

Failed Suppression of Salient Stimuli Precedes Behavioral Errors

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Abstract

■ Our visual system is constantly confronted with more information than it can process. To deal with the limited capacity, attention allows us to enhance relevant information and suppress irrelevant information. Particularly, the suppression of salient irrelevant stimuli has shown to be important as it prevents attention to be captured and thus attentional resources to be wasted. This study aimed at directly connecting failures to suppress distraction with a neural marker of suppression, the distractor positivity (Pd). We measured participants' EEG signal while they performed a visual search task in which they had to report a digit inside a shape target while ignoring distractors, one of which could be a salient color singleton. Reports of target digits served as a behavioral index of enhancement, and reports of color distractor digits served as a

behavioral index of failed suppression, each measured against reports of neutral distractor digits serving as a baseline. Participants reported the target identity more often than any distractor identity. The singleton identity was reported least often, suggesting suppression of the singleton below baseline. Suppression of salient stimuli was absent in the beginning and then increased throughout the experiment. When the singleton identity was reported, the Pd was observed in a later time window, suggesting that behavioral errors were preceded by failed suppression. Our results provide evidence for the signal suppression hypothesis that states salient items have to be actively suppressed to avoid attentional capture. Our results also provide direct evidence that the Pd is reflecting such active suppression. ■

INTRODUCTION

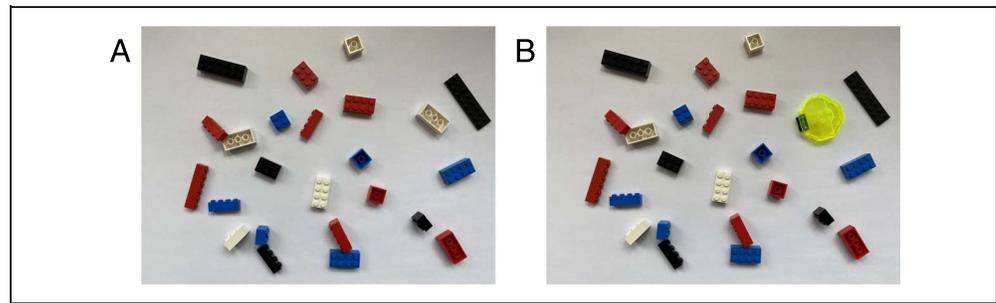
The selection of relevant information is a principal bottleneck in the visual processing stream because not all input can be dealt with at once. For example, trying to find a toy brick of a specific color and size in a pile of bricks can be challenging because bricks similar in color and shape compete with the “target brick” (see Figure 1A). However, attentional resources can be directed to specific locations (Carrasco, 2011; Posner, Snyder, & Davidson, 1980) or features (Wolfe, 2007; Found & Müller, 1996) to facilitate the processing of relevant information, which in turn leads to differences in underlying neural correlates. When looking for a blue brick, for example, selective attention enables us to focus on blue objects by enhancing the neural representation of blue (Desimone & Duncan, 1995). The enhancement of blue in this example is only one side of the coin, in which processing is biased in favor of relevant sensory signals. But how does the brain deal with the huge amount of irrelevant information? The other side of the coin is that typically a large number of irrelevant objects needs to be ignored (Duncan & Humphreys, 1989), particularly those that are salient, because they will more likely be distracting from your task

(Theeuwes, 2010). For example, when looking for a blue brick, a shiny, bright neon brick may capture our attention and thus impede visual search (see Figure 1B). A good strategy would be to suppress this irrelevant object so that relevant information can be processed more efficiently. Although suppression is a crucial component of human visual processing (Gaspelin & Luck, 2019), the role of suppression in attention is only just starting to emerge and does not feature in current models of visual attention (Wolfe, 2007; Itti & Koch, 2001).

Within the visual attention literature, suppression has received far less interest than enhancement. One reason is a lack of direct evidence for suppression as a fundamentally independent process from enhancement. Consider our example again. Can differences in visual priority across the visual field simply be accounted for by different levels of enhancement (higher priority for blue bricks than for bright neon ones), or is suppression (below baseline priority for neon bricks) as an independent process required to explain differences in behavior? Most previous research is inconclusive; however, more recent studies show evidence for active suppression below baseline (Gaspelin, Leonard, & Luck, 2017). In this study, participants were asked to make saccades to a target object presented among nontargets, and the majority of saccades were directed toward the target. In some cases, however, one of the nontargets was given a unique color, making it very

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Figure 1. Everyday examples of visual search for a toy brick. Trying to find a target brick (e.g., a 2×3 black brick) appears to be easier when presented with regular (A) compared with salient (B) presumably distracting toy bricks.



salient and inducing the potential danger of distraction. Interestingly, fewer saccades were made toward the salient nontarget than toward the neutral nontargets that served as a baseline. This suggests that salient nontargets had a negative priority, induced by active suppression. The findings indicate that if a particularly salient object is present that can capture our attention, signal suppression is used to counteract an imminent attentional capture (Gaspelin & Luck, 2018b; Sawaki & Luck, 2010).

Another potential reason for the lack of research on suppression has been the absence of neural markers that would allow for isolating suppression effects from enhancement. For example, the N2pc, a prominent marker of attention deployment in the ERP of the EEG signal, appears at electrodes contralateral to a target, approximately 200–300 msec after onset of the target. Because search displays typically include distractors in the opposite hemifield to the target, an increased N2pc could be due to either more target enhancement in one hemifield or more distractor suppression in the other hemifield. Based on the principle that lateralized signals can be used to differentiate between processing of items in different locations in the visual field (Woodman & Luck, 2003), Hickey and colleagues (Hickey, Di Lollo, & McDonald, 2009; Hickey, McDonald, & Theeuwes, 2006) were the first to disentangle target and distractor processing by using a systematic lateralization technique. In a subset of trials, the target would be the only laterally presented stimulus (the distractor being on the vertical midline). By this means, activity contralateral to the target (the “pure” target-N2pc) could be isolated because any items on the vertical midline would not affect the lateralized ERP. Crucially, in another subset of trials, the salient distractor would be the only laterally presented stimulus (target on vertical midline). A novel ERP component, the distractor positivity (Pd) was identified, which reflected pure distractor activity.

A large body of evidence links the Pd to suppression. For example, in trials in which a salient distractor did not cause RT costs (i.e., it has been successfully suppressed), a Pd was found. However, in trials with high RT costs, suggesting failed suppression, an inverse Pd (i.e., a greater negativity contralateral to a distractor) indicative of involuntary attentional capture was observed (Sawaki, Geng, & Luck, 2012). In line with this, a study combining EEG and

eye tracking showed that when observers erroneously made an eye movement to a salient distractor, no Pd was observed, but when they correctly made a saccade to the target, a Pd was observed contralateral to the singleton (Weaver, van Zoest, & Hickey, 2017). Moreover, within individuals, the Pd is larger in fast trials (Feldmann-Wüstefeld, Brandhofer, & Schubö, 2016; Gaspar & McDonald, 2014), suggesting that the Pd reflects effective suppression that allows rapid target identification. Participants who are particularly distractible show larger Pd components in line with the notion that, for them, more resources are required to suppress an irrelevant salient item (Burra & Kerzel, 2014). Furthermore, when less suppression is required for a salient distractor because its location is known in advance, the Pd amplitude elicited by the distractor is reduced (Heuer & Schubö, 2019). Finally, a macaque study combining ERPs and single-unit recordings showed an equivalent of the Pd in the neuron discharge rate that was closely related to the suppression of a salient irrelevant item (Cosman, Lowe, Zinke, Woodman, & Schall, 2018).

Although behavioral work supports the existence of active suppression (Gaspelin et al., 2017; Gaspelin, Leonard, & Luck, 2015) and the Pd now provides a neural marker of this suppression (Hickey et al., 2009), demonstrating a direct link between the Pd and below-baseline representation would allow establishing the Pd as a fundamental neural marker of active suppression. First evidence for such a direct link comes from a recent study by Gaspelin and Luck (2018a) in which the below-baseline report of letters at singleton locations in a probe task was correlated with the Pd elicited by singletons in a search task. Gaspelin and Luck measured behavioral performance and neural suppression in distinct tasks. They measured below-baseline performance in a letter report task in which all locations were relevant and the Pd component in a visual search task in which only the target location was relevant. In the current study, we will go one step further and measure behavior and suppression at the same time; thus, we will be able to measure the below-baseline performance and the Pd as a neural marker of suppression with the exact same task and in the exact same trials. To that end, we will use a compound search task in which each of the six shapes presented will have a unique digit embedded. Participants have to report the

digit inside the predefined target shape (a diamond) while ignoring all other items that serve as distractors, including a salient distractor (a color singleton) that will appear in 50% of the trials. Critically, when participants report incorrect digits, we will be able to associate the response to either a neutral distractor (in the same color as the target) or to the singleton distractor (in red, blue, or green). Because the target is a shape singleton and participants are asked to ignore a color singleton, this should encourage singleton detection mode, that is, participants will search for any unique “pop out,” and this strategy causes the color singleton to capture attention (Lamy & Egeth, 2003; Bacon & Egeth, 1994; Folk & Remington, 1998). This should result in a relatively high number of trials in which participants report the singleton number in the probe task, which is necessary to obtain a reliable Pd. By this means, we can directly link the behavioral response to the neural processing of targets and distractors. For example, we will compare the Pd elicited by the same visual search display as a function of whether the target identity (correct responses), the distractor identity (incorrect responses), or the singleton identity (incorrect responses) will be reported. A smaller Pd in color-reported trials would indicate that the lack of suppression coincides with the accidental report of the singleton identity.

METHODS

Participants

Forty volunteers naïve to paradigm and objective of the experiment participated for payment or course credit. One additional participant had to be excluded because of technical problems (markers were not correctly transferred to the EEG recording computer). The remaining 36 participants (7 men) were aged 19–27 years ($M = 23.1$ years, $SD = 2.5$ years), and all but four were right-handed. All participants had normal or corrected-to-normal visual acuity ($\text{visus} \geq 1$) and showed no signs of acritochromacy (both tested with an Oculus Binoptometer 3). The exper-

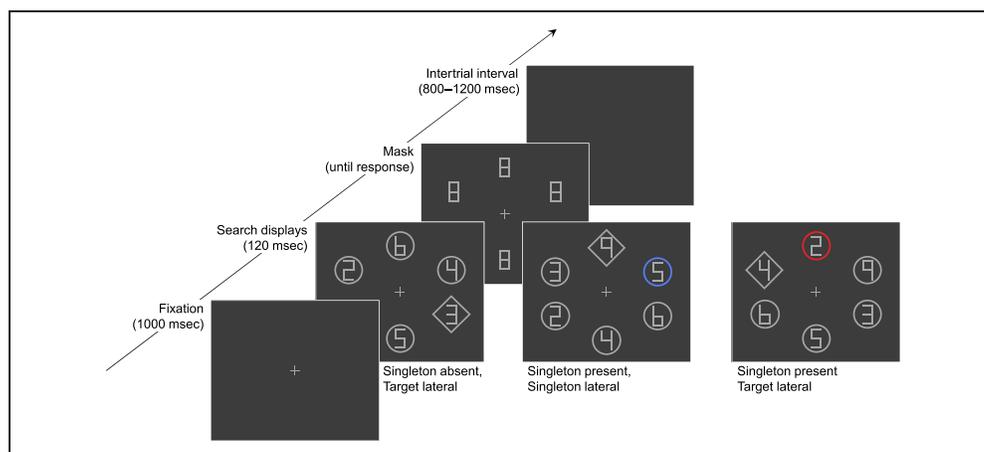
iment was conducted with the written understanding and consent of each participant in accordance with the ethical standards of the Declaration of Helsinki and was approved by the Ethic Committee of the Faculty of Psychology, Philipps University Marburg.

Apparatus and Stimuli

Participants were seated in a comfortable chair in a dimly lit, electrically shielded and sound attenuated chamber. Participants responded with button presses on an ergonomic customizable response pad (Ergodex DX1) that was placed on their lap. Six buttons labeled “2,” “3,” “4,” “5,” “6,” and “9” were placed in numeric order from left to right on the keyboard. No other keys were placed on the keyboard. Participants used their right index finger to press one of the buttons in each trial. Stimulus presentation and response collection were controlled by a Windows PC using E-Prime 2 routines. All stimuli were presented on a LCD-TN screen (Samsung Syncmaster 2233) placed at ~ 100 cm distance from participants.

Search displays (see Figure 2) comprised six stimuli arranged on an imaginary oval around a central fixation cross with two stimuli on the vertical midline (4.4° above/below fixation), two stimuli in the left hemifield, and two stimuli in the right hemifield (4.9° left/right from vertical midline, 2.0° above/below horizontal midline). All stimuli were presented on a dark gray (HSV: 160, 0, 56; ~ 4 –5 candela) background. Stimuli were compound objects consisting of a digit ($0.7^\circ \times 1.1^\circ$) embedded in a diamond-shaped (target) or a circular (distractor) outline (1.8°). Digits (2, 3, 4, 5, 6, 9) were medium gray (HSV: 160, 0, 126) seven-segment display character representations (see Figure 2) similar to those used for digital clocks. Targets and neutral distractors were medium gray (HSV: 160, 0, 126), whereas color distractors could be red (HSV: 0, 195, 125), blue (HSV: 150, 240, 160), or green (HSV: 99, 240, 77). Colors and medium gray were matched for luminance (~ 27 –30 candela). As color distractors were the only colored items, we from here on refer to them as “color singletons.” Mask

Figure 2. Trial procedure for a singleton-absent trial, a singleton-present trial with a lateral color distractor, and a color-present trial with a lateral target. Singletons were present in 50% of the trials. In half of the singleton-present trials, singletons were presented laterally (with a target on the vertical midline). In the other half, singletons were presented on the vertical midline (with a lateral target).



displays comprised six digital 8 embedded in a circle (both gray; HSV: 160, 0, 126) presented at the same location as the digits in the search display such that search items and mask items were exactly congruent.

Design and Procedure

The experiment comprised 20 blocks of 36 trials (720 trials in total). A target was present in all trials. Half of the trials (360 trials) did not have color singletons (from hereon called “singleton-absent trials”) in which all five distractors were neutral and the target appeared equally often on the vertical midline (180 trials) and in a lateral position (180 trials). The remaining half of the trials (360 trials) had color singletons (singleton-present trials), in which four distractors were neutral and one distractor was colored (red, blue, or green; each 120 trials). In half the singleton-present trials (180 trials), the target was presented on the vertical midline, and the color singleton in a lateral, neighboring position. In the remaining half of the singleton-present trials (180 trials), the color singleton was presented on the vertical midline and the target in a lateral, neighboring position. This systematic lateralization of target and color singleton allowed isolation of target and color distractor-related activity in the lateralized ERP (Hilimire, Hickey, & Corballis, 2012; Hickey et al., 2009). Note that the goal of the experiment was not to compare the ERPs as a function of an independent variable but as a function of which response was given: Report of the target, a neutral distractor or the color singleton.

Each trial started with a fixation cross presented for 1000 msec (see Figure 2). A search display followed for 120 msec and was replaced by a mask display presented until one of the six buttons was pressed. An empty screen was shown for 800–1200 msec until a fixation cross announced the beginning of a new trial. Participants were instructed to report the identity of the digit embedded in the diamond-shaped target by pressing the accordingly labeled button. Participants were to respond as correctly as possible; RT was not stressed. All trial types (singleton present/absent, target lateral/vertical midline) were randomly distributed across the experiment. After each block, participants had a break of at least 10 sec and could decide when to continue. Every other block, participants were informed about their accuracy in the last two blocks.

Data Recording and Analysis

Behavioral Data

For each participant, the RT for singleton-absent and singleton-present trials was calculated separately and compared with a *t* test for dependent measures. In addition, the frequency of reporting the digit inside the target (target report trials), of reporting the digit inside one of the neutral distractors (neutral distractor report trials), and of reporting the digit inside the singleton (if

present; singleton report trials) was calculated, separately for singleton-absent and singleton-present trials. To account for the larger number of neutral distractors, the frequency of distractor report trials was divided by 5 (singleton-absent trials = trials with 5 distractors) or by 4 (singleton-present trials = trials with 4 distractors). The report frequencies were compared using a one-way ANOVA for repeated measures with two factor levels in singleton-absent trials (target vs. distractor report) and three factor levels in singleton-present trials (target vs. distractor vs. singleton report).

EEG

EEG was recorded from 64 Ag–AgCl electrodes (according to the International 10–10 System) using a BrainProducts actiCap system. Horizontal and vertical EOGs were recorded bipolarly from the outer canthi of the eyes and from above and below the observer’s left eye, respectively. All electrodes were referenced to Cz and re-referenced offline to the average of all electrodes. Electrode impedances were kept below 5 k Ω . Sampling rate was 1000 Hz. Data were hardware filtered with a low-pass (Butterworth) cutoff frequency of 250 Hz (–3 dB half power cutoff, filter order 5, 30 dB/oct roll-off slope) and a high-pass (passive RC-filter) cutoff frequency of 0.016 Hz (–3 dB half power cutoff, 6 dB/oct roll-off slope). EEG data were averaged offline within 700-msec epochs time-locked to the search display onset and including a 200-msec prestimulus baseline. Trials with blinks (absolute voltage criterion: 100 μ V) or saccades (absolute voltage criterion: 50 μ V; step criterion: 25 μ V) from 0–500 msec were excluded from data analysis. In addition, channel noise was excluded on an individual channel basis (absolute voltage criterion: 60 μ V). ERPs were calculated for eight conditions: (1) singleton-absent, target lateral, target report (trials available after rejection: 52 ± 21 SD); (2) singleton-absent, target lateral, neutral distractor report (117 ± 21 trials); (3) singleton-present, target lateral, target report (48 ± 18 trials); (4) singleton-present, target lateral, neutral distractor report (101 ± 16 trials); (5) singleton-present, target lateral, singleton report (23 ± 9 trials); (6) singleton-present, singleton lateral, target report (41 ± 15 trials); (7) singleton-present, singleton lateral, neutral distractor report (98 ± 18 trials); (8) singleton-present, singleton lateral, singleton report (28 ± 12 trials). Eight participants were excluded from EEG data analyses because they had fewer than 12 trials in one of the singleton report trials, the least frequent condition). These participants were not excluded from behavioral analyses as this would have systematically biased the results (as participants with particularly low singleton report frequency had to be excluded from EEG analyses—excluding them from behavioral analyses would deflate the singleton report frequency, the dependent variable). For the 31 participants with sufficient trials, the ERP was averaged separately for contra- and ipsilateral electrodes and for each of the eight conditions.

For all statistical analyses, degrees of freedom are Greenhouse–Geisser corrected. *t* tests were one-tailed. Partial eta squared (η^2) for ANOVAs and Cohen's *d* for *t* tests are reported as a measure of effect size.

RESULTS

Behavior

RTs (see Figure 3) were faster in singleton-absent trials ($M = 1247$ msec) than in singleton-present trials ($M = 1301$ msec), $t(38) = 4.5$, $p < .001$, $d = 0.72$, suggesting that attention was captured by the color singleton. Accuracy was 27.9% ($SD = 8.3\%$, min = 13.6%, max = 48.3%). Six of 39 participants performed within chance levels (as defined by accuracy lower than chance level + 3%). In singleton-absent trials, the target identity was reported more often (28.8%) than the distractor identity (14.2%), $F(1, 38) = 65.2$, $\eta^2 = .63$, $p < .001$. In singleton-present trials, different target, distractor, and singleton report frequencies were found, too, $F(2, 76) = 69.0$, $\eta^2 = .65$, $p < .001$. Follow-up *t* tests showed that target reports

(26.9%) were more frequent than distractor reports (14.9%), $t(38) = 8.2$, $p < .001$, $d = 1.30$, and singleton reports (13.4%), $t(38) = 8.9$, $p < .001$, $d = 1.45$. Critically, singleton reports were less frequent than distractor reports, $t(38) = 2.5$, $p = .008$, $d = 0.43$. This neutral distractor advantage (frequency of reporting a distractor – frequency of reporting a singleton) indicated that singleton report frequency was below baseline. To investigate whether suppression would be more efficient throughout the experiment, we analyzed the neutral distractor advantage for five epochs, each comprising of four blocks (144 trials). The neutral distractor advantage increased throughout the experiment ($M_1 = -0.3\%$, $M_2 = 1.0\%$, $M_3 = 1.5\%$, $M_4 = 2.8\%$, $M_5 = 2.7\%$), $F(4, 152) = 3.3$, $\eta^2 = .08$, $p = .012$ (see Figure 3C). Within-subject contrasts revealed a linear trend, $F(1, 38) = 14.7$, $\eta^2 = .28$, $p < .001$, but no quadratic ($p = .513$) or cubic trend ($p = .802$).

Determining Time Windows for EEG Analyses

We used a data-driven condition-blind approach to determine analysis windows. Inspection of the difference waves in target-lateral trials showed a relatively narrow N2pc component both in singleton-absent and singleton-present trials. Across conditions (i.e., the factor report), the N2pc peak was at 232 and 233 msec, respectively. Visual inspection showed that N2pc was relatively narrow, which is why time windows were determined as ± 25 msec from the peak, that is, 207–257 and 208–258 msec. Visual inspection of the difference wave in distractor-lateral trials showed a broad Pd component that peaked (across report condition) at 250 msec. To track time dynamics, we chose two time windows for the Pd, one prior to the peak (174–249 msec) and one starting at the peak (250–325 msec).

N2pc

In singleton-absent trials with lateral targets (see Figure 4, left column), a main effect of Laterality revealed a reliable N2pc ($M_{\text{contra}} = -2.3 \mu\text{V}$, $M_{\text{ipsi}} = -2.0 \mu\text{V}$), $F(1, 30) = 10.5$, $\eta^2 = .26$, $p = .003$. There was no interaction of Laterality and Report ($p = .988$), showing no reliable differences in N2pc amplitudes between trials with target and distractor reports.

In singleton-present trials with lateral targets (see Figure 4, middle column), a main effect of Laterality revealed a reliable N2pc ($M_{\text{contra}} = -1.2 \mu\text{V}$, $M_{\text{ipsi}} = -0.8 \mu\text{V}$), $F(1, 30) = 5.8$, $\eta^2 = .16$, $p = .022$. There was no interaction of Laterality and Report ($p = .570$), showing no reliable differences in N2pc amplitudes between trials with target, neutral distractor, and singleton reports.

Pd

In singleton-present trials with lateral singletons (see Figure 4, right column), a main effect of Laterality revealed

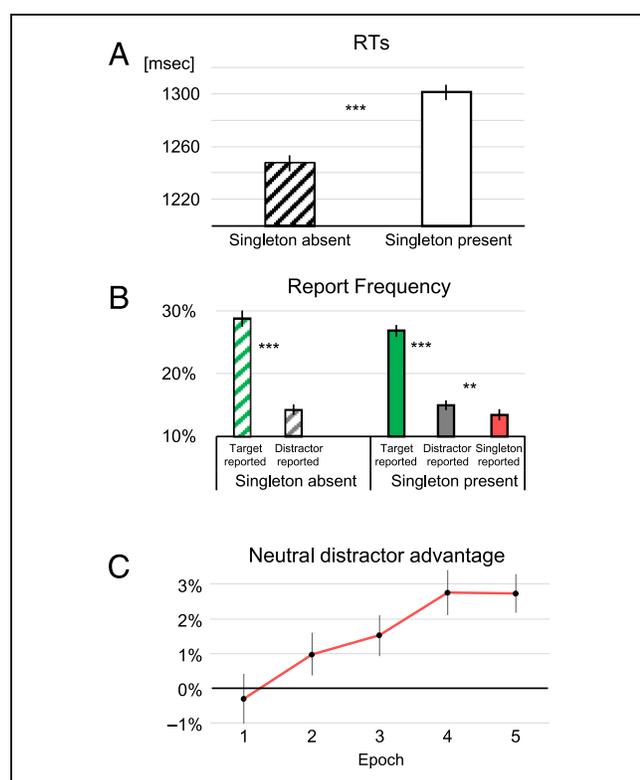


Figure 3. Behavioral results. (A) RTs for singleton-absent trials and singleton-present trials. (B) The frequency of target, neutral distractor, and singleton report (corrected for guessing). (C) The neutral distractor advantage for five epochs of four experimental blocks (144 trials). The neutral distractor advantage is the difference between the frequency to report a neutral distractor and to report a singleton identity. Error bars denote *SEM* corrected for within-subject variance (Cousineau, 2005). Asterisks denote statistical significance for direct comparisons (** $p < .001$, ** $p < .01$).

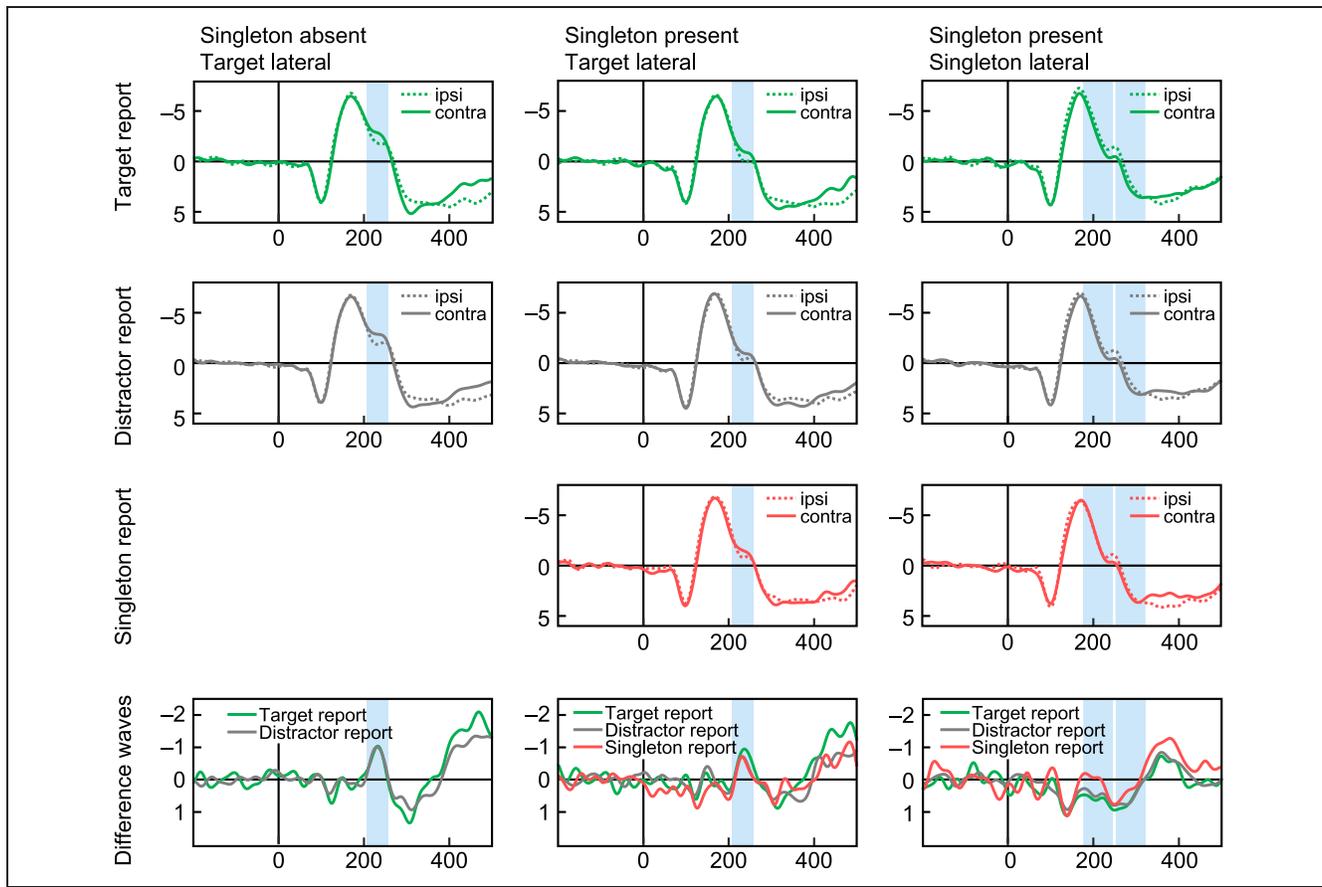


Figure 4. ERPs of the EEG. The upper three rows show waveforms for electrode separately for contra- and ipsilateral sites (PO7, PO8). Dotted lines denote ipsilateral sites, and solid lines denote contralateral sites. The lowest row shows the same data as Rows 1–3 but for the difference of contra- and ipsilateral sites. In all panels, green lines denote trials in which the target was reported, gray lines denote trials in which the neutral distractor was reported, and red lines denote trials in which the singleton was reported (note that in singleton-absent trials, singletons could not be reported as there were not any present). Blue shade indicates the time windows that were used for statistical analyses. All waveforms are 30 Hz low pass filtered for display purposes only.

a reliable Pd in the early time window of 174–249 msec ($M_{\text{contra}} = -2.6 \mu\text{V}$, $M_{\text{ipsi}} = -3.0 \mu\text{V}$), $F(1, 30) = 9.8$, $\eta^2 = .25$, $p = .004$. An interaction of Laterality and Report showed that Pd amplitude varied as a function of which item was reported, $F(2, 60) = 3.4$, $\eta^2 = .10$, $p = .040$. Follow-up t tests showed that the Pd was significantly smaller in singleton report trials ($0.1 \mu\text{V}$; red lines in Figure 4) than in target report trials ($0.6 \mu\text{V}$; green lines in Figure 4), $t(30) = 2.2$, $p = .018$, $d = 0.40$, or neutral distractor report trials ($0.4 \mu\text{V}$; gray lines in Figure 4), $t(30) = 2.2$, $p = .018$, $d = 0.40$. There was no difference between target report and distractor report trials, $t(30) = 0.7$, $p = .239$, $d = 0.13$. Furthermore, a reliable Pd was only found in target report ($p = .003$) and distractor report trials ($p = .002$), but not in singleton report trials ($p = .299$).

In the late time window of 250–325 msec, a main effect of Laterality revealed a reliable Pd ($M_{\text{contra}} = 2.0 \mu\text{V}$, $M_{\text{ipsi}} = 1.6 \mu\text{V}$), $F(1, 30) = 8.5$, $\eta^2 = .22$, $p = .007$. There was no interaction of Laterality and Report ($p = .418$), showing no reliable differences in Pd amplitudes be-

tween trials with target, neutral distractor, and singleton reports.

Exploratory Analyses

Bilateral Pd

Visual inspection showed that when targets were presented laterally, the bilateral EEG signal was more positive when singletons were presented on the vertical midline (middle column in Figure 4) than when no singletons were present (left column in Figure 4). To confirm whether this difference was statistically significant, we ran a t test for dependent measures and compared the EEG signal across Laterality (contra/ipsi) and report (target/singleton/distractor) between [singleton absent, target lateral] and [singleton present, target lateral trials], using the same time windows as for N2pc analyses described above. When singletons were absent, the signal was more negative ($-2.3 \mu\text{V}$) than when singletons were presented on the vertical midline ($-1.0 \mu\text{V}$), $t(30) = 6.4$, $p < .001$, $d = 1.16$. Within singleton present trials, the

bilateral Pd also seems to be smaller for singleton report trials than for target or distractor report trials. *t* Tests for dependent measures, however, showed that none of these differences were significant (all *ps* > .077).

Contralateral Delay Activity

Visual inspection revealed lateralized ERPs after the N2pc/Pd time windows: Electrodes showed a more negative voltage contra- than ipsilateral to the lateralized stimuli in all conditions. This contralateral delay activity (CDA) is typically found in working memory tasks contralateral to memorized stimuli (Vogel & Machizawa, 2004), and its amplitude reflects the number of items currently stored in working memory (Feldmann-Wüstefeld, Vogel, & Awh, 2018). A CDA elicited by salient singletons has also been found in slow response trials in visual search tasks (Gaspar & McDonald, 2014) and has been linked with accidentally storing irrelevant information in working memory. To explore whether the CDA observed in this study was related to the behavioral outcome, we analyzed the CDA similarly to the N2pc/Pd analyses, but for all conditions. We ran an ANOVA with the within-subject factors Laterality and Report separately for (i) singleton-absent trials; (ii) singleton-present, target-lateral trials; and (iii) singleton-present, singleton-lateral trials. Two time windows were chosen, one from 325 to 500 msec and one from 501 to 675 msec.

First, both in the early, $F(1, 30) = 13.8$, $\eta^2 = .32$, $p = .001$, and in the late, $F(1, 30) = 33.3$, $\eta^2 = .53$, $p < .001$, time window of singleton-absent trials, a main effect of Laterality revealed a reliable CDA. No interaction of Laterality and Report was found in either time window ($p > .057$), indicating that CDA amplitude did not vary as a function of which item was reported.

Second, both in the early, $F(1, 30) = 6.5$, $\eta^2 = .18$, $p = .016$, and late, $F(1, 30) = 52.7$, $\eta^2 = .64$, $p < .001$, time window of singleton-present, target-lateral trials, a main effect of Laterality revealed a reliable CDA. No interaction of Laterality and Report was found ($p = .115$) in the early time window. In the late time window, however, an interaction of Laterality and Report was found, suggesting that CDA amplitude varied as a function of which item was reported, $F(2, 60) = 3.8$, $\eta^2 = .11$, $p = .027$. Follow-up *t* tests showed that the CDA was significantly larger in target report trials ($-1.5 \mu\text{V}$) than in singleton report trials ($-0.9 \mu\text{V}$), $t(30) = 2.3$, $p = .015$, $d = 0.41$, or neutral distractor report trials ($-0.9 \mu\text{V}$), $t(30) = 2.5$, $p = .009$, $d = 0.45$. There was no difference between singleton report and distractor report trials, $t(30) = 0.2$, $p = .436$, $d = 0.03$. A reliable CDA was regardless of the digit reported (all *ps* ≤ .001).

Third, in the early time window of singleton-lateral trials (used for Pd analyses above), a main effect of Laterality revealed a reliable CDA, $F(1, 30) = 8.4$, $p = .007$, $\eta^2 = .22$. An interaction of Laterality and Report showed that CDA amplitude varied as a function of which item was reported, $F(2, 60) = 3.6$, $p = .033$, $\eta^2 = .11$. Follow-up

t tests showed that the CDA was significantly larger in singleton report trials ($-0.7 \mu\text{V}$) than in target report trials ($-0.1 \mu\text{V}$), $t(30) = 2.7$, $p = .006$, $d = 0.48$, or neutral distractor report trials ($-0.2 \mu\text{V}$), $t(30) = 1.7$, $p = .046$, $d = 0.31$. There was no difference between target report and neutral distractor report trials, $t(30) = 0.6$, $p = .292$, $d = 0.10$. Furthermore, a reliable CDA was only found in singleton report trials ($p < .001$), but not in target report ($p = .209$) or in distractor report trials ($p = .052$). In the late time window of singleton-lateral trials, no significant effects were found (all *ps* > .240), indicating that no reliable CDA was present anymore.

DISCUSSION

In this study, we examined how suppression affects behavioral performance in a visual search task. Participants saw compound search displays with one target and five distractors and had to report the digit inside the target. When one of the distractors had a unique color (i.e., it was a color singleton), RTs were slowed down, suggesting that the presence of salient items induced attentional costs. Critically, we found that the singleton identity was overall less frequently reported than that of a neutral (nonsalient) distractor (serving as the baseline), suggesting an active suppression of irrelevant features below baseline, in accordance with the signal suppression hypothesis (Gaspelin & Luck, 2018b; Gaspelin et al., 2017; Sawaki & Luck, 2010). Conversely, when individuals failed to report the target identity and rather (erroneously) reported the singleton identity, we found a decreased Pd component in the EEG signal (a neural measure of suppression) preceding the response. Importantly, our results provide evidence of a direct link of the Pd component to attentional suppression below baseline and highlight the importance of suppression for good attentional performance.

Previous research has suggested that suppression plays an important role in the visual system and can happen at multiple cognitive levels from early center-surround suppression (Anton-Erxleben, Stephan, & Treue, 2009; Desimone & Duncan, 1995) to selective attention (Gaspar & McDonald, 2014; Hickey et al., 2009) and later processes like working memory (Feldmann-Wüstefeld & Vogel, 2019; Gaspar, Christie, Prime, Jolicœur, & McDonald, 2016). However, it is not clear whether differences in visual priority (probability to attend/select an item according to salience models; e.g., Itti & Koch, 2001) can be accounted for by different levels of enhancement or whether suppression as a fundamentally independent process is required to explain differences in behavior. Critical for conclusive results regarding suppression is the establishment of a baseline and the demonstration that processing of some stimuli goes below that baseline. This was first done by Gaspelin et al. (2015) using the “capture-probe paradigm,” a visual search task in which participants have to search for a target and report the position of a dot inside the target in most of

the trials. In a large subset of trials, an additional singleton is presented, which slows down RTs. Critically, in a few trials, target and distractors had embedded letters rather than simple lines. In these “probe trials,” participants had to report as many letters as possible. Fewer letters were reported from color singletons compared with neutral distractors, suggesting below-baseline processing of the salient distractor (Gaspelin et al., 2015). Similar results were found for overt attention deployment (Gaspelin et al., 2017). This study’s aim was to link this behavioral evidence of active suppression to the Pd component.

The Pd has been used in a large body of studies as a marker of active suppression. The Pd is typically observed between 200 and 350 msec after the onset of displays with lateral salient distractors and targets presented on the vertical midline (so that the lateralized signal solely reflects distractor processing). As the N2pc, a “negativity” contralateral to an item, reflects enhancement (Mazza, Turatto, & Caramazza, 2009; Eimer, 1996; Luck & Hillyard, 1994), it may make intuitively sense that a “positivity” contralateral to an item reflects suppression, yet evidence for a direct connection of the Pd to suppression is scarce. Evidence comes from studies showing a correlation between behavioral measures and the Pd. For example, within individuals, the Pd is larger in fast trials (Feldmann-Wüstefeld et al., 2016; Gaspar & McDonald, 2014), suggesting that the Pd reflects successful suppression that allows rapid target identification. Similarly, Sawaki et al. (2012) showed that, in trials in which a salient distractor did not cause RT costs, there was a Pd, suggesting successful suppression of the distractor. In addition, no Pd was observed when observers erroneously made an eye movement to a salient distractor, but when they correctly made a saccade to the target, a Pd was observed contralateral to the singleton (Weaver et al., 2017). Participants who are particularly distractible show larger Pd components in line with the notion that for them, more resources are required to suppress an irrelevant salient item (Burra & Kerzel, 2014). Conversely, participants who have a particularly high working memory capacity also show larger Pd amplitudes elicited by items that are not to be encoded into working memory, suggesting that successful suppression contributes to an efficient encoding of relevant information into working memory (Feldmann-Wüstefeld & Vogel, 2019). More direct evidence for a connection of the Pd with suppression comes from a study that measured the Pd component in the probe trials of an capture-probe paradigm (Gaspelin & Luck, 2018a). They found that the same singleton that would elicit a Pd in search trials (in which a target feature needs to be reported) is reported less often than neutral distractors in probe trials. Furthermore, below-baseline report of letters at singleton locations in probe trials was correlated with the Pd elicited by singletons in search trials.

In the current study, we aimed at measuring the below-baseline behavioral report of singleton identity in the same trials as the Pd. To that end, we used a similar

paradigm as Gaspelin and Luck (2018a) but had participants report the identity of the target in every single trial. In contrast to the capture probe paradigm, participants were never to report the identity of distractors but performed the same task in every single trial: to report the identity of the target. However, assigning a unique digit to every single item in the search display allowed us to conclude which distractor was attended in an incorrect trial, the neutral distractor (baseline) or the singleton (potentially suppressed). Besides measuring behavior and Pd in the same task, our paradigm had another crucial difference to that of Gaspelin and Luck. The salient distractor varied across three different color features whereas it was constant in Gaspelin and Luck’s study. Thus, in this study, participants could not downregulate representations of a specific hue but rather had to apply suppression to the unpredictable color used in a given trial. This is of high theoretical interest as it has been shown that suppression is subject to statistical learning of location and/or features (Failing, Feldmann-Wüstefeld, Wang, Olivers, & Theeuwes, 2019; Stilwell, Bahle, & Vecera, 2019; Ferrante et al., 2018; Wang & Theeuwes, 2018). For example, a distractor in a frequently presented color causes less RT costs than a rare color (Stilwell et al., 2019). Because neither location nor color of the singleton was predictable in this study, our data suggest that the results from Gaspelin and Luck can be generalized; the Pd reflects suppression on a higher level and not just learned suppression of a specific feature.

The key finding of this study was that in trials in which the identity of a salient color distractor (rather than the identity of the target, or neutral distractor) was reported, failed suppression preceded the erroneous response. Failed suppression was measured using the Pd amplitude in two time windows. In the early time window, no Pd was found in trials in which the singleton identity was reported, whereas a reliable Pd was found in trials in which either the target or a neutral distractor was reported. In the later time window, a reliable Pd was found regardless which identity was reported and no differences in the Pd were found between trials with reports of target, distractor, or singleton. This suggests that suppression is eventually applied in all trials, but the delay in the emergence of the Pd is what causes the erroneous behavior, namely, the report of the singleton identity rather than then target identity. A novel finding in this study was also that the bilateral EEG signal in target lateral trials was more positive in the N2pc time window when color singletons were presented in the vertical midline versus when no color singletons were presented. This could be a “bilateral Pd.” That is, both hemispheres may be instantiating suppression of the distractor on the vertical midline, creating bilateral positivity in the ERP. Future research will have to scrutinize whether the bilateral Pd has a different functional role from the lateralized Pd.

In line with the EEG results, we found that the singleton identity was overall less frequently reported than that

of a nonsalient distractor, suggesting a suppression of irrelevant features below baseline as predicted by the signal suppression hypothesis (Gaspelin & Luck, 2018b; Gaspelin et al., 2017; Sawaki & Luck, 2010). The signal suppression hypothesis states that a top-down driven mechanism is required to suppress salient stimuli such as the color singleton to avoid attentional capture. In this study, participants seem to have applied suppression as evident in the below-baseline frequency of reporting a singleton identity and as evident in the presence of a Pd component, indicative of suppression (Liesefeld, Liesefeld, Töllner, & Müller, 2017; Feldmann-Wüstefeld, Uengoer, & Schubö, 2015; Burra & Kerzel, 2014; Feldmann-Wüstefeld & Schubö, 2013; Hickey et al., 2009). Individuals were reporting equally many singleton as distractor identities in the beginning of the experiment, suggesting that suppression was not efficient yet. Later into the experiment, fewer singleton identities were reported, showing that top-down driven suppression increased over time, hinting at a potentially important role of learning in suppression. Note that the singleton color could not be predicted and randomly varied between red, green, and blue. Thus, our data provide strong evidence that salient stimuli can be efficiently suppressed even when no feature-based suppression template is available (Reeder, Olivers, & Pollmann, 2017; Arita, Carlisle, & Woodman, 2012). This is in line with the finding that participants can learn to efficiently suppress an entire feature dimension if that dimension is never relevant to the task (Feldmann-Wüstefeld et al., 2015). Similarly, data from this study suggest that the feature dimension color was actively suppressed, resulting in below-baseline report frequency of singleton identity.

The RT results on one side and the report frequency results and EEG results on the other side may seem at odds at first glance; longer RTs were found for singleton-present trials, indicating attentional capture, yet singletons were reported less frequently than neutral distractor identities, and no distractor-N2pc, but rather a Pd was found, suggesting efficient suppression. In previous studies that combined a letter probe and a visual search task to reveal below-baseline attention deployment at salient distractor locations (Gaspelin & Luck, 2018a; Gaspelin et al., 2015), a negative capture effect (faster RTs for color distractor present trials) was found. This was explained in the context of the signal suppression hypothesis that predicts that irrelevant salient items are actively suppressed to avoid capture (Gaspelin et al., 2015). Although the classical interpretation of longer RTs is attentional capture (Theeuwes, 2010), it may also be possible that the necessary suppression (as evident in the Pd and low singleton identity reports) that is applied to avoid attentional capture is time demanding, thus resulting in longer RTs in singleton-present trials. This nonspatial filtering costs account (Folk & Remington, 1998) is also supported by the fact that we did not find a distractor-N2pc in any condition that would be indicative of attentional capture (see also

Wykowska & Schubö, 2011). The absence of a distractor-N2pc that suggests nonspatial filtering costs would also imply that suppression is applied proactively (Wang, van Driel, Ort, & Theeuwes, 2019; Gaspelin & Luck, 2018b; Reeder et al., 2017) rather than reactively (Lahav, Makovski, & Tsai, 2012; Moher & Egeth, 2012). It is not clear, however, whether proactive suppression may operate on various features within a dimension (such as the three colors used in this study) simultaneously. Alternatively, it may be that irregularities in an entire dimension (any color singleton) can be proactively suppressed as it was found that when observers learn to suppress a specific color, other colors can be suppressed more efficiently, too (Feldmann-Wüstefeld et al., 2015). Either way, the present results suggest that the presence of the color singleton slows down attentional allocation to the target without actually attracting attention and that then, in a second step, suppression is applied to the color singleton.

The present results are also in line with a large body of studies showing that RT costs can occur even when suppression is applied (Feldmann-Wüstefeld et al., 2015; Hilimire & Corballis, 2014; Kiss, Grubert, Petersen, & Eimer, 2012; Sawaki et al., 2012). One aspect that may have particularly fostered RT costs in this study is the fact that distractor color varied randomly from trial to trial, preventing participants to apply a negative search template (Arita et al., 2012). As a result, it was presumably more difficult to suppress the color distractor than in Gaspelin et al. (2015) and Gaspelin and Luck (2018a) since its feature was not predictable. Moreover, Gaspelin and Luck measured negative capture in a search task that was shown until response, imposing relatively little attentional demands. In our paradigm, attentional capture was measured in a setup in which stimuli were presented for only 120 msec and then masked. This makes competition in attention deployment much more prominent and time sensitive in our paradigm, and fast responses to targets were shown to be more vulnerable to distraction to salient irrelevant items than slow responses (van Zoest & Donk, 2006; van Zoest, Donk, & Theeuwes, 2004).

Interestingly, N2pc amplitudes did not vary between trials in which the target, distractor, or singleton identity was reported. This suggests that target processing is not contributing to reporting the correct item. This may be partially due to the fact that the target was relatively easy to find, being a shape pop-out stimulus that did not vary between trials and thus allows application of a feature search mode (Lamy & Egeth, 2003). Making a target more difficult to find may increase the necessity to efficiently attend the target, and a relatively small N2pc amplitude in such a task may be predictive of how successfully the target identity is reported. Nevertheless, the present data clearly show that the successful suppression of salient irrelevant items is crucial to successfully do a visual search task, and failing to do so can lead to behavioral errors. It should be noted that the target-N2pc does not necessarily solely reflect target enhancement. In the original Pd paper (Hickey et al.,

2009), the authors argued that both Pd and target-N2pc may reflect different types of distractor processing. One type occurs at the cortical location of distractor processing, acting to inhibit the distractor representation. The other type occurs at the cortical location of the target, acting to shelter the target representation from inhibitory signals stemming from distractors (see also Luck & Kappenman, 2012). The exploratory CDA analyses provided further evidence for what may result from failed suppression. As our task was relatively difficult, all digits may have had to undergo working memory identification, and in fact, a CDA was elicited both by targets and singletons. Targets elicited smaller CDA amplitudes when a singleton was reported, suggesting less efficient encoding of relevant information into working memory. It was previously shown that attentionally more demanding tasks elicit more sustained CDAs as information is required to be maintained in working memory longer (Prime & Jolicoeur, 2010; Mazza, Turatto, Umiltà, & Eimer, 2007). Accordingly, in this study when the target was not maintained long enough in working memory to be sufficiently processed, this may have resulted in an erroneous response. In this study, singletons elicited larger CDA amplitudes when a singleton was reported, suggesting accidental encoding of irrelevant information into working memory. This is in line with a previous study that found salient distractors elicited a CDA in slow trials but not in fast trials (Gaspar & McDonald, 2014; see also Mazza et al., 2007). The authors interpreted this in terms of better performance in trials in which distractors failed to gain access to working memory. Our results are in line with this notion and further suggest that if irrelevant information gains access to working memory because of failed suppression, it is also more likely maintained and then later erroneously reported. Conversely, if relevant information is efficiently encoded into working memory, the correct information is more likely retrieved.

In conclusion, we provide further evidence that suppression is a qualitatively different mechanism from enhancement within selective attention. Our study is the first to measure the Pd component in trials in which active suppression of irrelevant information below baseline was found, albeit this study remains correlational. The key finding is that singleton identity was less often reported than identity of a nonsalient distractor. At the same time, in trials in which the identity of the wrong, salient item was reported, suppression was applied too late. Suppression of the salient distractor increased throughout the experiment, highlighting the important role of learning to suppress irrelevant, potentially distracting information.

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