



More than just channeling: The role of subcortical mechanisms in executive functions – Evidence from the Stroop task

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ABSTRACT

The literature has long emphasized the role of the cerebral cortex in executive functions. Recently, however, several researchers have suggested that subcortical areas might also be involved in executive functions. The current study explored the possibility that subcortical mechanisms have a functional role in adaptive resolution of Stroop interference. We asked 20 participants to complete a cued task-switching Stroop task with variable cue-target intervals (CTI). Using a stereoscope, we manipulated which eye was shown the relevant dimension and which was shown the irrelevant dimension. This technique allowed us to examine the involvement of monocularly segregated – subcortical – regions of the visual processing stream. The interference effect was modulated by this eye-of-origin manipulation in the 0 CTI condition. This finding provides a novel indication for the notion that subcortical regions have a functional role in the resolution of Stroop interference. This indication suggests that cortical regions are not solely involved and that a dynamic interaction between cortical and subcortical regions is involved in executive functions.

1. Introduction

Executive functions serve as an umbrella term for referring to a set of abilities required to guide behavior flexibly toward a goal, freeing individuals from the constraints of automaticity (Banich, 2009; Miller & Cohen, 2001; Miyake et al., 2000). One very common task used to study executive functions in the laboratory is the Stroop task. In the classic version of the Stroop task, participants view color words printed in a color not denoted by the name. Participants are requested to name the color of the ink as fast as possible while ignoring the meaning of the word. Reaction time (RT) is commonly prolonged in incongruent trials (e.g., RED printed in blue ink) compared with neutral trials (e.g., XXXX printed in blue ink) due to the interference caused by the incongruent semantic information of the word's meaning. This effect is known as the interference effect (MacLeod, 1991). In congruent trials, when both word color and word meaning are the same (e.g., BLUE printed in blue ink), RT is commonly shorter than in neutral trials. This effect, known as the facilitation effect, is smaller and more fragile than the interference effect (Dalrymple-Alford & Budayr, 1966; Kalanthroff & Henik, 2013). Both the interference and the facilitation effects indicate that word reading is an obligatory process that affects the performance on this task, and that executive functions are required

to suppress the task-irrelevant information (Kalanthroff, Goldfarb, & Henik, 2013). As Stroop showed in his original (1935) paper, the interference effect is not present when participants are asked to respond to the written word and ignore the color of the ink (MacLeod, 1991; Stroop, 1935). Specifically, it has been shown that word reading is faster than color naming (reading the word “RED” is faster than naming the color of a red patch). This finding led researchers to conclude that reading is a more automatic process than color naming (Cohen, Dunbar, & McClelland, 1990; MacLeod, 1991; Stroop, 1935). The word and the color can also be presented as spatially separated from each other. Studies have long employed a spatially separated version of the Stroop task, and consistently found the same pattern of results as in the spatially combined Stroop task. Furthermore, widespread cognitive batteries have included the spatially separated Stroop task version, and the validation of this task has been demonstrated (e.g., Dwolatzky et al., 2003; Dyer, 1973; Goldfarb & Henik, 2006; Luo, 1999).

With respect to neural processes, the literature has long emphasized the role of the cerebral cortex in executive functions (Banich, 2009; Barch, Braver, et al., 2001; Bush, Luu, & Posner, 2000; Duncan & Owen, 2000; Fan, McCandliss, Flombaum, Thomas, & Posner, 2001; MacDonald, Cohen, Stenger, & Carter, 2000; Stuss & Alexander, 2007;

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Paus, Petrides, Evans, & Meyer, 1993; Picard & Strick, 1996). Several dissociable cortical brain networks were suggested to underlie executive functions. The dorsal attention network (Corbetta & Shulman, 2002), including parts of the intraparietal cortex and superior frontal cortex, was suggested to be involved in preparing and applying goal-directed selection to stimuli and responses. The fronto-parietal network (e.g., Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008), including the dorsolateral prefrontal cortex and intraparietal sulcus, is thought to be involved in task switching, initiation, and adjustments within trials. The cingulo-opercular network was suggested to be involved in stabilizing background maintenance for task performance as a whole (e.g., Dosenbach et al., 2008; Petersen & Posner, 2012). One influential model of executive functions suggests that the anterior cingulate cortex (ACC) monitors conflict situations and signals this information, via the magnitude of its activity, to different structures in the frontal cortex that are involved in conflict resolution (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter, Botvinick, & Cohen, 1999; MacDonald et al., 2000). In addition, a specific functional organization of the prefrontal cortex (PFC) in executive functions was also previously studied. Stuss and Alexander (2007) suggested that while initiating and sustaining a response relies on medial frontal regions, task setting relies on left lateral regions, and monitoring relies on right lateral regions of the PFC. Banich (2009) suggested that executive functions involve a temporal cascade of selection processes that are implemented in the PFC. The rostro-caudal axis of PFC has been claimed to support a control hierarchy (for a review see Badre, 2008). As can be seen, the cortex has received substantial attention in the literature on executive functions while subcortical regions are traditionally thought to be irrelevant to executive processes.

Until recently, the role of subcortical regions was considered to be merely channeling information to the cortex. However, in recent years, accumulating evidence suggests that subcortical regions may also be involved in executive functions. First, evolutionarily older species (e.g., fish and amphibians) lack a cortex and yet often face the need to inhibit or suppress irrelevant information in order to survive. Hence, executive functions are crucial to their survival and are most likely governed by subcortical regions. In addition, recent evidence supports the involvement of subcortical regions in attention processes. For example, in a recent study we showed that archer fish – a species that lacks a fully developed cortex – are able to perform a reflexive attention task and demonstrate both facilitation and inhibition of return (Gabay, Leibovich, Ben-Simon, Henik, & Segev, 2013). Another piece of evidence for the involvement of subcortical regions in executive functions comes from study of patients with ischemic vascular disease. This study demonstrated an association between subcortical regions and a decline in executive function (e.g., Kramer, Reed, Mungas, Weiner, & Chui, 2002). Furthermore, a recent review suggests a mechanistic model in which executive functions are underlain by an interaction between the PFC and the subcortical basal ganglia (BG; Hazy, Frank, & O'Reilly, 2007). Another piece of evidence for the involvement of subcortical structures comes from a study that examined large-scale data from 5809 human-imaging studies. This work revealed that the pattern of cortical activation reliably predicts activation in striatal (subcortical) regions. The authors conclude that these results confirm an overlooked involvement of the posterior caudate nucleus in executive functions (Pauli, O'Reilly, Yarkoni, & Wager, 2016). As far as we know, no previous study has examined the involvement of subcortical regions in executive functions using behavioral tasks.

In humans, the involvement of subcortical regions in cognitive processes can be studied using a stereoscope, a device that allows visual information to be displayed to each eye separately. This involvement relies on the fact that visual input is segregated monocularly until it reaches binocular striate and extrastriate regions (Horton, Dagi, McCrane, & de Monasterio, 1990; Menon, Ogawa, Strupp, & Uğurbil, 1997). Thus, subcortical regions are eye-dependent while higher cortical regions are mostly insensitive to the eye-of-origin of the visual

information. As such, presenting different visual information to each eye separately is an effective method for isolating the involvement of monocular (mostly subcortical) versus binocular (mostly cortical) neural channels. Thus, given that dividing the visual information is a manipulation that affects subcortical brain areas, if these areas are functionally involved in a specific cognitive task, then dividing the visual information will affect the performance on this task. By contrast, if subcortical areas are not involved in the performance on a specific cognitive task (e.g., if they only channel information to higher brain areas), then segregating the visual information to different eyes will not affect the performance on that specific task. For example, this technique was previously used to explore the involvement of subcortical structures in different cognitive processes such as perceptual learning (Karni & Sagi, 1991), spatial attention (Gabay & Behrmann, 2014; Saban, Sekely, Klein, & Gabay, 2016; Self & Roelfsema, 2010) and multisensory perception (Batson, Beer, Seitz, & Watanabe, 2011). To the best of our knowledge, the involvement of subcortical regions in the Stroop (color-naming) and reverse-Stroop (word-reading) tasks has never been directly investigated in humans.

The goal of the present study is to explore the involvement of lower-level, subcortical, monocularly segregated structures in executive functions, and specifically in the Stroop task. Based on the studies reviewed above, we hypothesize that subcortical regions will be found to be involved in the resolution processes of Stroop interference. To heighten the conflict in the Stroop task, we administered the color-word cued-task-switching paradigm. In this paradigm, which has been shown to result in larger Stroop effects, participants are asked to identify either the color or the word meaning of Stroop stimuli while frequently switching between the two tasks (e.g., Allport, Styles, & Hsieh, 1994; Gilbert & Shallice, 2002; Kalanthroff & Henik, 2014; Ruff, Woodward, Laurens, & Liddle, 2001; Yeung & Monsell, 2003). In addition, we manipulated the interval between the task cue and the target Stroop stimulus (i.e., cue – target interval, CTI; Meiran, 1996) such that in half of the trials the CTI was 0 ms. This was done to ensure that CTI would not be used for preparation (Kalanthroff & Henik, 2014) that is likely to involve recruitment of cortical regions (e.g., Coull, Frith, Büchel, & Nobre, 2000). As in some of the above-referenced studies, we used the stereoscope to probe the involvement of the lower-level (eye-specific stage) of the visual processing stream in executive process underlying the Stroop task. In the different-eye condition, different monocular channels process the word and the color information. Hence, the ability of monocular (subcortical) regions to detect the relevant dimension (without interference from the irrelevant dimension) should be enhanced in this condition. Accordingly, we predict that the interference from the irrelevant word will be greater in the same-eye condition (both ink color and written word are presented to the same monocular channel) than in the different-eye condition (ink color is presented to one eye while the word is presented to the other eye). In addition, we predict that this effect will be limited to the CTI = 0 condition, as elongation of CTI will increase the involvement of cortical regions and might provide enough time for more strategic processes to influence performance.

2. Methods

2.1. Participants

Twenty participants (mean age 25.2, standard deviation 4.21; 10 females) volunteered to participate in the study in exchange for payment or course credit. All participants had normal or corrected-to-normal vision, right-handed dominance, no history of attention deficit or dyslexia, and all were native Hebrew speakers. The University of Haifa Institutional Research Board approved the study.

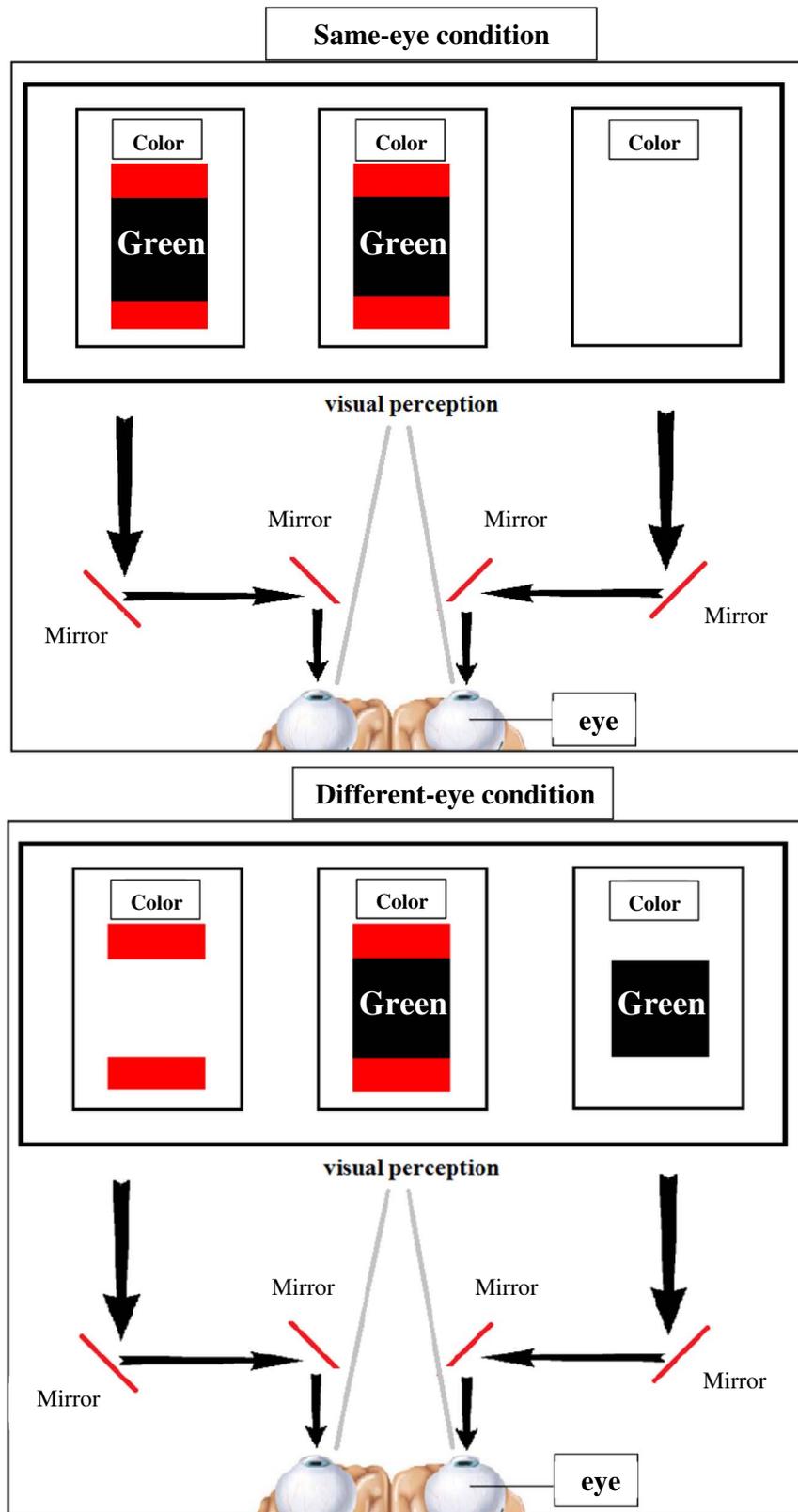


Fig. 1. Schematic illustration of the experimental apparatus and visual pathways from the screen to the eyes. Upper panel shows same-eye condition, in which visual information is presented to the same eye; lower panel shows different-eye condition, in which visual information is presented to different eyes.

2.2. Apparatus and software

Data collection and stimuli presentation were controlled using an HP Z200 computer, with a Windows 7 operating system. Stimuli were presented on a Samsung LCD monitor (model S24C650PL) with a

resolution of 1680 × 1050. Responses were made on a DELL Keyboard (model RT7D50 SK-8115). The computer monitor was positioned 57 cm in front of a stereoscope (model ScreenScope LCD SA200LCD), so that the participant's direct view of the monitor was blocked (see Fig. 1). Each eye was presented with half of the screen presentation.

2.3. Stimuli and procedure

Participants were shown a word stimulus (GREEN, RED, or XXXX in Hebrew) in between two peripheral color patches (red, green, or white). The appearance of the meaningless letter string (XXXX) or the two white patches served as neutral conditions for the color and word tasks, respectively (see Kalanthroff & Henik, 2014). There were eight combinations of words and color patches: two congruent, four neutrals (two for each task), and two incongruent. The different congruency conditions were equally frequent and randomly presented. Prior to the onset of the target stimulus, a word cue (“COLOR” vs. “WORD” in Hebrew) was presented, signaling the relevant task in the upcoming trial - identifying the color or the word (while ignoring the irrelevant dimension; see Fig. 1). Using the stereoscope, we manipulated which eye was shown the relevant dimension and which eye was shown the irrelevant dimension (see Fig. 1). In the different-eye condition, the color patches were shown to one eye while the word was shown to the other eye. In the same-eye condition, the entire stimulus was shown to one eye while a black screen was shown to the second eye. The word cue was shown to both eyes simultaneously in all conditions. The experiment included 40 practice trials (which were not analyzed) and 448 experimental trials. During practice, participants received feedback on accuracy and RT. Before the training block, we conducted two tests in order to make sure that the participants' percept was well-fused: first, we asked participants whether they saw a single rectangle or two overlapping rectangles when looking through the stereoscope (note that two rectangles were presented throughout the task, one to each eye, and all stimuli were presented inside those rectangles). If participants reported seeing two overlapping rectangles the stereoscope was calibrated in order to achieve a fused percept of a single rectangle. Second, participants were also instructed to close one eye (this was done for each eye separately) and asked if they saw a full rectangle (to make sure that the visual display was full for each eye separately). If participants reported seeing only a part of the rectangle, the stereoscope was recalibrated. These tests assured us that the percept was well-fused during the task. Each trial started with a 1000 ms fixation (a white plus sign at the center of a black screen), followed by a task cue. The interval between the task cue and the target stimulus (cue-target interval) varied between trials (0 vs. 1500 ms). After that, the Stroop target stimulus was presented for 3000 ms or until the participant pressed the key. Participants responded to the color task using their right hand by pressing the “7” and “9” keys with their index and middle fingers, respectively. Participants responded to the word task using their left hand by pressing the “M” and “B” keys with their index and middle fingers, respectively. Keys were marked with colored stickers. Note that in 64 trials, the relevant dimension was comprised of a natural stimulus (i.e., neutral XXXX when WORD was the relevant task or a white color patch when COLOR was the relevant task). Hence, there was no possible response, and participants were instructed not to respond in those trials.

3. Results

RT was calculated from the appearance of the Stroop stimulus to the response. Mean RTs of correct responses were calculated for each participant in each condition. Trials in which RT was longer than 2500 ms or shorter than 100 ms were excluded from the analyses (16%). Accuracy rate was 89% across all experimental trials. See Table 1 for a detailed description of accuracy rates for the different conditions. No indication of a speed-accuracy tradeoff was found. Rather, as expected, responses to incongruent conditions were less accurate than responses to neutral conditions.

In order to investigate our a-priori predictions, we carried out a four-way analysis of variance (ANOVA) with repeated measures on RT data, with CTI (0 vs. 1500 ms), congruency (congruent, neutral, vs. incongruent), eye-of-origin (same vs. different), and task (color vs.

Table 1

Reaction time (standard error) [% accuracy] for the different conditions.

		Same-eye		Different-eye	
		Color task	Word task	Color task	Word task
CTI = 0 ms	Congruent	1190 (27)	1280 (26)	1194 (29)	1248 (25)
		[93]	[91]	[91]	[92]
	Neutral	1190 (26)	1261 (24)	1196 (27)	1274 (25)
		[92]	[96]	[92]	[96]
	Incongruent	1312 (32)	1294 (25)	1231 (30)	1334 (27)
		[84]	[90]	[83]	[92]
CTI = 1500 ms	Congruent	862 (27)	951 (27)	876 (26)	1000 (31)
		[95]	[92]	[94]	[93]
	Neutral	887 (27)	1004 (27)	883 (24)	1002 (25)
		[93]	[95]	[94]	[97]
	Incongruent	964 (31)	1039 (26)	951 (32)	1068 (28)
		[89]	[93]	[88]	[93]

word) as within-subjects factors. Replicating previous findings, the main effects of task, CTI, and congruency were significant with moderate to very large effect sizes ($F(1,19) = 43.99$, $P < 0.001$, $\eta_p^2 = 0.69$; $F(1,19) = 177.18$, $P < 0.001$, $\eta_p^2 = 0.90$; $F(2,38) = 6.39$, $P < 0.01$, $\eta_p^2 = 0.25$ for task, CTI, and congruency, respectively). The main effect of eye-of-origin was not significant ($F(1,19) = 0.17$, $P = 0.68$). Planned comparisons revealed a significant interference effect (i.e., incongruent RT > neutral RT) but no significant facilitation effect (i.e., neutral RT > congruent RT; $F(1,19) = 7.11$, $P < 0.05$, $\eta_p^2 = 0.26$; $F(1,19) = 0.22$, $P = 0.64$ for interference and facilitation effects, respectively). The four-way interaction was significant ($F(2,38) = 3.57$, $P < 0.05$, $\eta_p^2 = 0.15$).

To further investigate the four-way interaction we conducted two separate three-way ANOVAs for each CTI condition, with task, congruency, and eye-of-origin as within-subjects factors. A significant interaction was found only for the 0 ms CTI condition ($F(2, 38) = 5.38$, $P < 0.01$, $\eta_p^2 = 0.22$; $F(2, 38) = 0.27$, $P = 0.76$; for the 0 and 1500 CTI, respectively). To further investigate this interaction in the 0 ms CTI condition with respect to the Stroop effects of facilitation and interference, we conducted separate two-way ANOVAs for each of the different tasks (color and word), with eye-of-origin and congruency as within-subjects factors. For the facilitation effect we found that the two-way interaction between congruency (congruent vs. neutral) and eye-of-origin was not significant for both the color task and the word task ($F(1,19) = 0.01$, $P = 0.89$; $F(1,19) = 1.87$, $P = 0.19$; for color and word tasks, respectively). However, for the interference effect we found that the two-way interaction between congruency (incongruent vs. neutral) and eye-of-origin was significant for the color task but not for the word task ($F(1, 19) = 4.66$, $P < 0.05$, $\eta_p^2 = 0.2$; $F(1, 19) = 1.78$, $P = 0.2$; for color and word tasks, respectively). As can be seen in Fig. 2 and Table 1, these effects indicate a larger interference effect on the same-eye condition compared to the different-eye condition, but only in the color task. To further investigate the origin of this effect, we then conducted three planned comparisons in the color task to compare congruent RT, neutral RT, and incongruent RT between the eye-of-origin conditions (same eye vs. different eye). These analyses revealed longer RTs for incongruent trials in the same-eye condition compared to the different-eye condition ($T(19) = 3.27$, $P < 0.01$, Cohen's $d = 0.61$) but no differences between the two eye-of-origin conditions for neutral RT and congruent RT ($T(19) = 0.38$, $P = 0.7$; $T(19) = 0.26$, $P = 0.79$) for neutral and congruent RT, respectively).

4. Discussion

The aim of the present study was to test whether the interference and facilitation effects can be modulated by eye-of-origin manipulation. We administered a combined two-color manual Stroop task in a cued task-switching design with variable CTIs. The results showed robust main effects of task, CTI, and congruency. Notably, similar to previous

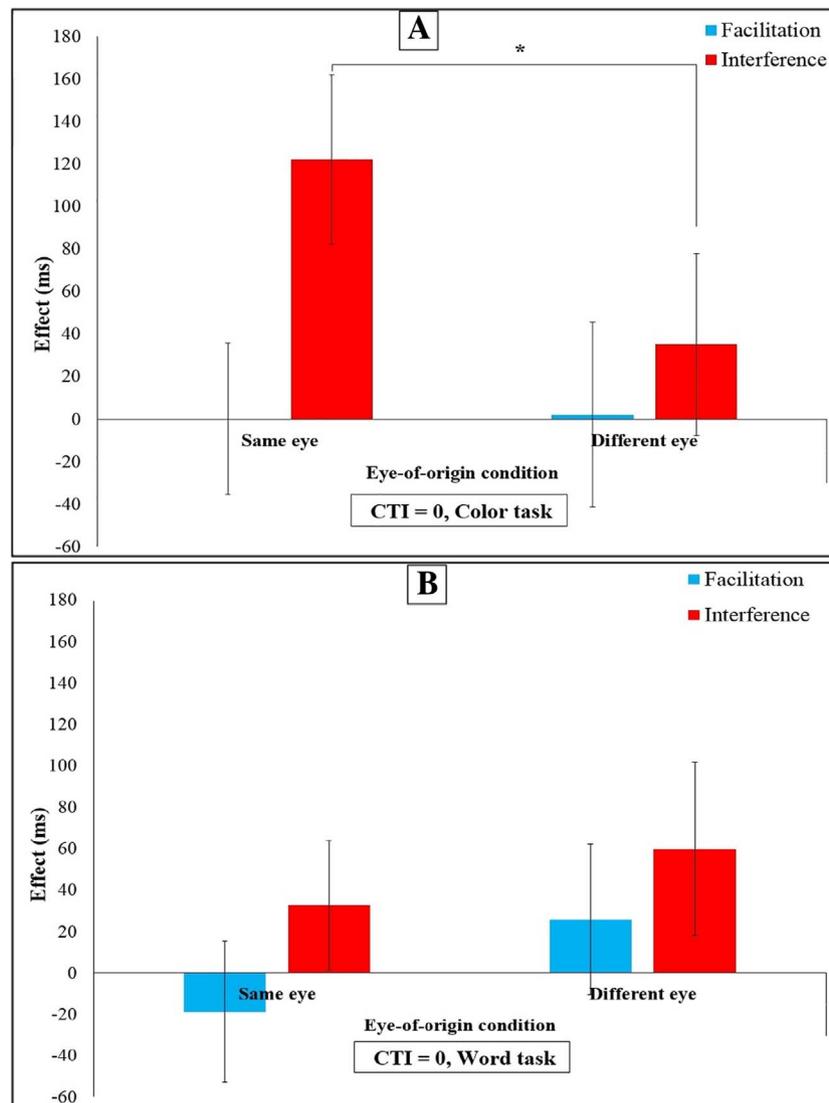


Fig. 2. Interference (incongruent RT – neutral RT) and facilitation (neutral RT – congruent RT) effects as a function of each eye-of-origin, in the color (see panel A) and word (see panel B) tasks, in the 0 CTI condition. Error bars represent one standard error from the mean using a method to compute the error bars in a within-subject design (Cousineau, 2005). * = significant at $P < 0.05$.

studies that used a similar task-switching Stroop task, we found a large interference effect but no facilitation effect—a pattern that was previously attributed to increased task conflict in the task-switching paradigm (see Goldfarb & Henik, 2007; Kalanthroff & Henik, 2014). We also found an interesting interaction between CTI, eye-of-origin, and congruency in the color task. Specifically, in the 1500 ms CTI condition, eye-of-origin did not have any effect on performance. Most importantly, in the 0 ms CTI condition, results yielded a much smaller interference effect in the different-eye condition compared to the same-eye condition. It is important to mention that our findings were limited to the color task (the Stroop task). A better understanding of control processes in the word task requires future research.

Moreover, one interesting question is how monocular (subcortical) channels are involved in the processing of word and color information? Indeed, the results of this study reflect a surprising finding. Recent findings suggest that both subcortical and cortical structures are involved in color representation (Goddard, Mannion, McDonald, Solomon, & Clifford, 2010). Another recent study reports that subcortical mechanisms can affect basic reading processes (Hornickel, Skoe, Nicol, Zecker, & Kraus, 2009). In addition, it was recently demonstrated that reading can be accomplished even without conscious perception (e.g., Sklar et al., 2012), which might imply the involvement of lower

portions of the visual system. Furthermore, a recent study (Zemmoura, Herbet, Moritz-Gasser, & Duffau, 2015), investigated reading abilities of patients during surgery of diffuse low-grade gliomas (LGG). The authors concluded that (i) the inferior temporal gyrus (ITP) and its subcortical white matter should be involved in a reading task and (ii) further studies should consider this region as an important anatomical pathway to the visual word form area (VWFA). Hence, it is possible that this subcortical region has a functional role in reading and hence in the interference of words reading in the Stroop task. It seems that the involvement of subcortical regions in executive functions is poorly documented. The examination of subcortical regions' contribution to executive functions has focused mainly on patients with degenerative disorders of the basal ganglia, such as PD or HD (for a review see Heyder, Suchan, & Daum, 2004). The contribution of the basal ganglia has been demonstrated in selection and inhibition of competing cognitive and motor programs. Hence, it is possible that the basal ganglia, a subcortical region, has a functional role also in the Stroop task. It is left to future research to examine a more well-defined neuro-anatomical mechanism underlying these observed effects.

Previous studies have also suggested that cortical involvement facilitates cognitive expectations (e.g., Coull et al., 2000). Since CTI can be used to recruit control by building specific expectations

(Kalanthoff & Henik, 2014), in the present study participants were able to use the long preparation time to reduce dependence on subcortical regions and to increase the involvement of cortical regions, regardless of the experimental eye-of-origin condition. In the 0 ms CTI condition, the cognitive system had no time to recruit control, and preparation processes were blocked. Therefore, the effect of the manipulation to lower subcortical areas administered via the stereoscope was masked in the long CTI condition and visible only in the 0 ms CTI condition. This conclusion is consistent with previous suggestions regarding the influence of CTI on performance (Kalanthoff & Henik, 2014; Meiran, 1996). Interestingly, to examine whether our findings vary parametrically from a 0 ms CTI to a longer CTI, further investigations of the effect at different CTIs could provide additional insight into the temporal dynamic of the effect. Importantly, our decision to use 0 ms and 1500 ms as CTIs was based on previous studies showing that smaller differences (e.g., 0 ms and 300 ms) do not induce a significantly different effect (e.g., Kalanthoff & Henik, 2014).

In the 0 ms CTI condition, when participants performed the color task, the interference effect was significantly modulated by the eye-of-origin manipulation. That is, the interference effect was greater in the same-eye condition than in the different-eye condition. When the two dimensions (color and word) were segregated into different monocular channels, the competition between the dimensions was abolished at lower monocular regions and a significantly smaller interference was evident. By contrast, when the two dimensions were presented in a single monocular channel, the competition between the dimensions influenced performance. This pattern of results indicates the involvement of low-level parts of the visual stream in conflict resolution when the cognitive system needs to decide the color of a stimulus. These findings provide evidence for the notion that monocular portions of the visual stream are involved in the resolution of cognitive interference, and specifically in the Stroop task. This leads to the conclusion that subcortical regions play a functional role in executive functions, rather than merely channeling information to the cortex. This novel suggestion calls for revising our understanding of the functionality of subcortical regions.

To conclude, the present study supports the notion that subcortical regions have a functional role in executive functions as measured by the Stroop task. In line with previous investigations, our results suggest that cortical mechanisms are not exclusively responsible for executive functioning, and that a dynamic interaction between cortical and subcortical regions may be involved in executive functions.

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