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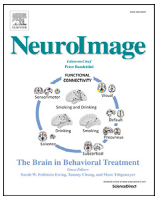

It takes two to tango: Suppression of task-irrelevant features requires (spatial) competition

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ABSTRACT

In a recent electrophysiological study, we reported on global facilitation but local suppression of color stimuli in feature-based attention in human early visual cortex. Subjects attended to one of two centrally located superimposed red/blue random dot kinematograms (RDKs). Task-irrelevant single RDKs in the same colors were presented in the left and right periphery, respectively. Suppression of the to-be-ignored color was only present in the centrally located RDK but not in the one with the same color in the periphery. This result was at odds with the idea of active suppression of task-irrelevant features across the entire visual field. In the present study, we introduced competition in the periphery by superimposing the RDKs at the task-irrelevant location as well. With such competition, we found suppression of the task-irrelevant color in the centrally and peripherally located RDKs. Results clearly demonstrate that suppression of task-irrelevant features at task-irrelevant locations requires (spatial) competitive interactions and is not an inherent neural mechanism in feature-based attention as was found for global facilitation.

Introduction

Global facilitation of a to-be-attended feature throughout the entire visual field has been shown as a key neural mechanisms in feature-based attention (see Andersen et al., 2013; Saenz et al., 2002; Treue and Martinez-Trujillo, 1999). In visual search, global facilitation is the key property of the "guided search model" (Wolfe, 1994). According to this model, searching a visual display for a target object that consists of different features (i.e. conjunction search), results in parallel enhancement of each feature of the object throughout the search display. Object constituent features act additively on an activation map, causing the target object to stand out from distractors. Thus, target objects can be localized much faster than in a purely serial search. (Treisman and Gelade, 1980). Such additive facilitation of features with feature-conjunction stimuli was also proposed by the "feature similarity gain model" (Treue, 2001; Treue and Martinez-Trujillo, 1999) and has been shown in human visual cortex by means of objective electrophysiological (EEG) recordings (Andersen et al., 2008, 2015).

While experimental evidence for global facilitation of task-relevant features is pretty much consistent, evidence on global suppression of task-irrelevant features is quite inconclusive. Some behavioral studies have failed to find results that would support global suppression (Beck and Hollingworth, 2015; Becker et al., 2015). In these studies, the authors reported that a behavioral benefit with negative cues (i.e. cueing of task-irrelevant features) can only be found when subjects were able to group stimuli spatially (Beck and Hollingworth, 2015), or used these cues as strategic shifts towards the to-be-attended features (Becker et al., 2015). In the same vein, Noonan et al. (2016) found evidence for distractor suppression in a block design only but not in trial-by-trial cueing, suggesting that active suppression of to-be-ignored features might depend on repetitive previous experience. Prior to these studies, Moher and Egeth (2012) cued subjects to ignore a certain color of a letter and observed that reaction times slowed down compared to neutral cues, when naming a target letter of a different color. This finding may rather imply attention capture of negatively cued stimuli than active suppression. In a subsequent dot-probe task, they demonstrated that an always valid cue to ignore a certain color (i.e. negative cue) automatically pulled attention towards the colored letter, which was withdrawn subsequently, instead of withdrawing it right from cue onset. In other words, the negative cue led to the same result as the instruction to not think of pink elephants walking down on Broadway.

Conversely, some electrophysiological studies found evidence for

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global suppression in feature-based attention. Moher et al. (2014) used a probe design by presenting either the ignored, the attended, or a neutral color as a 100 ms probe in the to-be-ignored visual hemifield. Subjects were instructed to attend to one color of two differently colored superimposed RDKs in the opposite visual hemifield. The amplitude of the P1 component (a positive deflection in the visual evoked potential with a latency of about 100 ms) was only reduced for probes of the to-be-ignored color, with no differences for neutral color or probes in the to-be-attended color. However, the P1 component is well known to be a sensitive neural marker for spatial attention (Hillyard and Anllo-Vento, 1998) with greater amplitudes for stimuli that occur at the attended location compared to when that location was unattended. While the greater P1 amplitude for the attended color probes was due to the global facilitation effect (see Zhang and Luck, 2009), the reduced P1 amplitude for the to-be-ignored color probes can alternatively be explained by spatial instead of feature-based attention mechanisms. The neutral color probes, on the other hand, were highly salient, given that this color was not in the attended display. Such transient salient probes are well known to involuntarily pull attention to that location (Yantis, 1998). The sudden onset of these probes, could result in greater P1 amplitudes compared to the P1 of to-be-ignored color probes that were part of the display and thus less salient. In fact, it was recently shown that salient but task-irrelevant distractors first pull attention towards their location and are subsequently suppressed (Gaspar and McDonald, 2014; Liesefeld et al., 2017).

In another EEG study, Störmer and Alvarez (2014) used frequency tagging to investigate suppressive interactions in color-based attention to overcome problems with sudden onset probes. They used a design identical to that used in Moher et al. (2014) but flickered two superimposed RDKs in the attended hemifield and a single one in the to-be-ignored hemifield at three different frequencies. Such frequency-tagged stimuli elicit steady-state visual evoked potentials (SSVEPs) that have the same frequency as the respective flickering stimulus (Regan, 1989) and their amplitudes are modulated by spatial- (Müller et al., 1998a, 2003) as well as feature-based attention (Andersen et al., 2009; Müller et al., 2006). Unsurprisingly, they found SSVEP amplitudes to be the greatest in the unattended visual hemifield when the color matched the target color (global facilitation). However, when the color either matched the distractor color or was 30° apart from the target in color space, SSVEP amplitudes were smallest. Störmer and Alvarez (2014) interpreted these findings as evidence for surround suppression in color space and for global suppression of the to-be-ignored color. However, the problem with that interpretation is the lack of a baseline or a reference measure in their study. Without such a reference, it is impossible to decide whether differences in amplitude are due to a pure facilitation effect of the attended color without any suppression of the to-be-ignored color, or whether the differences are due to the suppression of the to-be-ignored color (Forschack et al., 2017; Müller et al., 1998b).

Two recent studies that also used frequency tagging and included a reference or baseline measure, were unable to confirm global suppression of to-be-ignored features (Forschack et al., 2017; Painter et al., 2014). Painter et al. (2014) used a neutral third color that was never task-relevant in their display. Relative to this neutral color, SSVEP amplitudes of the to-be-ignored color did not significantly differ, but the to-be-attended color exhibited significantly greater SSVEP amplitudes for all stimuli in the display (global facilitation). In our recent study (Forschack et al., 2017), we employed a shifting design (Andersen and Müller, 2010; Müller, 2008; Müller et al., 1998b) in which subjects were cued to shift attention to one of two colors (red or blue) in centrally located RDKs after a certain baseline period. In the left and right periphery, we presented isolated red or blue RDKs, respectively, that flickered at different frequencies. These peripheral RDKs were never task-relevant. When subjects shifted attention to one color in the central display, we replicated the facilitation of the to-be-attended color, followed by a suppression of the to-be-ignored color relative to pre-cue baseline for centrally located RDKs (Andersen and Müller, 2010). For peripheral RDKs, we only found a global facilitation effect of feature-based attention but no suppression of the to-be-ignored color. These results, together with the ones by Painter et al. (2014), are clearly at odds with the idea of a global suppression mechanism.

In our last paper, we reasoned that the lack of competitive interactions might have resulted in the absence of suppression in the peripheral RDKs. In the central display, red and blue RDKs competed for processing resources and suppression of the unattended color followed a biased competition mechanism (Desimone, 1998; Desimone and Duncan, 1995). Given that peripheral RDKs displayed only one color without a competitor, there was no need to suppress the task-irrelevant color at that task-irrelevant location. The present experiment was set up to test that possibility. To this end, we now superimposed red and blue RDKs in the periphery as well. Identical to the last study, subjects awaited a shifting cue and shifted attention to the cued color of centrally presented RDKs. Under conditions of competitive interaction, we found a suppression of SSVEP amplitude of the to-be-ignored color relative to the pre-cue baseline in the peripheral task irrelevant displays.

Methods

Participants

In order to directly compare the present study to our previous one (Forschack et al., 2017), we recorded 23 subjects with a mean age of 25.7 ± 5.6 years (range 19–40) that entered the analysis. All participants received class credits or financial reimbursement for their participation. The experiment was conducted in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki) and the local ethics committee (University of Leipzig).

Stimuli and procedure

Stimuli were presented on a 19-inch CRT monitor set to a resolution of 640-by-480 pixels, color depth of 32 bits and refresh rate of 120 Hz. Stimuli consisted of two overlapping red and blue, centrally presented RDKs that filled an area of 4.8° by 9.6° of visual angle (width by height) at a distance of 80 cm. In the left periphery 7.8° of visual angle from central fixation two additional overlapping red/blue RDKs of the same size were presented (see Fig. 1A). Each of the four RDKs consisted of 75 rectangles with an edge size of 0.325° of visual angle. In each RDK rectangles were presented with an on/off flicker with a specific frequency and were thereby frequency tagged to allow for later analysis of distinct SSVEPs: center red: 11.5 Hz, center blue: 13.5 Hz, periphery red: 8.5 Hz, periphery blue: 6.5 Hz. In each RDK, squares were drawn randomly to prevent any depth cues and moved in a random direction with a speed of 0.051° per frame of screen refresh. Dots moving over the edge of the rectangular field reappeared on the other side. RDKs were presented as pure red and blue against a grey background color (see Fig. 1A). For each subject luminance values for each RDK at each position (periphery and center) were individually set to be isoluminant to the grey background (5.8 cd/m^2) with a procedure based on heterochromatic flicker photometry (Wagner and Boynton, 1972).

The experimental detection task began after participants signed a written consent, were informed of the nature of the experiment and had EEG electrodes attached. In each trial, all four flickering RDKs were presented simultaneously with a white fixation cross in the center of the screen. After a time-jittered window of 1258–1750 ms after stimulation onset, the fixation cross either changed to red or blue indicating the color of the centrally to-be-attended RDK. This pre-cue time window allowed for SSVEP signals to build up and served as an unbiased baseline time window (see also below). In the time window following the color cue (additional 1783 ms), participants had to report brief episodes (300 ms) of coherent motion of 60% of the dots of the to-be-attended color by pressing the spacebar of a standard keyboard (response hand was changed after half of experimental trials). Coherent motion events in the unattended RDK had to be ignored and served as distractors. Up to two

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