

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

3
4 **Hamidreza Ramezanpour**

5 Centre for Vision Research, York University, Toronto, Ontario, Canada
6 School of Kinesiology and Health Science, Faculty of Health, York University, Toronto,
7 Ontario, Canada
8 VISTA: Vision Science to Application, York University, Toronto, Ontario, Canada

9
10 **Shawn Blizzard**

11 Centre for Vision Research, York University, Toronto, Ontario, Canada
12 School of Kinesiology and Health Science, Faculty of Health, York University, Toronto,
13 Ontario, Canada

14
15 **Devin Heinze Kehoe**

16 Centre for Vision Research, York University, Toronto, Ontario, Canada
17 School of Kinesiology and Health Science, Faculty of Health, York University, Toronto,
18 Ontario, Canada
19 VISTA: Vision Science to Application, York University, Toronto, Ontario, Canada

20
21 **Mazyar Fallah**

22 Centre for Vision Research, York University, Toronto, Ontario, Canada
23 School of Kinesiology and Health Science, Faculty of Health, York University, Toronto,
24 Ontario, Canada
25 VISTA: Vision Science to Application, York University, Toronto, Ontario, Canada
26 Department of Psychology, Faculty of Health, York University, Toronto, Ontario, Canada
27 Department of Human Health and Nutritional Sciences, College of Biological Science,
28 University of Guelph, Guelph, Ontario, Canada

29 **Corresponding authors:** Hamidreza Ramezanpour and Mazyar Fallah. Email:
30 hamidram@yorku.ca and mfallah@uoguelph.ca. Address: York University, 4700 Keele Street,
31 Toronto, Ontario M3J 1P3, Canada.

32 **Abstract**

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

46

47 **Keywords:** target-distractor similarity, saccade, Stroop, color saliency, top-down control

48

49

50

51

52

53

54

55

56

57

58

59

60

61

62

63 **Introduction**

64 The brain can only process a small amount of information impinging on our visual system at a
65 given moment. The oculomotor system programs fast ballistic eye movements, saccades, to shift
66 the high acuity part of the retina, the fovea, to the locations of interest in the visual scene, thereby
67 allowing a high-resolution image of that particular location for further analysis. Previous studies
68 have shown that the oculomotor system selects a target which is either more salient because of its
69 visual properties (bottom-up attention or “pop-out”) or because it has higher behavioral relevance
70 (top-down attention) compared to the surrounding objects (Wolfe, 2010). Competition between
71 bottom-up and top-down processes leads to the formation of a spatial priority map in which the
72 location of the target with the highest weight is selected to program a saccade vector (Fecteau &
73 Munoz, 2006). This competition is reflected by longer saccade latencies to a saccade target in the
74 presence of a salient distractor or by the number of erroneous saccades to a distractor (Godijn &
75 Theeuwes, 2002; Van der Stigchel et al., 2006).

76 One of the elementary attributes of visual objects that guide target selection is color (Elliot et al.,
77 2007; Tchernikov & Fallah, 2010). Theories of primates’ evolution state that the Trichromacy, the
78 ability to distinguish red-green-blue, has evolved to enable our old world primate ancestors to
79 dissociate ripe fruits and green leaves from their natural background (Osorio & Vorobyev, 1996;
80 Regan et al., 2001). Color, as a result of these visual associations, has been shown to influence our
81 cognition and behavior (Elliot et al., 2007; Ghasemian et al., 2021; Mehta & Zhu, 2009). For
82 instance, studies in monkeys and humans have revealed that visual attention and eye movements
83 can be influenced by color (Bichot et al., 2005; Desimone & Duncan, 1995; Frey et al., 2008).
84 These influences are the result of color biasing the saliency map during target selection (Kehoe,
85 Rahimi, et al., 2018; Koch & Ullman, 1985; Tchernikov & Fallah, 2010). It is noteworthy to
86 mention that these color effects are not just random. There are behavioral and neurophysiological
87 evidence for the existence of a systematic color hierarchy for attentional selection with red sitting
88 at the top of the hierarchy (Lindsey et al., 2010; Pomerleau et al., 2014; Tchernikov & Fallah,
89 2010). For example, different colors can have a differential effect on the speed of smooth pursuit
90 eye movements and target selection even in the absence of clear external instruction on what to
91 select, suggesting a bottom-up nature of color encoding for the pursuit target selection (Tchernikov
92 & Fallah, 2010). This hierarchical color target selection has been shown to not be limited to low-
93 level visual processing. One study, using a stop signal task, showed that red color stop signals lead

94 to faster response inhibition than green color stop signals, suggesting that the color hierarchy is
95 present at higher stages of cognitive processing most probably due to visual associations which
96 assigned a certain value to each color for different cognitive tasks (Blizzard et al., 2017).
97 Studies on the color-specific effects on attentional control notwithstanding, the question of whether
98 different colors can modulate saccade trajectories is not well understood yet. We know from
99 previous studies that saccade trajectory deviations in the presence of competing stimuli can be an
100 indicator of competition between saccade targets in the oculomotor system. For a review please
101 see (Van der Stigchel et al., 2006; Walker & McSorley, 2008). These studies demonstrated that
102 the instruction to attend to a location other than the saccade target could modulate the extent and
103 direction of saccadic curvature (Sheliga et al., 1994, 1995, 1997; Tipper et al., 2001). Hence,
104 measuring saccade trajectories in the presence of distractors can be used as a noninvasive method
105 to assess executive functions and target selection in the brain (Kehoe & Fallah, 2017). It is
106 specifically interesting to investigate how/if colors compete for target selection during executive
107 control and if this competition lasts until the very last stages of generating a motor output i.e.,
108 oculomotor control of saccades. In a study on how the oculomotor system might encode color
109 saccade targets, Kehoe and colleagues used a memory-guided saccade task with color targets and
110 distractors (Kehoe, Rahimi, et al., 2018). They found that the oculomotor system encodes color in
111 perceptual color space similar to how the visual system does. Using a memory-guided saccade
112 task independent of sustained sensory inputs suggested that the color signals might reach the
113 oculomotor system via high-level cortical areas involved in visual working memory such as the
114 prefrontal cortex. Furthermore, cueing attention to a certain color elicited surround suppression in
115 the oculomotor color space as predicted by the selective tuning model of attention (Tsotsos, 2011).
116 The involvement of prefrontal circuitry in biasing target selection according to color saliency gets
117 further support from a study showing that response inhibition, a major prefrontal cortex function,
118 is sensitive to differences in color salience (Blizzard et al., 2017). These studies investigated a
119 subset of the executive functions produced by prefrontal cortex: attentional selection and response
120 inhibition. Our goal is to extend this further to conflict resolution and cognitive interference.
121 The Stroop task can be used to assess the ability to inhibit cognitive interference where there is a
122 competition between color words (“RED”, “GREEN”) and the color of the words (Hermens &
123 Walker, 2012; Hodgson et al., 2009; Stroop, 1935). The main aim of this study was to investigate
124 how the effects of color on executive functions drive the oculomotor system. We specifically asked

125 whether color effects on saccade programming would arise through the competition inherent in the
126 Stroop task. We used a modified version of the Stroop task in which we presented a distractor in
127 addition to the target. The distractor could either match the target feature needing to be attended
128 or not. This would allow us to determine whether color effects on saccade programming, if found,
129 are a function of distractor-target similarity.

130 **Methods**

131 Twenty students (18-37 years old, 8 men and 12 women) volunteers from York University
132 participated in the experiment in exchange for course credit. All participants had normal or
133 corrected to normal vision. Their color vision was assessed by Ishihara color plates (Ishihara,
134 2006). Written informed consent was obtained prior to participation in accordance with the
135 Declaration of Helsinki. All research was approved by York University's Human Participants
136 Review Committee. One participant was excluded from the analysis because of poor quality eye
137 data.

138 *Apparatus and measurement*

139 Stimulus presentation was controlled using a computer running Presentation software
140 (Neurobehavioral Systems, Berkeley, CA, www.neurobs.com). Eye position was sampled at
141 500Hz 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,
142 1024 x 768 pixels). Participants viewed stimuli in a dimly lit room from a viewing distance of 57
143 cm with a headrest stabilizing their head position. Stimuli color and luminance were calibrated
144 using a spectrophotometer (PR-655, Photo Research, Syracuse, NY).

146 *Visual stimuli and experimental tasks*

147 The visual stimuli were constructed offline using Matlab (The Mathworks, www.mathworks.com)
148 and consisted of colored bars or words that subtended $3.2^\circ \times 1.1^\circ$ visual angle. The word letters
149 were spaced such that the overall word's size would roughly fit to the size of the bars. The colors
150 used in this experiment consisted of isoluminant red (CIE coordinates: $x=0.63, y=0.3; L=12.07$
151 cd/m^2) and green (CIE coordinates: $x=0.29, y=0.59; L=12.00 cd/m^2$) as target colors and gray (CIE
152 coordinates: $x=0.28, y=0.30; L=11.20 cd/m^2$) as the baseline color. "RED" and "GREEN" were
153 used as target words. The cue was always presented at the center of the screen while the target and
154 distractor were presented at the upper left and upper right quadrant of the screen. The coordinates

155 of target and distractor were chosen in each trial randomly from the set of [-5.67, 6.2] and [5.67,
156 6.2] degrees of visual angle (Cartesian (x,y) coordinates, see **Figure 1**).

157 **Word Task.** In this task, after successfully fixating on a small central fixation point for 500 ms,
158 participants were shown a central cue consisting of a printed word: “RED” or “GREEN” in gray
159 color. If the participant failed to fixate at least 200 ms on the central cue within 2s after the trial
160 start, that trial was aborted and a new trial was presented. When they fixated on the central cue for
161 200 ms, the central cue disappeared and two words appeared on the screen, one serving as the
162 target that would match the semantic meaning of the central cue and the other one as the distractor
163 which always differed semantically from the target word. The participant’s task was to look at the
164 same word that they had previewed in the cue period while ignoring the color of the target and
165 distractor (see **Figure 1A**). Distractor and target words could be presented in the same color (DT-
166 match condition) or in different colors (DT-unmatched condition). The color of the target could
167 either match the semantic meaning of the central cue (congruent condition), or not (incongruent).

168 **Color Task.** In this task, after successfully fixating on a central fixation for 500ms, participants
169 were shown a central cue consisting of a red or a green horizontal bar, at the beginning of each
170 trial. Similar to the word task, after participants fixated on the central cue for 200ms, the central
171 cue disappeared and two words “RED” and “GREEN” appeared on the screen, one serving as the
172 target in that its color matched the color of the central cue and the other one as the distractor which
173 always differed from the target in color. The participant had to look at the word that has the same
174 color as the one they had previewed in the cue period while ignoring the semantic identity of the
175 target and distractor (see **Figure 1B**). Distractor and target could have the same semantic identity
176 (DT-match condition) or different (DT-unmatched condition). The target word could either match
177 semantically with the color of the central cue (congruent condition), or not (incongruent condition).

178 A few other examples from the set of possible conditions are illustrated in **Figure 1C-H**.

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

182 The tasks were done in separate blocks with randomized order. Each block started with an
183 instruction on the screen stating which task (color or word) held for that block. Each block
184 consisted of 64 trials and each participant completed 8 blocks. There were two practice blocks,
185 each consisting of 10 trials of the word task and the color task separately, at the beginning of each

186 experiment to familiarize the participant with the experiment. After the practice blocks and before
187 starting the two main tasks, each participant performed a block of 20 trials consisting of visually
188 guided saccade to one of two spatial targets (grey bars) located at the same location and the same
189 size as the words in the main experiment. Since saccades naturally have a small amount of
190 curvature even in the absence of distracters, the purpose of this block was to measure baseline
191 saccade curvatures to be accounted for in the later analyses.

192

193 **Analysis**

194 **Saccade Detection.** All analyses were done using customized Matlab algorithms. One participant
195 was removed from further analysis due to poor quality eye data. All subsequent analyses were
196 performed on the remaining 19 participants. Trials that contained blinks were excluded from
197 further analysis. Saccades were defined based on a velocity threshold of $20^\circ/\text{s}$ for at least 8ms and
198 a peak velocity exceeding $50^\circ/\text{s}$. Saccades were excluded from further analysis if their amplitude
199 was smaller than 1° visual angle, or if they were accompanied by more than one corrective saccade
200 or only one corrective saccade larger than 1° visual angle. Also, saccades with less than 100ms
201 latency were excluded. Other exclusion criteria were pre-saccadic drift larger than 2° and endpoint
202 deviations larger than 2° . Finally, we excluded all saccades where their initial angle was more than
203 2.5 standard deviations further from the correct target direction, to account for saccades corrected
204 mid-flight. These strict exclusion criteria were used to make sure that any modulatory effects of
205 experimental condition on saccade trajectories were not related to task irrelevant saccadic
206 preparation (i.e, short amplitude, short latency or poor fixational stability). In total, 6242 saccades
207 remained for further analysis ($mean \pm std = 328 \pm 143$ trials per participant).

208 **Saccade Metrics.** In this study we looked at several saccade metrics: saccade reaction times,
209 endpoint deviation, max curvature, and sum curvature. These metrics have been used previously
210 in several studies (Kehoe, Aybulut, et al., 2018; Kehoe, Rahimi, et al., 2018; Kehoe & Fallah,
211 2017). To analyse saccade curvatures, saccade starting points were translated back to the origin
212 and then trigonometrically rotated such that endpoint was aligned to the positive y-axis. Saccade
213 reaction time was defined as the time between target/distractor onset and saccade initiation.
214 Endpoint deviation was calculated for each saccade as the Euclidean distance between the saccade
215 landing point and the target location. Max curvature was quantified by the maximum orthogonal
216 deviation from a straight line between the start and endpoint of saccade trajectories. Sum curvature

217 was calculated by summing of all orthogonal deviations from a straight line between the start and
218 endpoint of the saccade trajectory (**Figure 2A**). Example saccades made by one of the participants
219 can be seen in **Figure 2B**. The saccade peak velocity-amplitude relationship (main sequence), and
220 peak velocity-duration relationship for the same example participant can be seen in **Figure 2C**.

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

230

231 **Results**

232 *Accuracy and Reaction Times*

233 Participants performed the task with high accuracy well above the chance level of 50% ($p < 0.001$,
234 Wilcoxon signed-rank test, since the data did not follow a normal distribution (kstest, $p < 0.05$))
235 with correct response accuracy of $77.5\% \pm 2.35$. As shown in **Figure 3A**, their performance in the
236 word task ($62.56\% \pm 13.7$) was significantly worse than the color task ($90.6\% \pm 9.8$) suggesting a
237 higher difficulty level in the word task. The greater difficulty of the word task was also reflected
238 in longer average reaction times (241 ± 38 ms) than in the color task (221 ± 20 ms), see **Figure**
239 **3B**. In order to further quantify how different experimental conditions might affect participants'
240 performance and reaction times, we performed a linear Pearson correlation analysis. As can be
241 seen in **Figure 3C**, there was in general a strong positive linear correlation between the
242 participants' performance and their reaction times ($\rho = 0.61$, $p = 0.005$ for the color task and ($\rho = 0.69$,
243 $p = 0.001$ for the word task) suggesting that stronger inhibitory control (better performance) is
244 reflected in slower responses.

245 In order to characterize the traditional Stroop interference effect, we compared the performance
246 and reaction times between the congruent and incongruent conditions. Participants' performance
247 was significantly lower in the incongruent condition for the word task ($p_{\text{Bonferroni-corrected}} < 0.001$, t-

248 test, since the data followed a normal distribution (kstest, $p > 0.05$). Consistent with the accuracy
249 results, reaction times were significantly longer in the incongruent condition in the word task
250 ($p_{\text{Bonferroni-corrected}} < 0.05$, t-test, since the data followed a normal distribution (kstest, $p > 0.05$), **Figure**
251 **4A**). Separating this analysis for red color and green color targets revealed that the significantly
252 lower performance in the incongruent condition was mainly driven by the green condition
253 ($p_{\text{Bonferroni-corrected}} < 0.001$, t-test, since the data followed a normal distribution (kstest, $p > 0.05$),
254 **Figure 4B**), or when distractor and targets were unmatched ($p_{\text{Bonferroni-corrected}} < 0.001$, t-test, since
255 the data followed a normal distribution (kstest, $p > 0.05$), **Figure 4D**). We did not see any effects
256 of color in conjunction with the incongruent effect on reaction times ($p_{\text{Bonferroni-corrected}} > 0.05$, t-test,
257 since the data followed a normal distribution (kstest, $p > 0.05$)). Moreover, there was no effect of
258 congruency on the color task ($p_{\text{Bonferroni-corrected}} > 0.05$, Wilcoxon signed-rank test, since the data did
259 not follow a normal distribution (kstest, $p < 0.05$), see **Figure 5A-G**).

260 Furthermore, a four-way repeated measure ANOVA (factors: color, task, congruency and
261 distractor-target similarity) showed main effects of task ($df=1$, $F=92.62$, $p < .001$), congruency
262 ($df=1$, $F=37.68$, $p < 0.001$) and similarity ($df=1$, $F=6.5$, $p < 0.05$), as well as two-way interactions of
263 congruency \times task ($df=1$, $F=23.26$, $p < .001$), congruency \times similarity ($df=1$, $F=26.11$, $p < .001$) and
264 congruency \times color ($df=1$, $F=24.03$, $p < .001$) on performance. Performance was also significantly
265 influenced by three-way interactions of congruency \times task \times color ($df=1$, $F=17.42$, $p < .001$) and
266 congruency \times task \times similarity ($df=1$, $F=19.55$, $p < .001$). Finally, there was a four-way interaction
267 effect of congruency \times task \times color \times similarity ($df=1$, $F=25.54$, $p < .001$). Posthoc t-tests (since the
268 data followed a normal distribution (kstest, $p > 0.05$)) revealed that the participants make
269 significantly more errors during the word task when the target is green (color) in three different
270 conditions: incongruent ($df=18$, $p_{\text{Bonferroni-corrected}} < 0.05$, **Figure 6A**), DT-unmatched ($df=18$,
271 $p_{\text{Bonferroni-corrected}} < 0.05$, **Figure 6B**) and their interaction i.e., incongruent, DT-unmatched ($df=18$,
272 $p_{\text{Bonferroni-corrected}} < 0.01$, **Figure 6C**).

273 Similarly, a four-way repeated measure ANOVA (factors: color, task, congruency and distractor-
274 target similarity) showed main effects of task ($df=1$, $F=13.23$, $p < 0.001$), congruency ($df=1$,
275 $F=4.48$, $p < 0.05$) and similarity ($df=1$, $F=6.5$, $p < 0.05$), also two-way interactions of congruency \times
276 task ($df=1$, $F=22.46$, $p < 0.001$), and congruency \times color ($df=18.33$, $F=18.46$, $p < 0.001$) for the
277 reaction time measures. Furthermore, reaction times were significantly influenced by a three-way
278 interactions of congruency \times task \times color ($df=1$, $F=5.9$, $p < 0.05$) and congruency \times color \times

279 similarity ($df=1$, $F=6.3$, $p<0.05$). Finally, there was a four-way interaction effect of congruency \times
280 task \times color \times similarity ($p<0.01$). Posthoc t-tests (since the data followed a normal distribution
281 (kstest, $p>0.05$)) also revealed significantly longer reaction times for red color than green color in
282 the congruent condition and when distractor and targets were unmatched ($RT_{red\ color}=240$ ms and
283 $RT_{green\ color}=233$ ms, $df=18$, $p_{Bonferroni-corrected}<0.05$, see **Figure 6D**). We also observed that this
284 significant effect was even stronger in the word task ($RT_{red\ color}=260$ ms and $RT_{green\ color}=240$ ms,
285 $df=18$, $p_{Bonferroni-corrected}<0.05$, **Figure 6E**).

286 *Saccade Metrics*

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

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

297 Saccade curvature reflects competition between the saccade target and a distractor, wherein
298 increased strength of the distractor results in increased curvature towards it. Based on this a-priori
299 hypothesis, even though the ANOVA did not show any overall effects of color on curvature
300 metrics, and given the consistent effect of color in the word task and especially in DT-unmatched
301 condition (see **Figure 6**) we performed additional posthoc tests. There was a statistically
302 significant effect of color on the curvature metrics in the DT-unmatched condition in the word task
303 ($p_{Bonferroni-corrected}=0.006$, $df=18$, t-test, since the data did not follow a normal distribution (kstest,
304 $p>0.05$)). Saccade trajectories were more curved for green (color) targets (sum curvature $mean \pm$
305 $std = 6 \pm 2.4$ dva) compared to red (color) targets ($mean \pm std = 5.4 \pm 2.2$ dva). Then, we median
306 split subjects according to their performance into a speedy-inaccurate (subjects with weaker
307 inhibitory control) and a slow-accurate (subjects with stronger inhibitory control) group in order
308 to investigate whether it is the strength of inhibitory control in each participant which influences
309 their saccade trajectories and the effects of color. Repeating these analyses on the two groups

310 separately showed that while the speedy-inaccurate subjects' saccade trajectories were more
311 curved (sum curvature) for green (color) targets in the word task, DT-unmatched condition
312 ($p_{\text{Bonferroni-corrected}}=0.01$ t-test, see **Figure 7A** and also **Figure 7C** for DT-matched condition), slow-
313 accurate subjects' eye movements were not significantly affected by color in any of the conditions
314 including the DT-unmatched in the word task ($p_{\text{Bonferroni-corrected}}>0.05$, t-test, see **Figure 7B** and also
315 **Figure 7D** for DT-matched condition). The analysis of max curvature yielded similar results: i.e.,
316 significantly more curved saccades ($p_{\text{Bonferroni-corrected}}=0.004$, t-test) were seen in the DT-unmatched
317 condition in the word task for green (color) targets ("GREEN": max curvature $mean \pm std = 0.61$
318 ± 0.16 ; red (color): max curvature $mean \pm std = 0.58 \pm 0.17$).

319

320 **Discussion**

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

334 Participants' performance in the word task was significantly worse than the color task suggesting
335 a higher difficulty level in the word task. This higher difficulty in the word task was even more
336 pronounced in those conditions with higher competition between target and distractor features,
337 such as in the incongruent or DT-unmatched (**Figure 6A-C**), where participants were driven to
338 select a competing feature in error. In those conditions, the interference effects (resulting from
339 decreased inhibition) were greater for red (near chance level performance for the green target as
340 in **Figure 6A-C**). The combination of an incongruent color-word pairing with unmatched

341 distractor-target pairings produced the worse performance, reflecting the greatest amount of
342 interference. As such, performance on the task was dependent on the different colors of the target
343 and distractor, with red unmatched distractors producing the greatest interference such that it drove
344 performance as a whole down to chance levels. We split the data set by speed and accuracy based
345 on participants' performance across the conditions. Thus for these conditions where interference
346 was the strongest, even the slow-accurate participants showed lower performance, nearing 50%.
347 This however, is not the same as chance performance, as it reflects the interference between target
348 and distractor, as evidenced by overall task performance being higher.

349 Previous studies have shown that oblique saccades' dynamics differ from saccades on the cardinal
350 axes (Smit et al., 1990). Oblique saccades are generally more curved (M. C. Doyle & Walker,
351 2002; Smit & Van Gisbergen, 1990) because they involve different eye muscles coactivations
352 (Viviani et al., 1977). As an example, the average maximum of saccade curvature values in speedy
353 subjects for the green target in the word task, DT-unmatched condition, in our study (Figure 7A)
354 (after normalizing it to saccade amplitudes) was 0.07° degree visual angle, roughly two times
355 larger than the curvature values reported for cardinal saccades in the study by Doyle and Walker
356 (2002).

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

367 When participants were instructed to find one of the words "GREEN" or "RED", ignoring its color,
368 their performance significantly dropped if it was presented in green color and the distractor was
369 presented in red color (**Figure 6B-C**). This reduced performance was accompanied by much
370 longer reaction times when they had to find the word "GREEN" written in green color in the
371 presence of the word "RED" written in red color as the distractor (**Figure 6E**). The common

372 denominator of these conditions is red as the distractor color. As previously shown in (Blizzard et
373 al., 2017), response inhibition in a stop signal task is enhanced by the color red. Hence a red
374 distractor is a stronger competitor in oculomotor saccade programming. If active inhibition
375 required to suppress this unresolved competition is not effective enough, or it arrives late, then the
376 subjects may reach the decision threshold and initiate an incorrectly targeted saccade. It is also
377 possible that subjects would require more time to be able to fully suppress red distractors, which
378 in turn leads to longer reaction times. In the latter case, if conflict processing continues until just
379 before the saccade initiation, we would expect to see its influence on saccade trajectories and
380 indeed this was the case. We observed saccade curvatures were significantly larger in this
381 condition with a green target and a red distractor. Consistent with red distractors specifically
382 deriving stronger competition, we found no evidence for a symmetric effect of green distractors
383 and red targets. These findings are in full accordance with the notion that saccade deviations are a
384 consequence of additional inhibitory processes (M. C. Doyle & Walker, 2002; M. Doyle & Walker,
385 2001; McSorley et al., 2004; White et al., 2012). Our data supports that the color hierarchy not
386 only influences high order cognitive functions but also automatically feeds into oculomotor
387 programming as seen in the saccade trajectories.

388 We also observed that the reaction times were significantly longer in the word task. Previous
389 studies have suggested that attentional resources can be devoted both serially, i.e., focal attention
390 is allocated serially to salient locations to identify selected items, or in parallel, i.e., attention is
391 distributed diffusively to all locations simultaneously during visual search (Bichot et al., 2005;
392 Wolfe, 2010). It might be that the color task utilizes attentional resources in a more parallel way
393 than the word task and hence, target selection will be faster based on color cues. This idea is further
394 supported by the fact that color detection in parafoveal vision is as good as foveal (Kugler et al.,
395 2015; Martin et al., 2001) and hence a divided attention strategy may suffice to find the relevant
396 target efficiently. We should note that participants are allowed to make only one saccade to the
397 correct target. Hence color detection in parafoveal vision is probably happening in pre-attentive
398 processing (Treisman, 1985).

399 There is ample evidence for the existence of a color hierarchy for attentional selection with red
400 sitting at the top of the hierarchy (Lindsey et al., 2010; Pomerleau et al., 2014; Tchernikov &
401 Fallah, 2010). We also observed the differential effect of red and green colors at three different
402 levels but all in the word task while target and distractor were unmatched. Interestingly, the

403 absence of the Stroop interference effect in the color task in our study may suggest that in some
404 circumstances, behavioral demands and interactions between different perceptual domains may
405 override the Stroop effect. In our case, it may be that the color mapping system is more robust than
406 the word system and does not allow for interference of the incongruent word domain easily (see
407 (Yantis, 1993) for a discussion on the interactions between color driven attention capture and the
408 observer's goals). Another possibility is that focusing attention on the color domain may result in
409 faster programming of saccade vectors (pop-out effect), hence not leaving enough time in the
410 presaccadic window to integrate the information on the word identities as distractors. The
411 differential Stroop effect seen in the word and color tasks may be as well a consequence of the
412 differential sensitivity of the peripheral versus foveal vision to color and form information. Studies
413 demonstrated that complex form representation is highly dependent on the foveal scrutiny (we use
414 foveal vision while reading text) while homogenous color patches can be well discriminated even
415 in parafoveal space (Kugler et al., 2015; Lee et al., 2003; Martin et al., 2001). Recent theories
416 propose that it is foveal versus extrafoveal exploring during development which constrains the
417 location of category selective areas in inferotemporal cortex (Conway, 2018) and how they are
418 recruited during the performance of cognitive control or visual attention tasks (Ramezanpour &
419 Fallah, 2022). Differential sensitivity of the peripheral versus foveal vision to color and form
420 information may also lead to faster and less erroneous responses to color. Another factor which
421 may have affected the reaction time and accuracy measures is the relatively lower speed of word
422 identity perception than color perception. Word perception needs to recruit longer latency neurons
423 in the inferotemporal cortex which are sensitive to complex forms (Schmolsky et al., 1998;
424 Tamura & Tanaka, 2001; Vogels & Orban, 1994) while color perception can be achieved by
425 shorter latency neurons such as those in visual area V4 (Schmolsky et al., 1998).

426 While a set of frontal lobe structures has been associated with the Stroop task, two areas
427 consistently are thought to play the most important functions: the anterior cingulate cortex (ACC)
428 and the dorsolateral prefrontal cortex (dlPFC) (Laird et al., 2005; Nee et al., 2007; Roberts & Hall,
429 2008). The latest findings and theories suggest that ACC is mainly involved in conflict monitoring
430 while the dlPFC is recruited when interference occurs in order to resolve conflict in a top down
431 manner, by biasing information processing in lower level brain areas to favor the most relevant
432 criteria for performing the task (Botvinick et al., 2001, 2004). When it comes to eye movements,
433 target selection in the presence of distractors has been shown to recruit other prefrontal circuitries

434 involving the frontal eye field (FEF) (Cohen et al., 2010). Whether color modulation of saccade
435 trajectories is dependent upon processing within FEF or input from other areas requires future
436 neuroimaging or electrophysiological recordings. However, a recent study is suggestive that, at
437 least in monkeys, prefrontal area 8Av/45 underlies encoding of the color of a visual stimulus,
438 regardless of its behavioral relevance (Schwedhelm et al., 2020). Such signals in the area 8Av/45
439 might be inherently reflecting the color hierarchy observed in the visual system and its influences
440 over cognitive functions.

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

459

460 **Conclusions**

461 The current study demonstrates that effects of red and green colors on saccade curvature are
462 mediated by competition between features and objects. Red distractors exhibit stronger
463 competition with green targets when planning saccades, as seen both in the behavioral measures
464 as well as saccade curvature metrics. When the results of this cognitive interference task are taken

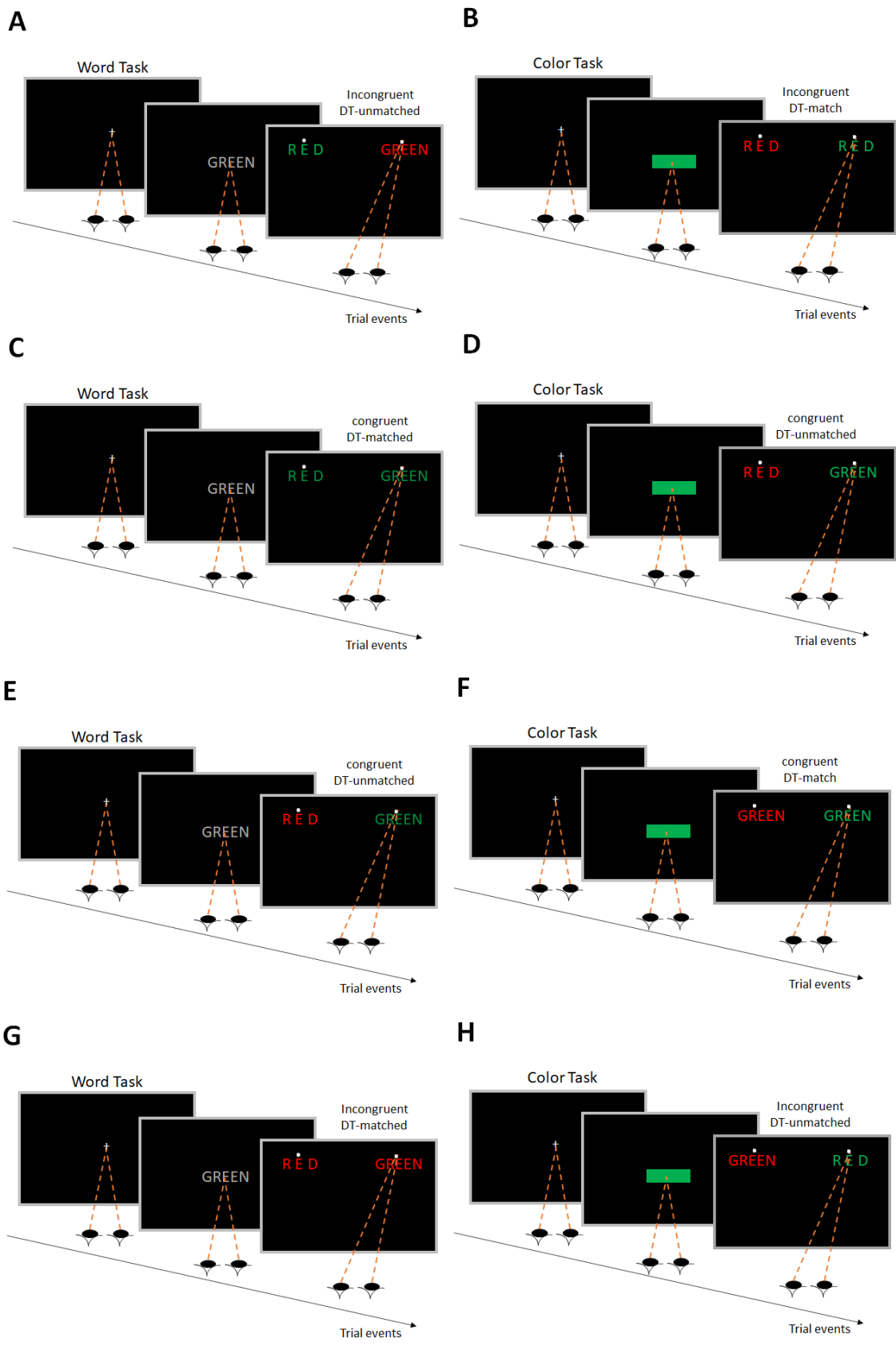
465 together with prior studies of response inhibition and attentional selection, it suggests that color
466 inherently modulates the range of executive functions which are thought to be supported by
467 prefrontal circuitry.

468

469 **Acknowledgments:** H.R. was supported by a Vision: Science to Applications (VISTA)
470 postdoctoral fellowship award. M.F. was supported by an NSERC Discovery Grant and CIHR
471 Project Grant.

472 **Conflict of interest:** none.

473 **Data availability:** The datasets generated during and/or analysed during the current study are
474 available from the corresponding author on reasonable request.



476 **Figure 1. Saccadic Stroop task.**

477 (A) Word task: In this task, after successfully fixating on a central fixation for 500ms, participants were shown a central cue, a
478 printed word “RED” or “GREEN” in gray color. After participants fixated on the central cue for 200ms, the central cue disappeared
479 and two words appeared on the screen, one serving as the target that would match the semantic meaning of the central cue and the
480 other one as the distractor which always differed semantically from the target word. The participant’s task was to look at the *word*
481 that has the same semantic meaning as the one they had previewed in the cue period, while ignoring the color of the target and
482 distractor. This exemplary trial is considered an incongruent and DT-unmatched condition since the word “RED” as the target has
483 a green color (incongruency) and the distractor word is “GREEN” (B) Color task: In this task, after successfully fixating on a
484 central fixation for 500ms, participants were shown a central cue, a red or a green bar, at the beginning of each trial. Similar to the
485 word task, after participants fixated on the central cue for 200ms, the central cue disappeared and two words appeared on the screen,
486 one serving as the target that would match the *color* of the central cue and the other one as the distractor which always differed
487 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
488 cue period, while ignoring the semantic identity of the target and distractor. This example trial is from the incongruent, DT-match
489 condition). (C-H) A few other examples from the set of possible conditions.

490

491

492

493

494

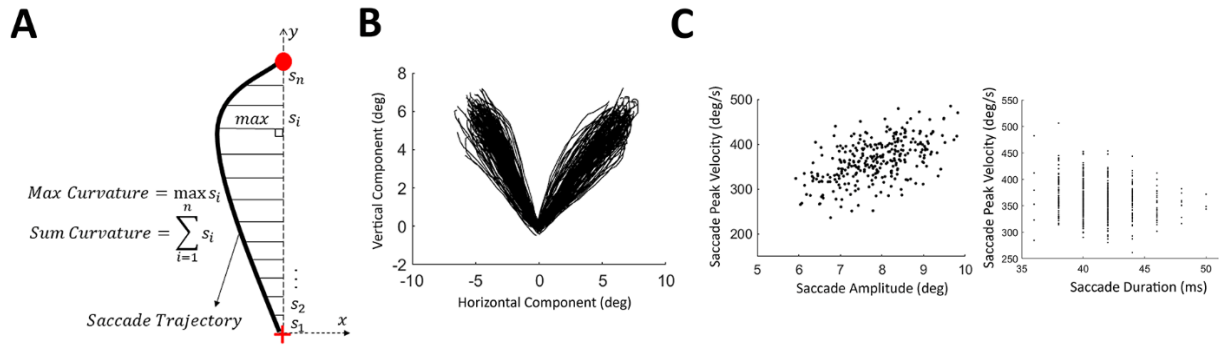
495

496

497

498

499



500

501 **Figure 2. Saccadic Characteristics.**

502 (A) Derivation of saccade curvature metrics. Saccade start and end points are represented by red + and closed circles. The saccade
 503 has been translated and trigonometrically rotated so that it starts from the Cartesian origin and the end point lies on the positive y-
 504 axis. Orthogonal deviations from each eye position sample to a straight line between the start and end point of the saccade
 505 are indicated by horizontal lines (s_i). (B) Example of saccades made by one of the participants. (C) Saccade peak velocity-amplitude
 506 relationship (main sequence), and saccade peak velocity-duration relationship for the same example participant in (B).

507

508

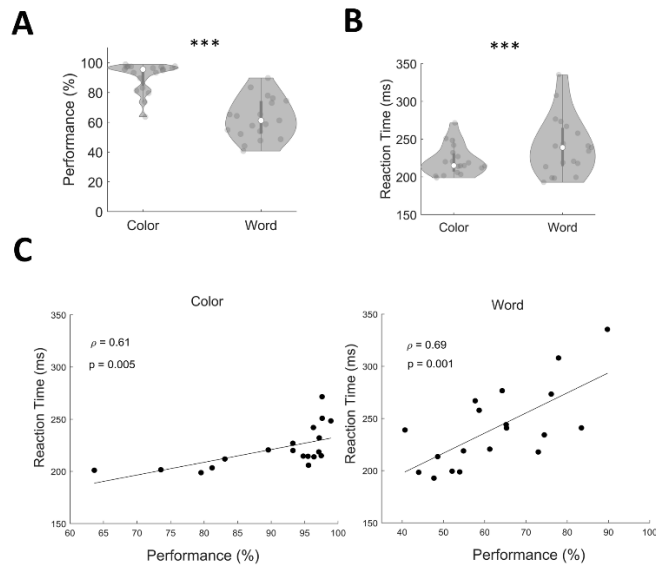
509

510

511

512

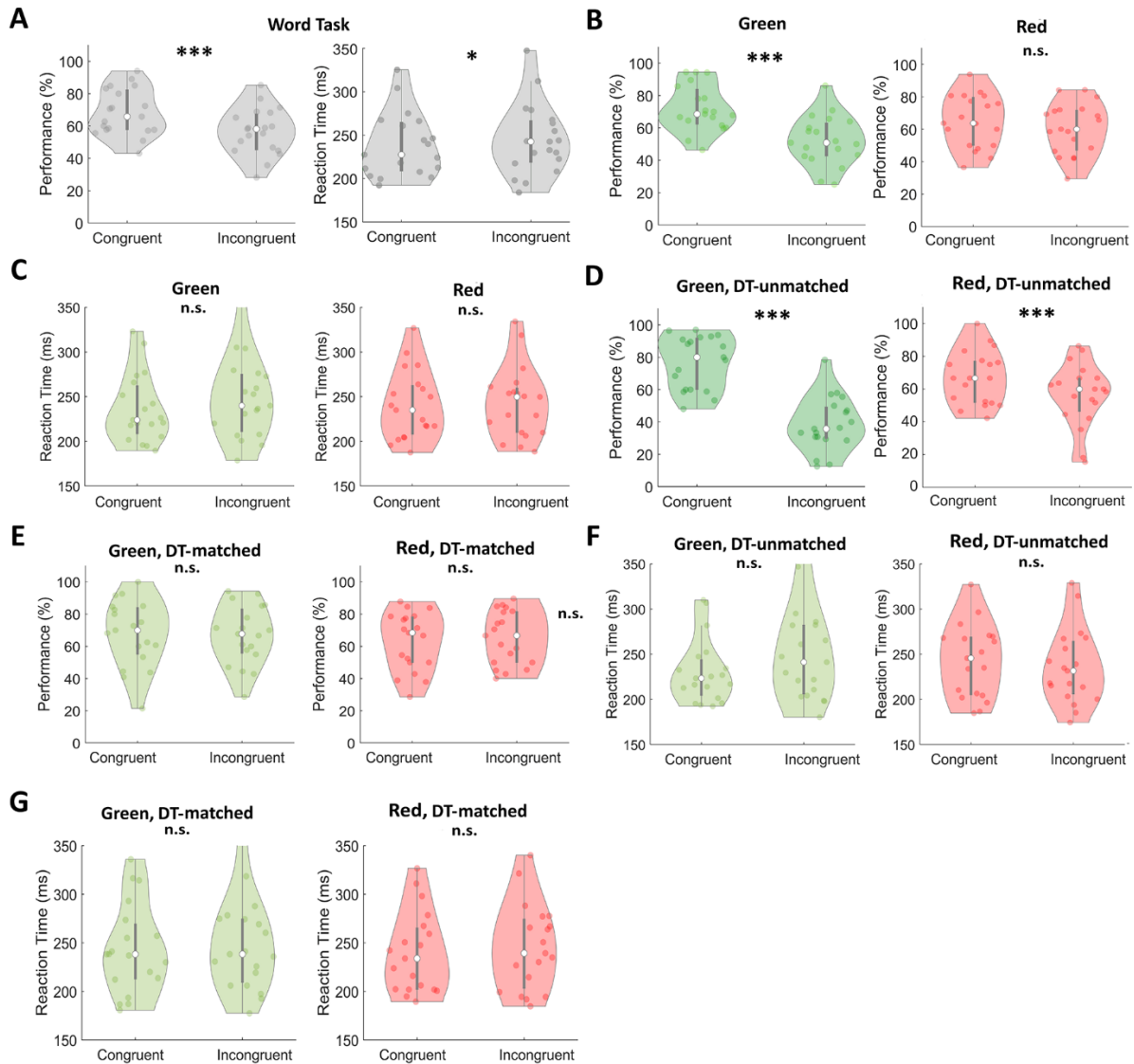
513



514

515 **Figure 3. Task specific performance and reaction times**

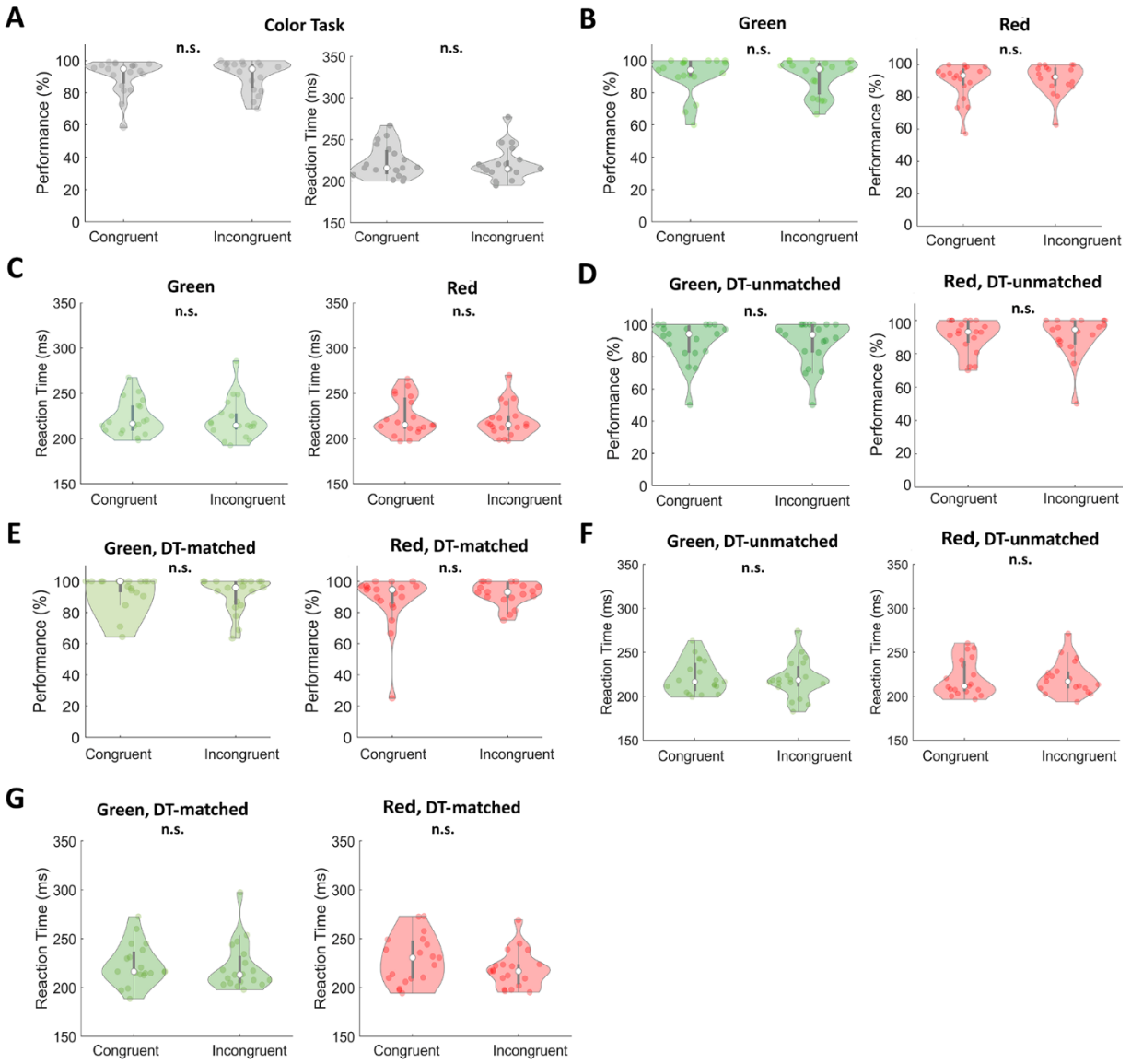
516 (A) Accuracy in the color task was significantly much higher than the word task. In the violin plot, the white dot in the middle is
 517 the median value and the thick black bar in the centre represents the interquartile range. The thin black line extended from it
 518 represents the upper (max) and lower (min) adjacent values in the data. *** denotes the significance level of $p < 0.001$ (Wilcoxon
 519 signed-rank test since the data did not follow a normal distribution (kstest, $p < 0.05$)). (B) Reaction times were significantly longer
 520 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
 521 normal distribution (kstest, $p < 0.05$)). (C) A significant positive correlation between reaction times and performance was observed
 522 for both tasks.



523
524

Figure 4. Stroop interference effect in the word task

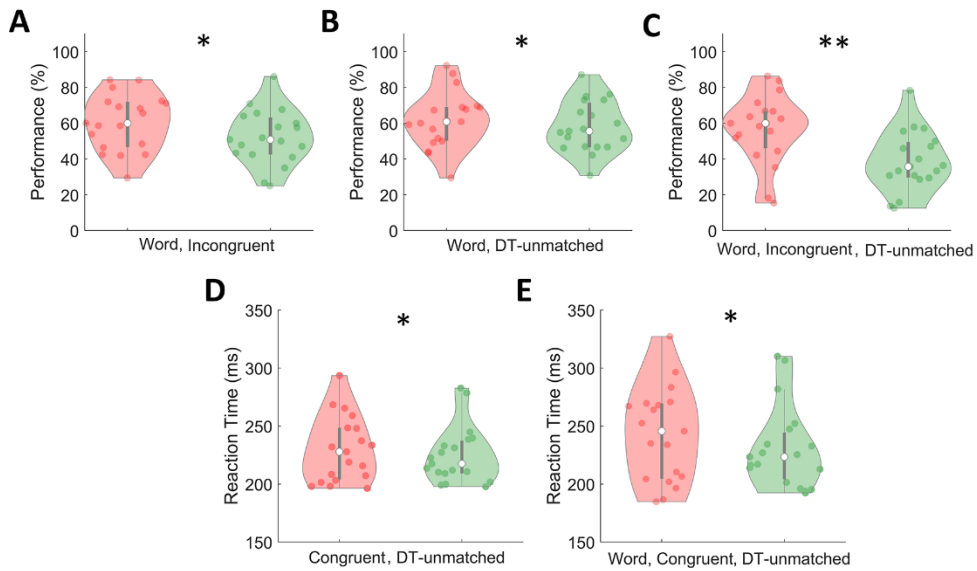
525 (A) Effects of Stroop interference on performance and reaction time (worse performance and slower reaction time in the
526 incongruent vs congruent condition). The interference effect was significant for both performance and reaction times in the
527 word task across both colors. (B) The Stroop interference effect was much stronger in the word task when the target was green (color).
528 (C) The Stroop interference effect on reaction times did not reach significance for either color targets individually. (D) The Stroop
529 interference effect on performance in the word task was strongest when the target was green (color) and the distractor was red
530 (color) (E) The Stroop interference effect on performance was absent when the target and the distractor did not match in color. (F-
531 G) The Stroop interference effect on reaction time did not reach a statistically significant level when targets were separated by
532 color.



533

534 **Figure 5. Stroop interference effect in the color task**

535 (A-G) The Stroop interference effect on performance and reaction time in the color task was not significant in any of the conditions.



536
537

Figure 6. Color-specific differences in the subjects' performance and reaction times

538 (A) Color-specific differences were only observed in the word task: incongruent conditions. Performance was significantly lower
 539 when the participants had to detect the green color target as compared to the red color target. Please note that in the incongruent
 540 conditions, the target word meaning and its color do not match (e.g., the “RED” word printed in green color). (B) Performance
 541 was significantly lower in the DT-unmatched condition. Participants made more errors when instructed to detect the green color
 542 target as compared to the red color target. (C) The most significant drop in performance was the conjunction of incongruent and
 543 DT-unmatched conditions. In this case, performance was again significantly lower when detecting the green color target. (D-E)
 544 Reaction times were significantly longer for red color versus green color targets in the congruent condition and when the distractor
 545 and the target were unmatched. This effect driven by the word task. Every single point represents one participant.

546

547

548

549

550

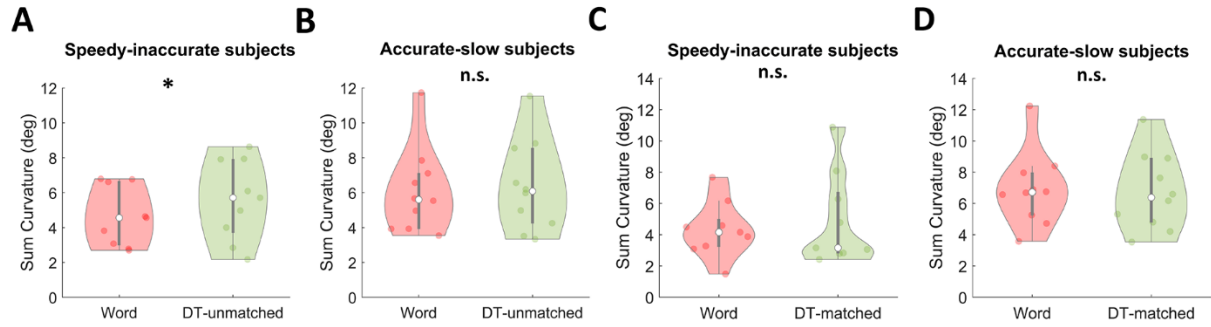
551

552

553

554

555



556

557

Figure 7. Color-specific effects on saccade sum curvature metrics

558

In the speedy subjects (A) and not the accurate ones (B), saccade trajectories were more curved in the word task for the green

559

(color) target when the distractor was red (color) ($p_{\text{Bonferroni-corrected}} < 0.05$, t-test). Color did not have any effect on saccade curvatures,

560

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).

561

562

563

564

565

566

567

568

569

570

571

572

573

574

575

576

577

578

579

580

581

582

583

584

585

586

587

588 **References**

- 589 Bichot, N. P., Rossi, A. F., & Desimone, R. (2005). Parallel and Serial Neural Mechanisms for Visual Search
590 in Macaque Area V4. *Science*, *308*(5721), 529–534. <https://doi.org/10.1126/science.1109676>
- 591 Blizzard, S., Fierro-Rojas, A., & Fallah, M. (2017). Response Inhibition Is Facilitated by a Change to Red Over
592 Green in the Stop Signal Paradigm. *Frontiers in Human Neuroscience*, *10*.
593 <https://doi.org/10.3389/fnhum.2016.00655>
- 594 Botvinick, M. M., Braver, T. S., Barch, D. M., Carter, C. S., & Cohen, J. D. (2001). Conflict monitoring and
595 cognitive control. *Psychol Rev*, *108*(3), 624–652.
- 596 Botvinick, M. M., Cohen, J. D., & Carter, C. S. (2004). Conflict monitoring and anterior cingulate cortex: An
597 update. *Trends in Cognitive Sciences*, *8*(12), 539–546. <https://doi.org/10.1016/j.tics.2004.10.003>
- 598 Cohen, J. Y., Crowder, E. A., Heitz, R. P., Subraveti, C. R., Thompson, K. G., Woodman, G. F., & Schall, J. D.
599 (2010). Cooperation and Competition among Frontal Eye Field Neurons during Visual Target
600 Selection. *The Journal of Neuroscience*, *30*(9), 3227–3238.
601 <https://doi.org/10.1523/JNEUROSCI.4600-09.2010>
- 602 Conway, B. R. (2018). The Organization and Operation of Inferior Temporal Cortex. *Annual Review of*
603 *Vision Science*, *4*, 381–402. <https://doi.org/10.1146/annurev-vision-091517-034202>
- 604 Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of*
605 *Neuroscience*, *18*, 193–222. <https://doi.org/10.1146/annurev.ne.18.030195.001205>
- 606 Doyle, M. C., & Walker, R. (2002). Multisensory interactions in saccade target selection: Curved saccade
607 trajectories. *Experimental Brain Research*, *142*(1), 116–130. [https://doi.org/10.1007/s00221-001-](https://doi.org/10.1007/s00221-001-0919-2)
608 [0919-2](https://doi.org/10.1007/s00221-001-0919-2)
- 609 Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away
610 from irrelevant distractors. *Experimental Brain Research*, *139*(3), 333–344.
611 <https://doi.org/10.1007/s002210100742>
- 612 Elliot, A. J. (2015). Color and psychological functioning: A review of theoretical and empirical work.
613 *Frontiers in Psychology*, *6*, 368. <https://doi.org/10.3389/fpsyg.2015.00368>
- 614 Elliot, A. J., Maier, M. A., Moller, A. C., Friedman, R., & Meinhardt, J. (2007). Color and psychological
615 functioning: The effect of red on performance attainment. *Journal of Experimental Psychology.*
616 *General*, *136*(1), 154–168. <https://doi.org/10.1037/0096-3445.136.1.154>
- 617 Fecteau, J. H., & Munoz, D. P. (2006). Saliency, relevance, and firing: A priority map for target selection.
618 *Trends in Cognitive Sciences*, *10*(8), 382–390. <https://doi.org/10.1016/j.tics.2006.06.011>
- 619 Fortier-Gauthier, U., Dell’acqua, R., & Jolicœur, P. (2013). The “red-alert” effect in visual search: Evidence
620 from human electrophysiology. *Psychophysiology*, *50*(7), 671–679.
621 <https://doi.org/10.1111/psyp.12050>
- 622 Frey, H.-P., Honey, C., & König, P. (2008). What’s color got to do with it? The influence of color on visual
623 attention in different categories. *Journal of Vision*, *8*(14), 6.1-17. <https://doi.org/10.1167/8.14.6>
- 624 Ghasemian, S., Vardanjani, M. M., Sheibani, V., & Mansouri, F. A. (2021). Color-hierarchies in executive
625 control of monkeys’ behavior. *American Journal of Primatology*, *83*(2), e23231.
626 <https://doi.org/10.1002/ajp.23231>

627 Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a
628 competitive integration model. *Journal of Experimental Psychology. Human Perception and*
629 *Performance*, 28(5), 1039–1054. <https://doi.org/10.1037//0096-1523.28.5.1039>

630 Hallett, P. E., & Adams, B. D. (1980). The predictability of saccadic latency in a novel voluntary oculomotor
631 task. *Vision Research*, 20(4), 329–339. [https://doi.org/10.1016/0042-6989\(80\)90019-X](https://doi.org/10.1016/0042-6989(80)90019-X)

632 Hermens, F., & Walker, R. (2012). The site of interference in the saccadic Stroop effect. *Vision Research*,
633 73, 10–22. <https://doi.org/10.1016/j.visres.2012.09.017>

634 Hodgson, T. L., Parris, B. A., Gregory, N. J., & Jarvis, T. (2009). The saccadic Stroop effect: Evidence for
635 involuntary programming of eye movements by linguistic cues. *Vision Research*, 49(5), 569–574.
636 <https://doi.org/10.1016/j.visres.2009.01.001>

637 Hurvich, L. M., & Jameson, D. (1957). An opponent-process theory of color vision. *Psychological Review*,
638 64, Part 1(6), 384–404. <https://doi.org/10.1037/h0041403>

639 Ishihara, S. (2006). *The Series of Plates Designed as a Test for Colour Deficiency (Concise Ed.)*, Tokyo:
640 Kanehara Trading Inc.

641 Kehoe, D. H., Aybulut, S., & Fallah, M. (2018). Higher order, multifeatureal object encoding by the
642 oculomotor system. *Journal of Neurophysiology*, 120(6), 3042–3062.
643 <https://doi.org/10.1152/jn.00834.2017>

644 Kehoe, D. H., & Fallah, M. (2017). Rapid accumulation of inhibition accounts for saccades curved away
645 from distractors. *Journal of Neurophysiology*, 118(2), 832–844.
646 <https://doi.org/10.1152/jn.00742.2016>

647 Kehoe, D. H., Rahimi, M., & Fallah, M. (2018). Perceptual Color Space Representations in the Oculomotor
648 System Are Modulated by Surround Suppression and Biased Selection. *Frontiers in Systems*
649 *Neuroscience*, 12. <https://doi.org/10.3389/fnsys.2018.00001>

650 Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: Towards the underlying neural circuitry.
651 *Human Neurobiology*, 4(4), 219–227.

652 Kugler, G., 't Hart, B. M., Kohlbecher, S., Bartl, K., Schumann, F., Einhäuser, W., & Schneider, E. (2015).
653 Visual Search in the Real World: Color Vision Deficiency Affects Peripheral Guidance, but Leaves
654 Foveal Verification Largely Unaffected. *Frontiers in Human Neuroscience*, 9.
655 <https://doi.org/10.3389/fnhum.2015.00680>

656 Laird, A. R., McMillan, K. M., Lancaster, J. L., Kochunov, P., Turkeltaub, P. E., Pardo, J. V., & Fox, P. T. (2005).
657 A comparison of label-based review and ALE meta-analysis in the Stroop task. *Human Brain*
658 *Mapping*, 25(1), 6–21. <https://doi.org/10.1002/hbm.20129>

659 Lee, H.-W., Legge, G. E., & Ortiz, A. (2003). Is word recognition different in central and peripheral vision?
660 *Vision Research*, 43(26), 2837–2846. [https://doi.org/10.1016/s0042-6989\(03\)00479-6](https://doi.org/10.1016/s0042-6989(03)00479-6)

661 Lindsey, D. T., Brown, A. M., Reijnen, E., Rich, A. N., Kuzmova, Y. I., & Wolfe, J. M. (2010). Color channels,
662 not color appearance or color categories, guide visual search for desaturated color targets.
663 *Psychological Science*, 21(9), 1208–1214. <https://doi.org/10.1177/0956797610379861>

664 Martin, P. R., Lee, B. B., White, A. J., Solomon, S. G., & Rüttiger, L. (2001). Chromatic sensitivity of ganglion
665 cells in the peripheral primate retina. *Nature*, 410(6831), 933–936.
666 <https://doi.org/10.1038/35073587>

667 McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: Spatial
668 separation and symmetry effects. *Experimental Brain Research*, *155*(3), 320–333.
669 <https://doi.org/10.1007/s00221-003-1729-5>

670 Mehta, R., & Zhu, R. J. (2009). Blue or red? Exploring the effect of color on cognitive task performances.
671 *Science (New York, N.Y.)*, *323*(5918), 1226–1229. <https://doi.org/10.1126/science.1169144>

672 Nee, D. E., Wager, T. D., & Jonides, J. (2007). Interference resolution: Insights from a meta-analysis of
673 neuroimaging tasks. *Cognitive, Affective, & Behavioral Neuroscience*, *7*(1), 1–17.
674 <https://doi.org/10.3758/CABN.7.1.1>

675 Osorio, D., & Vorobyev, M. (1996). Colour Vision as an Adaptation to Frugivory in Primates. *Proceedings:*
676 *Biological Sciences*, *263*(1370), 593–599. JSTOR.

677 Pomerleau, V. J., Fortier-Gauthier, U., Corriveau, I., Dell'Acqua, R., & Jolicœur, P. (2014). Colour-specific
678 differences in attentional deployment for equiluminant pop-out colours: Evidence from
679 lateralised potentials. *International Journal of Psychophysiology: Official Journal of the*
680 *International Organization of Psychophysiology*, *91*(3), 194–205.
681 <https://doi.org/10.1016/j.ijpsycho.2013.10.016>

682 Ramezanpour, H., & Fallah, M. (2022). The role of temporal cortex in the control of attention. *Current*
683 *Research in Neurobiology*, *3*, 100038. <https://doi.org/10.1016/j.crneur.2022.100038>

684 Regan, B. C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage
685 and the evolution of primate colour vision. *Philosophical Transactions of the Royal Society of*
686 *London. Series B*, *356*(1407), 229–283. <https://doi.org/10.1098/rstb.2000.0773>

687 Roberts, K. L., & Hall, D. A. (2008). Examining a supramodal network for conflict processing: A systematic
688 review and novel functional magnetic resonance imaging data for related visual and auditory
689 Stroop tasks. *Journal of Cognitive Neuroscience*, *20*(6), 1063–1078.
690 <https://doi.org/10.1162/jocn.2008.20074>

691 Ross, L. E., & Ross, S. M. (1980). Saccade latency and warning signals: Stimulus onset, offset, and change
692 as warning events. *Perception & Psychophysics*, *27*(3), 251–257.
693 <https://doi.org/10.3758/bf03204262>

694 Saini, H., Jordan, H., & Fallah, M. (2021). Color Modulates Feature Integration. *Frontiers in Psychology*, *12*,
695 2274. <https://doi.org/10.3389/fpsyg.2021.680558>

696 Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., & Leventhal, A. G.
697 (1998). Signal Timing Across the Macaque Visual System. *Journal of Neurophysiology*, *79*(6), 3272–
698 3278. <https://doi.org/10.1152/jn.1998.79.6.3272>

699 Schwedhelm, P., Baldauf, D., & Treue, S. (2020). The lateral prefrontal cortex of primates encodes stimulus
700 colors and their behavioral relevance during a match-to-sample task. *Scientific Reports*, *10*(1),
701 4216. <https://doi.org/10.1038/s41598-020-61171-3>

702 Sheliga, B. M., Craighero, L., Riggio, L., & Rizzolatti, G. (1997). Effects of spatial attention on directional
703 manual and ocular responses. *Experimental Brain Research*, *114*(2), 339–351.
704 <https://doi.org/10.1007/pl00005642>

705 Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental*
706 *Brain Research*, *98*(3), 507–522. <https://doi.org/10.1007/BF00233988>

707 Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain*
708 *Research*, *105*(2), 261–275. <https://doi.org/10.1007/BF00240962>

709 Smit, A. C., & Van Gisbergen, J. A. M. (1990). An analysis of curvature in fast and slow human saccades.
710 *Experimental Brain Research*, 81(2), 335–345. <https://doi.org/10.1007/BF00228124>

711 Smit, A. C., Van Opstal, A. J., & Van Gisbergen, J. A. M. (1990). Component stretching in fast and slow
712 oblique saccades in the human. *Experimental Brain Research*, 81(2), 325–334.
713 <https://doi.org/10.1007/BF00228123>

714 Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*,
715 18(6), 643–662. <https://doi.org/10.1037/h0054651>

716 Tamura, H., & Tanaka, K. (2001). Visual Response Properties of Cells in the Ventral and Dorsal Parts of the
717 Macaque Inferotemporal Cortex. *Cerebral Cortex*, 11(5), 384–399.
718 <https://doi.org/10.1093/cercor/11.5.384>

719 Tchernikov, I., & Fallah, M. (2010). A Color Hierarchy for Automatic Target Selection. *PLoS ONE*, 5(2).
720 <https://doi.org/10.1371/journal.pone.0009338>

721 Tipper, S. P., Howard, L. A., & Paul, M. A. (2001). Reaching affects saccade trajectories. *Experimental Brain*
722 *Research*, 136(2), 241–249. <https://doi.org/10.1007/s002210000577>

723 Treisman, A. (1985). Preattentive processing in vision. *Computer Vision, Graphics, and Image Processing*,
724 31(2), 156–177. [https://doi.org/10.1016/S0734-189X\(85\)80004-9](https://doi.org/10.1016/S0734-189X(85)80004-9)

725 Tsotsos, J. K. (2011). *A Computational Perspective on Visual Attention*. MIT Press.

726 Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us.
727 *Neuroscience and Biobehavioral Reviews*, 30(5), 666–679.
728 <https://doi.org/10.1016/j.neubiorev.2005.12.001>

729 Viviani, P., Berthoz, A., & Tracey, D. (1977). The curvature of oblique saccades. *Vision Research*, 17(5),
730 661–664. [https://doi.org/10.1016/0042-6989\(77\)90143-2](https://doi.org/10.1016/0042-6989(77)90143-2)

731 Vogels, R., & Orban, G. A. (1994). Activity of inferior temporal neurons during orientation discrimination
732 with successively presented gratings. *Journal of Neurophysiology*, 71(4), 1428–1451.
733 <https://doi.org/10.1152/jn.1994.71.4.1428>

734 Walker, R., Deubel, H., Schneider, W. X., & Findlay, J. M. (1997). Effect of remote distractors on saccade
735 programming: Evidence for an extended fixation zone. *Journal of Neurophysiology*, 78(2), 1108–
736 1119. <https://doi.org/10.1152/jn.1997.78.2.1108>

737 Walker, R., & McSorley, E. (2008). The Influence of Distractors on Saccade-Target Selection: Saccade
738 Trajectory Effects. *Journal of Eye Movement Research*, 2(3), Article 3.
739 <https://doi.org/10.16910/jemr.2.3.7>

740 Weaver, M. D., Lauwereyns, J., & Theeuwes, J. (2011). The effect of semantic information on saccade
741 trajectory deviations. *Vision Research*, 51(10), 1124–1128.
742 <https://doi.org/10.1016/j.visres.2011.03.005>

743 White, B. J., Theeuwes, J., & Munoz, D. P. (2012). Interaction between visual- and goal-related neuronal
744 signals on the trajectories of saccadic eye movements. *Journal of Cognitive Neuroscience*, 24(3),
745 707–717. https://doi.org/10.1162/jocn_a_00162

746 Wolfe, J. M. (2010). Visual search. *Current Biology: CB*, 20(8), R346–349.
747 <https://doi.org/10.1016/j.cub.2010.02.016>

748 Yantis, S. (1993). Stimulus-driven attentional capture and attentional control settings. *Journal of*
749 *Experimental Psychology: Human Perception and Performance*, 19(3), 676–681.
750 <https://doi.org/10.1037/0096-1523.19.3.676>

