color can affect saccade target selection and saccade trajectories. While those saccade modulations are based on perceptual color space, the level in the visual processing hierarchy at which color selection biases saccade programming remains unclear. As color has also been shown to influence manual response inhibition which is a key function of the prefrontal cortex, we hypothesized that the effects of color on executive functions would also inherently affect saccade programming. To test this hypothesis, we measured behavioral performance and saccade metrics during a modified saccadic Stroop task which reflects competition between color words ("RED" and "GREEN") and their color at the level of the prefrontal cortex. Our results revealed that the oculomotor system can differentially process red and green colors when planning a saccade in the presence of a competing distractor.

Keywords Target-distractor similarity · Saccade · Stroop · Color saliency · Top-down control

Introduction

The brain can only process a small amount of information impinging on our visual system at a given moment. The oculomotor system programs fast ballistic eye movements,

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saccades, to shift the high acuity part of the retina, the fovea, to the locations of interest in the visual scene, thereby allowing a high-resolution image of that particular location for further analysis. Previous studies have shown that the oculomotor system selects a target which is either more salient because of its visual properties (bottom-up attention or "pop-out") or because it has higher behavioral relevance (top-down attention) compared to the surrounding objects (Wolfe 2010). Competition between bottom-up and top-down processes leads to the formation of a spatial priority map in which the location of the target with the highest weight is selected to program a saccade vector (Fecteau and Munoz 2006). This competition is reflected by longer saccade latencies to a saccade target in the presence of a salient distractor or by the number of erroneous saccades to a distractor (Godijn and Theeuwes 2002; Van der Stigchel et al. 2006).

One of the elementary attributes of visual objects that guide target selection is color (Elliot et al. 2007; Tchernikov and Fallah 2010). Theories of primates' evolution state that the Trichromacy, the ability to distinguish red–green–blue, has evolved to enable our old world primate ancestors to dissociate ripe fruits and green leaves from their natural background (Osorio and Vorobyev 1996; Regan et al. 2001). Color, as a result of these visual associations, has been shown to influence our cognition and behavior (Elliot et al. 2007; Ghasemian et al. 2021; Mehta and Zhu 2009). For instance, studies in monkeys and humans have revealed that visual attention and eye movements can be influenced by color (Bichot et al. 2005; Desimone and Duncan 1995; Frey et al. 2008). These influences are the result of color biasing the saliency map during target selection (Kehoe et al. 2018a, b; Koch and Ullman 1985; Tchernikov and Fallah 2010). It is noteworthy to mention that these color effects are not just random. There are behavioral and neurophysiological evidences for the existence of a systematic color hierarchy for attentional selection with red sitting at the top of the hierarchy (Lindsey et al. 2010; Pomerleau et al. 2014; Tchernikov and Fallah 2010). For example, different colors can have a differential effect on the speed of smooth pursuit eye movements and target selection even in the absence of clear external instruction on what to select, suggesting a bottom-up nature of color encoding for the pursuit target selection (Tchernikov and Fallah 2010). This hierarchical color target selection has been shown to not be limited to low-level visual processing. One study, using a stop signal task, showed that red-color stop signals lead to faster response inhibition than green-color stop signals, suggesting that the color hierarchy is present at higher stages of cognitive processing most probably due to visual associations which assigned a certain value to each color for different cognitive tasks (Blizzard et al. 2017).

Studies on the color-specific effects on attentional control notwithstanding, the question of whether different colors can modulate saccade trajectories is not well understood yet. We know from previous studies that saccade trajectory deviations in the presence of competing stimuli can be an indicator of competition between saccade targets in the oculomotor system. For a review, please see (Van der Stigchel et al. 2006; Walker and McSorley 2008). These studies demonstrated that the instruction to attend to a location other than the saccade target could modulate the extent and direction of saccadic curvature (Sheliga et al. 1994, 1995, 1997; Tipper et al. 2001). Hence, measuring saccade trajectories in the presence of distractors can be used as a noninvasive method to assess executive functions and target selection in the brain (Kehoe and Fallah 2017). It is specifically interesting to investigate how/if colors compete for target selection during executive control and if this competition lasts until the very last stages of generating a motor output, i.e., oculomotor control of saccades. In a study on how the oculomotor system might encode color saccade targets, Kehoe and colleagues used a memoryguided saccade task with color targets and distractors (Kehoe et al. 2018a, b). They found that the oculomotor system encodes color in perceptual color space similar to how the visual system does. Using a memory-guided saccade task independent of sustained sensory inputs suggested that the color signals might reach the oculomotor system via high-level cortical areas involved in visual working memory such as the prefrontal cortex. Furthermore, cueing attention to a certain color elicited surround suppression in the oculomotor color space as predicted by the selective tuning model of attention (Tsotsos 2011). The involvement of prefrontal circuitry in biasing target selection according to color saliency gets further support from a study, showing that response inhibition, a major prefrontal cortex function, is sensitive to differences in color salience (Blizzard et al. 2017). These studies investigated a subset of the executive functions produced by prefrontal cortex: attentional selection and response inhibition. Our goal is to extend this further to conflict resolution and cognitive interference.

The Stroop task can be used to assess the ability to inhibit cognitive interference where there is a competition between color words ("RED", "GREEN") and the color of the words (Hermens and Walker 2012; Hodgson et al. 2009; Stroop 1935). The main aim of this study was to investigate how the effects of color on executive functions drive the oculomotor system. We specifically asked whether color effects on saccade programming would arise through the competition inherent in the Stroop task. We used a modified version of the Stroop task in which we presented a distractor in addition to the target. The distractor could either match the target feature needing to be attended or not. This would allow us to determine whether color effects on saccade programming, if found, are a function of distractor–target similarity.

Methods

Twenty students (18–37 years old, 8 men and 12 women) volunteers from York University participated in the experiment in exchange for course credit. All participants had normal or corrected to normal vision. Their color vision was assessed by Ishihara color plates (Ishihara 2006). Written informed consent was obtained prior to participation in accordance with the Declaration of Helsinki. All research was approved by York University's Human Participants Review Committee. One participant was excluded from the analysis because of poor quality eye data.

Apparatus and measurement

Stimulus presentation was controlled using a computer running Presentation software (Neurobehavioral Systems, Berkeley, CA, www.neurobs.com). Eye position was sampled at 500 Hz using an infrared eye tracker (Eyelink II, SR research, Ontario, Canada, www.sr-research.com). The visual stimuli were presented on a 21-inch cathode ray tube monitor (60 Hz, $1024 \times 768 \text{ pixels}$). Participants viewed stimuli in a dimly lit room from a viewing distance of 57 cm with a headrest stabilizing their head position. Stimuli color and luminance were calibrated using a spectrophotometer (PR-655, Photo Research, Syracuse, NY).

Visual stimuli and experimental tasks

The visual stimuli were constructed offline using Matlab (The Mathworks, www.mathworks.com) and consisted of colored bars or words that subtended $3.2^{\circ} \times 1.1^{\circ}$ visual angle. The word letters were spaced, such that the overall word's size would roughly fit to the size of the bars. The colors used in this experiment consisted of isoluminant red (CIE coordinates: x = 0.63, y = 0.3; L = 12.07 cd/m²) and green (CIE coordinates: x = 0.29, y = 0.59; L = 12.00 cd/ m^2) as target colors and gray (CIE coordinates: x = 0.28, y = 0.30; L = 11.20 cd/m²) as the baseline color. "RED" and "GREEN" were used as target words. The cue was always presented at the center of the screen, while the target and distractor were presented at the upper left and upper right quadrant of the screen. The coordinates of target and distractor were chosen in each trial randomly from the set of [- 5.67, 6.2] and [5.67, 6.2] degrees of visual angle [Cartesian (x,y) coordinates, see Fig. 1].

Word task

In this task, after successfully fixating on a small central fixation point for 500 ms, participants were shown a central cue consisting of a printed word: "RED" or "GREEN" in gray color. If the participant failed to fixate at least 200 ms on the central cue within 2 s after the trial start, that trial was aborted and a new trial was presented. When they fixated on the central cue for 200 ms, the central cue disappeared and two words appeared on the screen, one serving as the target that would match the semantic meaning of the central cue and the other one as the distractor which always differed semantically from the target word. The participant's task was to look at the same word that they had previewed in the cue period while ignoring the color of the target and distractor (see Fig. 1A). Distractor and target words could be presented in the same color (DT-match condition) or in different colors (DT-unmatched condition). The color of the target could either match the semantic meaning of the central cue (congruent condition), or not (incongruent).

Color task

In this task, after successfully fixating on a central fixation for 500 ms, participants were shown a central cue consisting of a red or a green horizontal bar, at the beginning of each trial. Similar to the word task, after participants fixated on the central cue for 200 ms, the central cue disappeared and two words "RED" and "GREEN" appeared on the screen, one serving as the target in that its color matched the color of the central cue and the other one as the distractor which always differed from the target in color. The participant had to look at the word that has the same color as the one they had previewed in the cue period while ignoring the semantic identity of the target and distractor (see Fig. 1B). Distractor and target could have the same semantic identity (DT-match condition) or different (DT-unmatched condition). The target word could either match semantically with the color of the central cue (congruent condition), or not (incongruent condition). A few other examples from the set of possible conditions are illustrated in Fig. 1C–H.

In both tasks, the locations of the target and distractor were randomly interleaved. Participants received auditory feedback on their correct or erroneous performance at the end of each trial and trials were aborted if they failed to respond within 500 ms after the target–distractor onset.

The tasks were done in separate blocks with randomized order. Each block started with an instruction on the screen stating which task (color or word) held for that block. Each block consisted of 64 trials and each participant completed 8 blocks. There were two practice blocks, each consisting of 10 trials of the word task and the color task separately, at the beginning of each experiment to familiarize the participant with the experiment. After the practice blocks and before starting the two main tasks, each participant performed a block of 20 trials consisting of visually guided saccade to one of two spatial targets (gray bars) located at the same location and the same size as the words in the main experiment. Since saccades naturally have a small amount of curvature even in the absence of distracters, the purpose of this block was to measure baseline saccade curvatures to be accounted for in the later analyses.

Analysis

Saccade detection

All analyses were done using customized Matlab algorithms. One participant was removed from further analysis due to poor quality eye data. All subsequent analyses were performed on the remaining 19 participants. Trials that contained blinks were excluded from further analysis. Saccades were defined based on a velocity threshold of 20° /s for at least 8 ms and a peak velocity exceeding 50° /s. Saccades were excluded from further analysis if their amplitude was smaller than 1° visual angle, or if they were accompanied by more than one corrective saccade or only one corrective saccade larger than 1° visual angle. Also, saccades with less than 100 ms latency were excluded.

Trial events



Trial events

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◄Fig. 1 Saccadic Stroop task. A Word task: In this task, after successfully fixating on a central fixation for 500 ms, participants were shown a central cue, a printed word "RED" or "GREEN" in gray color. After participants fixated on the central cue for 200 ms, the central cue disappeared and two words appeared on the screen, one serving as the target that would match the semantic meaning of the central cue and the other one as the distractor which always differed semantically from the target word. The participant's task was to look at the word that has the same semantic meaning as the one they had previewed in the cue period, while ignoring the color of the target and distractor. This exemplary trial is considered an incongruent and DT-unmatched condition, since the word "GREEN" as the target has a red color (incongruency) and the distractor word is "RED". B Color task: In this task, after successfully fixating on a central fixation for 500 ms, participants were shown a central cue, a red or a green bar, at the beginning of each trial. Similar to the word task, after participants fixated on the central cue for 200 ms, the central cue disappeared and two words appeared on the screen, one serving as the target that would match the color of the central cue and the other one as the distractor which always differed from the target in color. The participant's task was to look at the word that has the same color as the one they had previewed in the cue period, while ignoring the semantic identity of the target and distractor. This example trial is from the incongruent, DT-match condition). C-H A few other examples from the set of possible conditions

Other exclusion criteria were pre-saccadic drift larger than 2° and endpoint deviations larger than 2°. Finally, we excluded all saccades where their initial angle was more than 2.5 standard deviations further from the correct target direction, to account for saccades corrected mid-flight. These strict exclusion criteria were used to make sure that any modulatory effects of experimental condition on saccade trajectories were not related to task irrelevant saccadic preparation (i.e., short amplitude, short latency, or poor fixational stability). In total, 6242 saccades remained for further analysis (mean \pm std = 328 \pm 143 trials per participant).

Saccade metrics

In this study, we looked at several saccade metrics: saccade reaction times, endpoint deviation, max curvature, and sum curvature. These metrics have been used previously in several studies (Kehoe et al. 2018a, b; Kehoe et al. 2018a, b; Kehoe and Fallah 2017). To analyze saccade curvatures, saccade starting points were translated back to the origin and then trigonometrically rotated, such that endpoint was aligned to the positive y-axis. Saccade reaction time was defined as the time between target/distractor onset and saccade initiation. Endpoint deviation was calculated for each saccade as the Euclidean distance between the saccade landing point and the target location. Max curvature was quantified by the maximum orthogonal deviation from a straight line between the start and endpoint of saccade trajectories. Sum curvature was calculated by summing of all orthogonal deviations from a straight line between the start and endpoint of the saccade trajectory (Fig. 2a). Example saccades made by one of the participants can be seen in Fig. 2B. The saccade peak velocity–amplitude relationship (main sequence), and peak velocity–duration relationship for the same example participant can be seen in Fig. 2C.

Statistical analysis

Repeated-measure ANOVAs were used to assess the effects of experimental conditions on participants' saccadic reaction times, performance, and saccade metrics (max curvature, sum curvature, end points deviation). If any significant main effect was found by ANOVA, post hoc tests (*t* tests for variables with a normal distribution and non-parametric Wilcoxon signed-rank tests otherwise) were applied. We used the Kolmogorov–Smirnov test (kstest) to check if a variable had a normal distribution. When the data did not follow a normal distribution, non-parametric Wilcoxon signed-rank test was applied. Bonferroni corrections were used to adjust statistical significance thresholds when several analyses on the same dependent variable were performed. All of the analyses were performed in Matlab.

Results

Accuracy and reaction times

Participants performed the task with high accuracy well above the chance level of 50% (p < 0.001, Wilcoxon signedrank test, since the data did not follow a normal distribution (kstest, p < 0.05)) with correct response accuracy of $77.5\% \pm 2.35$. As shown in Fig. 3A, their performance in the word task $(62.56\% \pm 13.7)$ was significantly worse than the color task $(90.6\% \pm 9.8)$ suggesting a higher difficulty level in the word task. The greater difficulty of the word task was also reflected in longer average reaction times $(241 \pm 38 \text{ ms})$ than in the color task $(221 \pm 20 \text{ ms})$, see Fig. 3B. To further quantify how different experimental conditions might affect participants' performance and reaction times, we performed a linear Pearson correlation analysis. As can be seen in Fig. 3C, there was in general a strong positive linear correlation between the participants' performance and their reaction times ($\rho = 0.61$, p = 0.005 for the color task) and ($\rho = 0.69$, p = 0.001 for the word task), suggesting that stronger inhibitory control (better performance) is reflected in slower responses.

To characterize the traditional Stroop interference effect, we compared the performance and reaction times between the congruent and incongruent conditions. Participants' performance was significantly lower in the incongruent condition for the word task ($p_{\text{Bonferroni-corrected}} < 0.001$, *t* test, since the data followed a normal distribution (kstest,



Fig. 2 Saccadic characteristics. **A** Derivation of saccade curvature metrics. Saccade start and end points are represented by red + and closed circles. The saccade has been translated and trigonometrically rotated, so that it starts from the Cartesian origin and the end point lies on the positive y-axis. Orthogonal deviations from each eye

position sample to a straight line between the start and end point of the saccade are indicated by horizontal lines (s_i) . **B** Example of saccades made by one of the participants. **C** Saccade peak velocity– amplitude relationship (main sequence), and saccade peak velocity– duration relationship for the same example participant in **B**



Fig. 3 Task specific performance and reaction times. A Accuracy in the color task was significantly much higher than the word task. In the violin plot, the white dot in the middle is the median value and the thick black bar in the center represents the interquartile range. The thin black line extended from it represents the upper (max) and lower (min) adjacent values in the data. *** denotes the significance level of p < 0.001 [Wilcoxon signed-rank test, since the data did not follow a normal distribution (kstest, p < 0.05)]. B Reaction times were significantly longer in the word task in comparison to the color task [$p_{\text{Bonferroni-corrected}} < 0.001$, Wilcoxon signed-rank test, since the data did not follow a normal distribution (kstest, p < 0.05)]. C A significant positive correlation between reaction times and performance was observed for both tasks

p > 0.05)). Consistent with the accuracy results, reaction times were significantly longer in the incongruent condition in the word task ($p_{Bonferroni-corrected} < 0.05$, *t* test, since the data followed a normal distribution (kstest, p > 0.05), Fig. 4A). Separating this analysis for red-color and green-color targets revealed that the significantly lower performance in the incongruent condition was mainly driven by the green condition ($p_{Bonferroni-corrected} < 0.001$, *t* test, since the data followed a normal distribution (kstest, p > 0.05), Fig. 4B), or when distractor and targets were unmatched ($p_{Bonferroni-corrected} < 0.001$, *t* test, since the data followed a normal distribution (kstest, p > 0.05), Fig. 4D). We did not see any effects of color in conjunction with the incongruent effect on reaction times ($p_{Bonferroni-corrected} > 0.05$, *t* test, since the data followed a normal distribution (kstest, p > 0.05)). Moreover, there was no effect of congruency on the color task [$p_{Bonferroni-corrected} > 0.05$, Wilcoxon signed-rank test, since the data did not follow a normal distribution (kstest, p < 0.05), see Fig. 5A–G].

Furthermore, a four-way repeated-measure ANOVA (factors: color, task, congruency, and distractor-target similarity) showed main effects of task (df = 1, F = 92.62,



Fig. 4 Stroop interference effect in the word task. A Effects of Stroop interference on performance and reaction time (worse performance and slower reaction time in the incongruent vs congruent condition). The interference effect was significant for both performance and reaction times in the word task across both colors. B The Stroop interference effect was much stronger in the word task when the target was green (color). C The Stroop interference effect on reaction

p < 0.001), congruency (df = 1, F = 37.68, p < 0.001) and similarity (df = 1, F = 6.5, p < 0.05), as well as twoway interactions of congruency × task (df = 1, F = 23.26, p < 0.001), congruency × similarity (df = 1, F = 26.11, p < 0.001), and congruency × color (df = 1, F = 24.03, p < 0.001) on performance. Performance was also significantly influenced by three-way interactions of

times did not reach significance for either color targets individually. **D** The Stroop interference effect on performance in the word task was strongest when the target was green (color) and the distractor was red (color). **E** The Stroop interference effect on performance was absent when the target and the distractor did not match in color. **F**–**G** The Stroop interference effect on reaction time did not reach a statistically significant level when targets were separated by color

congruency × task × color (df = 1, F = 17.42, p < 0.001) and congruency × task × similarity (df = 1, F = 19.55, p < 0.001). Finally, there was a four-way interaction effect of congruency × task × color × similarity (df = 1, F = 25.54, p < 0.001). Post hoc t tests (since the data followed a normal distribution (kstest, p > 0.05)) revealed that the participants make significantly more errors during the word task when



Fig. 5 Stroop interference effect in the color task. A–G The Stroop interference effect on performance and reaction time in the color task was not significant in any of the conditions

the target is green (color) in three different conditions: incongruent (df = 18, $p_{Bonferroni-corrected} < 0.05$, Fig. 6A), DT-unmatched (df = 18, $p_{Bonferroni-corrected} < 0.05$, Fig. 6B), and their interaction, i.e., incongruent, DT-unmatched (df = 18, $p_{Bonferroni-corrected} < 0.01$, Fig. 6C).

Similarly, a four-way repeated-measure ANOVA (factors: color, task, congruency, and distractor-target similarity) showed main effects of task (df = 1, F = 13.23, p < 0.001), congruency (df = 1, F = 4.48, p < 0.05), and similarity (df = 1, F = 6.5, p < 0.05), also two-way interactions of congruency × task (df = 1, F = 22.46, p < 0.001), and

congruency × color (df = 18.33, F = 18.46, p < 0.001) for the reaction time measures. Furthermore, reaction times were significantly influenced by a three-way interactions of congruency × task × color (df = 1, F = 5.9, p < 0.05) and congruency × color × similarity (df = 1, F = 6.3, p < 0.05). Finally, there was a four-way interaction effect of congruen cy × task × color × similarity (p < 0.01). Post hoc t tests [since the data followed a normal distribution (kstest, p > 0.05)] also revealed significantly longer reaction times for red color than green color in the congruent condition and when distractor and targets were unmatched ($RT_{red color} = 240$ ms

Fig. 6 Color-specific differences in the subjects' performance and reaction times. A Color-specific differences were only observed in the word task: incongruent conditions. Performance was significantly lower when the participants had to detect the green-color target as compared to the red-color target. Please note that in the incongruent conditions, the target word meaning and its color do not match (e.g., the "RED" word printed in green color). B Performance was significantly lower in the DT-unmatched condition. Participants made more errors when instructed to detect the green-color target

and $RT_{green\ color} = 233 \text{ ms}$, df = 18, $p_{Bonferroni-corrected} < 0.05$, see Fig. 6D). We also observed that this significant effect was even stronger in the word task ($RT_{red\ color} = 260 \text{ ms}$ and $RT_{green\ color} = 240 \text{ ms}$, df = 18, $p_{Bonferroni-corrected} < 0.05$, Fig. 6E).

Saccade metrics

Endpoint deviation was calculated for each condition as described in the Methods section. The endpoint deviations in the word task and the color task were 1.14 ± 0.26 (dva) and 1.10 ± 0.25 (dva), respectively. A four-way repeated-measure ANOVA (factors: color, task, congruency, and distractor-target similarity) did not show any main effects or interactions on endpoint deviation (all p > 0.05). Pearson correlation did not show any significant linear relationship between endpoint deviation and performance (p > 0.05).

A four-way repeated-measure ANOVA (factors: color, task, congruency, and distractor-target similarity) did not show any main effects or interactions on sum curvature (all p > 0.05). Similarly, a four-way repeated-measure ANOVA (factors: color, task, congruency, and distractor-target similarity) did not show any main effects or interactions on max curvature (all p > 0.05).

Saccade curvature reflects competition between the saccade target and a distractor, wherein increased strength

as compared to the red-color target. **C** The most significant drop in performance was the conjunction of incongruent and DT-unmatched conditions. In this case, performance was again significantly lower when detecting the green-color target. **D**–**E** Reaction times were significantly longer for red-color versus green-color targets in the congruent condition and when the distractor and the target were unmatched. This effect driven by the word task. Every single point represents one participant

of the distractor results in increased curvature toward it. Based on this a-priori hypothesis, even though the ANOVA did not show any overall effects of color on curvature metrics, and given the consistent effect of color in the word task and especially in DT-unmatched condition (see Fig. 6), we performed additional post hoc tests. There was a statistically significant effect of color on the curvature metrics in the DT-unmatched condition in the word task $[p_{\text{Bonferroni-corrected}} = 0.006, \text{ df} = 18, t \text{ test, since the data did}$ not follow a normal distribution (kstest, p > 0.05)]. Saccade trajectories were more curved for green (color) targets (sum curvature mean \pm std = 6 \pm 2.4 dva) compared to red (color) targets (mean \pm std = 5.4 \pm 2.2 dva). Then, we median split subjects according to their performance into a speedyinaccurate (subjects with weaker inhibitory control) and a slow-accurate (subjects with stronger inhibitory control) group to investigate whether it is the strength of inhibitory control in each participant which influences their saccade trajectories and the effects of color. Repeating these analyses on the two groups separately showed that while the speedyinaccurate subjects' saccade trajectories were more curved (sum curvature) for green (color) targets in the word task, DT-unmatched condition ($p_{\text{Bonferroni-corrected}} = 0.01 t$ test, see Fig. 7A and also Fig. 7C for DT-matched condition), slowaccurate subjects' eye movements were not significantly affected by color in any of the conditions including the

Fig.7 Color-specific effects on saccade sum curvature metrics. In the speedy subjects (**A**) and not the accurate ones (**B**), saccade trajectories were more curved in the word task for the green (color) target when the distractor was red (color) ($p_{Bonferroni-corrected} < 0.05$, *t*

test). Color did not have any effect on saccade curvatures, neither in speedy subjects (C) nor in the accurate ones (D), when the target and the distractor matched in color (p > 0.05, t test)

DT-unmatched in the word task ($p_{Bonferroni-corrected} > 0.05$, *t* test, see Fig. 7B and also Fig. 7D for DT-matched condition). The analysis of max curvature yielded similar results: i.e., significantly more curved saccades ($p_{Bonferroni-corrected} = 0.004$, *t* test) were seen in the DT-unmatched condition in the word task for green (color) targets ["GREEN": max curvature mean \pm std = 0.61 \pm 0.16; red (color): max curvature mean \pm std = 0.58 \pm 0.17].

Discussion

In this study, we investigated the effects of color on executive functions and eye movements. Using a modified saccade Stroop paradigm, we showed that selecting a correct saccade target using a central word cue is in general much harder than a central color patch. More errors in the word task were accompanied by longer reaction times. A Stroop interference effect was only observed in the word task and it was more pronounced in the error rates compared to the reaction times. Breaking down the Stroop effect into the color and similarity conditions revealed that the main factor influencing higher error rate and longer reaction times in the incongruent condition in the word task was a green (color) target and an unmatched distractor. The differential effect of color in the DT-unmatched and incongruent condition was more strongly reflected in the group of less accurate but speedy subjects eye movements' trajectories, showing more curvature for the word "RED" printed in green color in the presence of the word "GREEN" printed in red color as the distractor (similar to Fig. 1A). These results show a differential effect of green versus red colors in how they interfere with searching for the words "GREEN" or "RED" in a saccadic Stroop task.

Participants' performance in the word task was significantly worse than the color task suggesting a higher

difficulty level in the word task. This higher difficulty in the word task was even more pronounced in those conditions with higher competition between target and distractor features, such as in the incongruent or DT-unmatched (Fig. 6A-C), where participants were driven to select a competing feature in error. In those conditions, the interference effects (resulting from decreased inhibition) were greater for red (near chance level performance for the green target as in Fig. 6A–C). The combination of an incongruent color-word pairing with unmatched distractor-target pairings produced the worse performance, reflecting the greatest amount of interference. As such, performance on the task was dependent on the different colors of the target and distractor, with red unmatched distractors producing the greatest interference, such that it drove performance as a whole down to chance levels. We split the data set by speed and accuracy based on participants' performance across the conditions. Thus, for these conditions where interference was the strongest, even the slow-accurate participants showed lower performance, nearing 50%. This, however, is not the same as chance performance, as it reflects the interference between target and distractor, as evidenced by overall task performance being higher.

Previous studies have shown that oblique saccades' dynamics differ from saccades on the cardinal axes (Smit et al. 1990). Oblique saccades are generally more curved (M. C. Doyle and Walker 2002; Smit and Van Gisbergen 1990), because they involve different eye muscles' coactivations (Viviani et al. 1977). As an example, the average maximum of saccade curvature values in speedy subjects for the green target in the word task, DT-unmatched condition, in our study (Fig. 7A) (after normalizing it to saccade amplitudes) was 0.07° degree visual angle, roughly two times larger than the curvature values reported for cardinal saccades in the study by Doyle and Walker (2002).

Our results replicated previous findings which showed that Stroop interference can also be seen in the oculomotor domain (Hodgson et al. 2009) and high-level semantic distractors can influence saccade trajectories (Weaver et al. 2011). Furthermore, the results show that written words can influence oculomotor saccade programming in a similar way to that previously observed for peripheral cues (Hallett and Adams 1980; Ross and Ross 1980; Walker et al. 1997). The fact that color affected interference in a saccadic Stroop task which engages executive control signals to resolve the conflict arising from the presence of a distractor may support the generalization of color inherently modulating executive functions deriving from high-level brain areas such as the prefrontal cortex, a finding in line with the previously established role of prefrontal cortex in computing behavioral relevance of color features (Schwedhelm et al. 2020).

When participants were instructed to find one of the words "GREEN" or "RED", ignoring its color, their performance significantly dropped if it was presented in green color and the distractor was presented in red color (Fig. 6B-B). This reduced performance was accompanied by much longer reaction times when they had to find the word "GREEN" written in green color in the presence of the word "RED" written in red color as the distractor (Fig. 6E). The common denominator of these conditions is red as the distractor color. As previously shown in Blizzard et al. (2017), response inhibition in a stop signal task is enhanced by the color red. Hence, a red distractor is a stronger competitor in oculomotor saccade programming. If active inhibition required to suppress this unresolved competition is not effective enough, or it arrives late, then the subjects may reach the decision threshold and initiate an incorrectly targeted saccade. It is also possible that subjects would require more time to be able to fully suppress red distractors, which in turn leads to longer reaction times. In the latter case, if conflict processing continues until just before the saccade initiation, we would expect to see its influence on saccade trajectories, and indeed, this was the case. We observed saccade curvatures were significantly larger in this condition with a green target and a red distractor. Consistent with red distractors specifically deriving stronger competition, we found no evidence for a symmetric effect of green distractors and red targets. These findings are in full accordance with the notion that saccade deviations are a consequence of additional inhibitory processes (M. C. Doyle and Walker 2002; M. Doyle and Walker 2001; McSorley et al. 2004; White et al. 2012). Our data support that the color hierarchy not only influences high-order cognitive functions but also automatically feeds into oculomotor programming as seen in the saccade trajectories.

We also observed that the reaction times were significantly longer in the word task. Previous studies have suggested that attentional resources can be devoted both serially, i.e., focal attention is allocated serially to salient locations to identify selected items, or in parallel, i.e., attention is distributed diffusively to all locations simultaneously during visual search (Bichot et al. 2005; Wolfe 2010). It might be that the color task utilizes attentional resources in a more parallel way than the word task, and hence, target selection will be faster based on color cues. This idea is further supported by the fact that color detection in parafoveal vision is as good as foveal (Kugler et al. 2015; Martin et al. 2001), and hence, a divided attention strategy may suffice to find the relevant target efficiently. We should note that participants are allowed to make only one saccade to the correct target. Hence, color detection in parafoveal vision is probably happening in pre-attentive processing (Treisman 1985).

There is ample evidence for the existence of a color hierarchy for attentional selection with red sitting at the top of the hierarchy (Lindsey et al. 2010; Pomerleau et al. 2014; Tchernikov and Fallah 2010). We also observed the differential effect of red and green colors at three different levels but all in the word task, while target and distractor were unmatched. Interestingly, the absence of the Stroop interference effect in the color task in our study may suggest that in some circumstances, behavioral demands and interactions between different perceptual domains may override the Stroop effect. In our case, it may be that the color mapping system is more robust than the word system and does not allow for interference of the incongruent word domain easily [see (Yantis 1993) for a discussion on the interactions between color driven attention capture and the observer's goals]. Another possibility is that focusing attention on the color domain may result in faster programming of saccade vectors (pop-out effect), hence not leaving enough time in the pre-saccadic window to integrate the information on the word identities as distractors. The differential Stroop effect seen in the word and color tasks may be as well a consequence of the differential sensitivity of the peripheral versus foveal vision to color and form information. Studies demonstrated that complex form representation is highly dependent on the foveal scrutiny (we use foveal vision while reading text), while homogenous color patches can be well discriminated even in parafoveal space (Kugler et al. 2015; Lee et al. 2003; Martin et al. 2001). Recent theories propose that it is foveal versus extrafoveal exploring during development which constrains the location of category selective areas in inferotemporal cortex (Conway 2018) and how they are recruited during the performance of cognitive control or visual attention tasks (Ramezanpour and Fallah 2022). Differential sensitivity of the peripheral versus foveal vision to color and form information may also lead to faster and less erroneous responses to color. Another factor which may have affected the reaction time and accuracy measures is the relatively lower speed of word identity perception than color perception. Word perception needs to recruit longer latency neurons in the inferotemporal cortex which are sensitive to complex forms (Schmolesky et al. 1998; Tamura and Tanaka 2001; Vogels and Orban 1994), while color perception can be achieved by shorter latency neurons such as those in visual area V4 (Schmolesky et al. 1998).

While a set of frontal lobe structures has been associated with the Stroop task, two areas consistently are thought to play the most important functions: the anterior cingulate cortex (ACC) and the dorsolateral prefrontal cortex (dlPFC) (Laird et al. 2005; Nee et al. 2007; Roberts and Hall 2008). The latest findings and theories suggest that ACC is mainly involved in conflict monitoring, while the dlPFC is recruited when interference occurs to resolve conflict in a top-down manner, by biasing information processing in lower level brain areas to favor the most relevant criteria for performing the task (Botvinick et al. 2001, 2004). When it comes to eye movements, target selection in the presence of distractors has been shown to recruit other prefrontal circuitries involving the frontal eye field (FEF) (Cohen et al. 2010). Whether color modulation of saccade trajectories is dependent upon processing within FEF or input from other areas requires future neuroimaging or electrophysiological recordings. However, a recent study is suggestive that, at least in monkeys, prefrontal area 8Av/45 underlies encoding of the color of a visual stimulus, regardless of its behavioral relevance (Schwedhelm et al. 2020). Such signals in the area 8Av/45 might be inherently reflecting the color hierarchy observed in the visual system and its influences over cognitive functions.

Where do color biases initially come from? Several studies have provided empirical evidence supporting the role of color opponent mechanisms on modulation of behavioral functions (Fortier-Gauthier et al. 2013; Lindsey et al. 2010; Pomerleau et al. 2014; Saini et al. 2021). Color opponency theories state that because of the circuity of cone photoreceptors (mutual inhibition), only one of opposing color pairs (e.g., red and green) can be detected by the early visual system (Hurvich and Jameson 1957). While this theory explains why differential processing of colors within opponent pairs might exist, it cannot provide an explanation of why red is prioritized over green and not vice versa. Other studies provided further evidence of an attentional color hierarchy that can bias oculomotor target selection (Kehoe et al. 2018a, b; Tchernikov and Fallah 2010). In contrast to color opponency, this type of color modulation cannot solely rely on early visual areas and are most probably accommodated by more intermediate levels of visual system hierarchy such as area V4. Last but not least, color biases might be based on implicit associations between repeated pairings of colors and specific outcomes (Elliot 2015). While the nature and origin of these associations may vary across the animal kingdom, there is evidence that, at least in primates, these color biases are evolutionarily preserved (Ghasemian et al. 2021). In recent work, macaque monkeys exhibited bias for red stop signals, mirroring human behavior (Blizzard et al. 2017). Further research is needed to shed more light on how experience-dependent learning may modify such innate evolutionarily preserved biases.

Conclusions

The current study demonstrates that effects of red and green colors on saccade curvature are mediated by competition between features and objects. Red distractors exhibit stronger competition with green targets when planning saccades, as seen both in the behavioral measures as well as saccade curvature metrics. When the results of this cognitive interference task are taken together with prior studies of response inhibition and attentional selection, it suggests that color inherently modulates the range of executive functions which are thought to be supported by prefrontal circuitry.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest None.

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