Attentional suppression is delayed for threatening distractors

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Abstract

According to the threat-capture hypothesis, fear-related stimuli have a high attentional priority. As a result, irrelevant-but-salient stimuli interfere more with a visual search task when they are perceived as threatening. We investigated the neural basis for behavioral interference in conditions that promote attentional suppression of distracting stimuli (i.e., easy search with fixed target/distractor roles). In Experiment 1, participants discriminated the shape of a neutral target (a flower), which competed for selection with a threat-related (spider) or neutral (leaf) distractor. In line with prior results, we observed larger interference from spider than leaf distractors. At an electrophysiological level, we found that participants actively suppressed both distractors as evidenced by the presence of a posterior positivity between 200-300 ms, the P_D . Critically, the P_D was delayed with spider compared to leaf distractors. Further, in the spider distractor condition, the offset of the P_D component correlated with response time to complete the search task when the spider was present. Experiment 2 was a control experiment where we confirmed that the results depended on the execution of the peripheral search task. When participants performed a localization task on the fixation cross, the decisive results from Experiment 1 were not replicated despite equal peripheral stimulation. Our results indicate that the behavioral delay incurred by threatening stimuli is accompanied by a delay of suppressive mechanisms. In contrast, we found no evidence for initial capture followed by suppression that may be predicted by hypervigilance-avoidance theory.

Introduction

Our brain can only process a limited amount of visual information. The necessary reduction of the amount of information is ascribed to visual selective attention (Desimone & Duncan, 1995; LaBerge, 1995). In recent years, there has been substantial interest in the effect of emotional saliency on attentional selection. Some objects may have higher attentional priority based on their physical saliency (e.g. Pashler, 1988; Theeuwes, 1992), but the affective value of an object is also central in establishing its attentional priority (e.g. Eastwood, Smilek, & Merikle, 2001; Fox et al., 2000). Higher attentional priority is given to stimuli associated with a risk of harm or threat to survival. The *threat-capture hypothesis* (Öhman & Mineka, 2001) suggests that threatening visual objects increase capture of attention compared to non-threatening stimuli. The account states that the preferential selection of threatening objects is rapid, resistant to active top-down attentional control and reliant on an evolutionary old defense system mediated by the limbic system, specifically the amygdala (LeDoux, 1996).

High attentional priority affects different aspects of attentional selection. In visual search tasks, threat-related attentional biases often result in facilitated orienting to threat-related targets, which allows for faster and more accurate responses. Facilitated attentional selection of fear-related targets is well established and is the basis of studies on the *anger superiority effect*, which refers to the faster processing of threatening (angry) faces compared to happy faces (Mineka & Ohman, 2002; Öhman, 1996; Öhman, Flykt, & Esteves, 2001; Williams, Watts, MacLeod, & Mathews, 1988).

Conversely, preferential processing of threatening stimuli may also elicit interference in visual search tasks. In particular, the threat-capture hypothesis predicts that threatening stimuli capture attention despite being irrelevant for the ongoing task. One possibility to

measure attentional captured by a salient-but-irrelevant stimulus is the *additional singleton paradigm*, which assesses the precedence of stimulus-driven (bottom-up) attention over goal-driven (top-down) attention (Theeuwes, 1991). It was observed that irrelevant angry faces produced more interference than happy faces (Burra, Barras, Coll, & Kerzel, 2016; Burra, Coll, Barras, & Kerzel, 2017; Hodsoll, Viding, & Lavie, 2011; Huang, Chang, & Chen, 2011).

In addition to certain facial expressions, animals such as snakes or spiders also carry threat value (Öhman et al., 2001). Spiders in particular are a common object of phobias, but are also rated negatively by healthy participants. Similar to angry faces, facilitated orienting to spider relative to neutral targets has been demonstrated in various tasks, such as the dot probe task (Lipp & Derakshan, 2005; Mogg & Bradley, 2006), visual search tasks (Öhman et al., 2001; Soares, Esteves, Lundqvist, & Ohman, 2009), or object identification tasks (Kolassa, Musial, Mohr, Trippe, & Miltner, 2005). Moreover, behavioral studies provided evidence for stronger attentional capture by spider relative to neutral distractors in visual search tasks (Lipp & Waters, 2007; Miltner, Krieschel, Hecht, Trippe, & Weiss, 2004; Rinck, Reinecke, Ellwart, Heuer, & Becker, 2005). That is, search was slower in the presence of a task-irrelevant spider as compared to a non-spider distractor. Thus, both facilitated target search and stronger distractor interference have been taken to support the high priority of threatening stimuli in attentional selection.

To provide further evidence for the rapid attentional processing of threat-related stimuli, studies were conducted using the N2pc component, a marker of attentional selection. The N2pc is observed at posterior-occipital electrodes approximately 180 to 300 ms after display onset (Eimer, 1996; Luck & Hillyard, 1994), and corresponds to a more negative voltage at electrode sites contralateral than ipsilateral to an attended item. The

N2pc revealed enhanced attentional selection of spiders at an early stage of visual processing in spider-fearful participants (Weymar, Gerdes, Low, Alpers, & Hamm, 2013). In the study of Weymar et al. (2013), the participants were required to detect the presence of an odd stimulus in an array of six items. The N2pc amplitude to spiders was larger for spider-fearful compared to non-fearful participants, confirming that threatening stimuli capture attention more than neutral stimuli. Similar results were observed with other phobias, such as blood or social phobia (Buodo, Sarlo, Munafo, & Palomba, 2009; Reutter, Hewig, Wieser, & Osinsky, 2017; Weymar et al., 2013),

Beyond attentional capture by salient distractors, recent research has focused on mechanisms that avoid distraction by salient stimuli. Most recently, Gaspelin and Luck (2018b) reviewed evidence for the idea that distraction by salient stimuli is avoided by their top-down suppression. Key evidence for distractor suppression is a contralateral positivity at the same electrode sites and in the same time range as the N2pc, which has been labelled P_D (Hickey, Di Lollo, & McDonald, 2009). The P_D has mostly been observed in variants of Theeuwes' (1992) additional singleton paradigm (Burra & Kerzel, 2013, 2014; Eimer & Kiss, 2008; Gaspar, Christie, Prime, Jolicoeur, & McDonald, 2016; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018a; Jannati, Gaspar, & McDonald, 2013; Sawaki, Geng, & Luck, 2012; Sawaki & Luck, 2010). However, a positivity was also observed earlier, between 100-200 ms, which may reflect a sensory saliency signal (Sawaki & Luck, 2010). The positivity may also occur later, between 300 and 400 ms, where it may reflect the termination of an attention shift (Hilimire, Mounts, Parks, & Corballis, 2011; Liesefeld, Liesefeld, Tollner, & Muller, 2017; Sawaki et al., 2012). In the present study, we refer to the early positivity between 100-200 ms as Ppc (Barras & Kerzel, 2017; Fortier-Gauthier, Moffat, Dell'Acqua, McDonald, & Jolicoeur, 2012; Gokce, Geyer, Finke, Muller, & Tollner, 2014; Jannati et al., 2013) even

though it is not quite clear whether it is functionally separate from the P_D in the 200-300 ms interval (Barras & Kerzel, 2017; Weaver, van Zoest, & Hickey, 2017).

Recent research has also uncovered the conditions that determine whether a salient stimulus can be suppressed. Burra and Kerzel (2013) showed that a color distractor elicits an N2pc (i.e., attentional capture) when the target and nontarget shapes switch roles in an unpredictable manner. In contrast, fixed roles of target and nontarget stimuli result in a P_D (Burra & Kerzel, 2013; Jannati et al., 2013), suggesting that the colored distractor was suppressed. Because random swaps between target and distractor result in slower search times while fixed targets result in efficient search (Lamy & Yashar, 2008; Pinto, Olivers, & Theeuwes, 2005), one may conclude that easy search tasks allow for suppression while difficult search results in capture (Barras & Kerzel, 2017). With fixed targets and threatening faces as distractors, however, both suppression (Bretherton, Eysenck, Richards, & Holmes, 2017; Burra et al., 2017) and capture (Burra et al., 2016; Eimer & Kiss, 2007) were observed, showing that motivational value may sometimes prevent distractor suppression even when the target is perfectly predictable.

In the present paper, we addressed the question whether attentional suppression of threatening stimuli differs from the attentional suppression of neutral stimuli. It is not clear what to predict based on the facilitated attentional deployment to threatening targets that we reviewed above. Possibly, the expected attentional suppression is cancelled by attentional capture resulting from the high attentional priority of threatening stimuli. It was shown that the P_D and N2pc component are additive so that capture and distraction jointly determine the amplitude and sign of the voltage difference (Gaspar & McDonald, 2014; Hickey, McDonald, & Theeuwes, 2006; Liesefeld et al., 2017). Thus, neutral stimuli may be suppressed, while attentional capture cancels the positivity either completely or partially.

Another prediction is made by the hypervigilance-avoidance hypothesis (e.g., Mogg & Bradley, 2006), which was developed in the context of anxiety. Fearful or phobic participants initially respond to the feared object (e.g., a spider) by hypervigilance combined with fear. Subsequently, they avoid the feared object by directing attention elsewhere. While we are not concerned with phobic populations, it is nonetheless possible to adopt the hypothesis to non-fearful participants. In particular, it may be possible that threatening stimuli result in attentional capture followed by suppression, whereas non-threatening stimuli can be immediately suppressed. Thus, there would be a sequence of capture followed by suppression for threatening stimuli. A similar sequence was observed when the distractor resembled the target and was therefore initially attended (Hilimire et al., 2011; Liesefeld et al., 2017).

Experiment 1

In this study, we compared the electrophysiological signatures of suppression with threatening and non-threatening distractors. To isolate distractor from target processing, the target was presented on the vertical meridian while the distractor was presented on a lateralized position. In this configuration, the difference between contra and ipsilateral posterior electrodes (i.e., N2pc or P_D) only reflects distractor processing (Woodman & Luck, 2003). Further, the target and distractor stimuli never swapped roles and the search task was easy, so that we expect a P_D to the distractor (Barras & Kerzel, 2017). Consistent with the hypervigilance-avoidance hypothesis, we predict that threatening distractors result in attentional capture (N2pc) followed by attentional suppression (P_D), while neutral stimuli only elicit suppression (P_D). Similar to Weymar et al. (2013), we used spiders as threatening distractors. As a non-threatening distractor, we selected a schematic leaf because it bears some visual resemblance to the spider stimulus. Participants were instructed to indicate the

position of a missing petal in the upper part a flower stimulus. Therefore, the leaf and the spider stimulus were irrelevant to the task and there was no incentive to attend to them (Theeuwes, 2010; Yantis & Egeth, 1999). The non-targets were also flower stimuli with a missing petal in the lower central position, which made them easy to discriminate from the target stimulus while at the same time balancing visual contrast and spatial frequency.

Materials and Method

Participants. Twenty-one students enrolled in a first year psychology class at the University of Geneva (all female) participated in the experiment. According to self-report, participants had normal or corrected-to-normal vision and were free of neurological or psychiatric conditions. All participants were naive regarding the purpose of the experiment. The local ethics committee of the University of Geneva had approved the study, and informed consent was obtained from participants prior to the experiment. Due to excessive eye blinks and saccades, three datasets were discarded, resulting in 18 participants (age: $M = 21.1$, $SD = 3.7$ years) for all subsequent analyses.

Stimuli. Six stimuli were presented at 4.5° of eccentricity on a black background. The approximate dimensions of the stimuli was $\sim 3^\circ$ horizontal x 4° vertical. The nontargets and targets were flowers with a missing petal. The distractors were a leaf and a spider (see Figure 1A). To match the luminance of distractor stimuli, the spider and leaf images were composed of the same number of black pixels (~ 16800). All pictures were black and white and the background was white (similar to Weymar et al., 2013).

Figure 1. A) Stimuli in the visual search task. The target was a flower with a missing petal in the upper part of the flower and participants were asked to judge whether the gap was on the left or right. Nontargets were flowers with a missing petal below the center. A spider and a leaf were used as distractor stimuli. The search array was displayed until a response was registered. B) Illustration of the trial sequence. The first trial shows a vertical target and lateral distractor. The second trial shows a distractor-absent trial with a lateral target. Event-related potentials were only analyzed in these configurations.

Stimuli and Procedure. The experiment took place in a dimly lit room. The Cogent toolbox (www.vislab.ucl.ac.uk/Cogent2000) for MATLAB was used to display the stimuli. All stimuli were displayed on a CRT screen. The target consisted of a flower with a missing petal

on the upper left or right. The missing petal of the target flower and the location of the target varied unpredictably. A distractor object (50% spider, 50% leaf) was present in two-thirds of the trials, similar to previous studies on attentional capture (see Burra et al., 2016; Burra et al., 2017; Burra & Kerzel, 2013, 2014; Hickey et al., 2006). On half of the distractor-present trials, the target was on the vertical midline and the distractor on a lateral position, which elicited a lateralized component to the distractor but not to the target. To make target and distractor positions unpredictable, the distractor appeared ipsilateral on 25% of the distractor-present trials and contralateral on the remaining 25% distractor-present trials. As the latter conditions do not provide information useful to testing our experimental hypothesis, they were not analyzed.

As depicted in Figure 1B, each trial began with a black fixation cross on a white background for a random interval between 600 and 1200 ms. Participants were instructed to report the orientation of the missing petal as quickly as possible while maintaining accuracy better than 90%. Participants were instructed to respond using their right hand to press one of two keys on a standard keyboard. Incorrect responses were indicated by visual feedback. The stimulus remained on the screen until a response was given, followed by 1000 ms of blank screen. Before the experiment, participants completed 96 trials of the task in which they were trained to avoid moving their eyes in the direction of the target. Each participant performed 12 blocks of 96 experimental trials for a total of 1152 trials. Prior to the experiment, participants completed a questionnaire regarding their fear of spiders (Fear of Spider Questionnaire, FSQ, Szymanski & O'Donohue, 1995) in its French Version (FSQ, Delroisse & Philippot, 2007).

After completing the experiment, participants evaluated the stimuli in order to assess their subjective experience of threat. Participants evaluated the degree to which the stimuli

were pleasant (from 0 = very unpleasant to 100 = very pleasant), arousing (from 0 = not stimulating to 100 = extremely stimulating), frightening (from 0 = no fear to 100 = extreme fear), and disgusting (from 0 = no disgust to 100 extreme disgust) (similar to Devue, Belopolsky, & Theeuwes, 2011).

Electrophysiological recording and analysis. EEG signals were recorded using an actiCHamp amplifier (Brain Products, Gilching, Germany) with active Ag/AgCl electrodes sampled at 1000 Hz. Twenty-seven electrodes were fixed on the scalp, one on the outer canthus of each eye (HEOG), one above and below the right eye (VEOG), and one on each earlobe. Cz served as the online reference and AFz as the ground. Electrode impedance was kept below 20 k Ω for EEG and H/VEOG.

Using BrainVision Analyzer 2.1 (Brain Products, Gilching, Germany), data were filtered with a Butterworth zero-phase shift low-pass filter (40 Hz with 24 dB/oct.). In order to exclude eye movement, blinks or general artifacts, we used the same rejection criteria as in our prior study (Burra et al., 2016; Burra et al., 2017). On average, 15.9% of the trials were discarded. Epochs started 100 ms before the onset of the display and ended 600 ms after, for a total time window of 700 ms. When necessary, we corrected for the non-sphericity of the data in the ANOVA using the Greenhouse-Geisser correction of the degrees of freedom.

The N2pc/P_D mean amplitudes were measured at pooled electrodes PO7/PO8 and P7/P8, where the signal was maximal (see topography, Figure 2C). At these sites, we extracted the mean amplitude at its apex, i.e. between 230 and 330 ms after stimulus onset. Visual inspection revealed an early positive component, so that we also analyzed the interval from 90 to 130 ms. Moreover, we measured ERP latency in the following way: First, we measured onset latency for all ERPs using the jackknife-based scoring method (Miller, Patterson, & Ulrich, 1998). This method does not only constitute the standard approach to

quantify LRP latency (see Smulders & Miller, 2012), but has the specific advantage that it provides especially robust latency estimates in general (see Kiesel, Miller, Jolicoeur, & Brisson, 2008). We derived ERP onset and offset latency for the P_D in the distractor conditions using a relative amplitude criterion of 75% of maximum amplitude before and after the peak of the component respectively. All jackknife-based latency (onset and offset) estimates were then submitted to a paired-sample t-test. The resulting t-values were corrected using the formula $t_c = t/(n-1)^2$, where t_c represents the corrected t value, and n represents the number of participants (Kiesel et al., 2008). Finally, we measured the correlation between behavioral response time (RT) and the onset and offset of distractor suppression. Individual onset and offset were extracted using

$$(1) o_i = n\bar{J} - (n-1)j_i,$$

where $\bar{J}$ is the mean of subaverage scores across n participants and j_i is the subaverage that excludes participant i 's waveform. The values of o_i will be referred to as the *retrieved individual* latency (Smulders, 2010). To avoid inflating the experimentwise Type 1 error rate, only the theoretically most relevant correlations were examined, i.e., the onset and offset of P_D were correlated with RTs in the respective distractor conditions.

Figure 2. Panels A and B present the difference waveforms between contralateral and ipsilateral electrodes with respect to the target (in the absence of a distractor), and with respect to the spider and leaf distractors. Panels A and B present the data from Experiments 1 and 2, respectively. The topography of the P_D between 230–330 ms in panel C shows that

the component peaked maximally at site P7/P8 and PO7/PO8. Panel D presents the difference between the differences waveforms to spider and leaf distractors for Experiments 1 and 2 (from panels A and B). Shaded areas indicate the analysis intervals of 50 ms duration. Panel E shows a scatter plot of the offset of the P_D to the spider distractor and RTs in Experiment 1.

Behavioral Results

Questionnaire. The mean spider fear score of participants in Experiment 1 was 59.5 (range: 22–90; SD: 24.92).

Ratings. We performed four one-way, repeated measures ANOVAs to evaluate effects of stimulus type (flower, leaf, spider) on rated pleasantness, arousal, fear and disgust. As expected, stimulus type had a significant effect on all measures (see Table 2), $F_s(2, 34) > 14.5$, $ps < .001$, $\eta_p^2 > .460$, Post-hoc analysis indicated that spiders were rated as more unpleasant, more arousing, more frightening and more disgusting than flowers and leaves, $ts(17) > 3.57$, $ps < .002$. Leaf and flower stimuli were not rated as significantly different from one another on any measure, $ts(17) > 1.88$, $ps > .08$.

Table 1. Mean ratings of the three stimuli in Experiment 1. Standard errors are given in parenthesis.

	Flower	Leaf	Spider
Pleasantness	57.3 (3.13)	64 (3.6)	21.4 (3.95)
Arousal	22 (5.34)	12.8 (5.83)	45.8 (5.8)
Fear	13 (4.8)	4.5 (4.3)	38.94 (6.3)

Disgust	17.1 (5.4)	9.2 (5.2)	41.6 (6.8)
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Reaction Times and Accuracy. A one-way (distractor type: no distractor, spider distractor, leaf distractor), repeated-measures ANOVA revealed that RTs were shorter on distractor-absent than distractor-present trials (618, 640, and 633 ms for no distractor, spider distractor, and leaf distractor, respectively), $F(2, 34) = 15.26, p < .001, \eta_p^2 = 0.473$. Critically, a paired t-test revealed that RTs were longer with the spider than with the leaf distractor (640 vs. 633 ms), $t(17) = 2.32, p = .03$, Cohen's $d = 0.55$. Additionally, accuracy was lower in the distractor-present conditions (0.96, 0.95, 0.94 for no distractor, spider distractor, leaf distractor, respectively), $F(2, 34) = 3.49, p = .042, \eta_p^2 = 0.171$. However, there was no significant difference between spider and leaf distractors, $t(17) = 1.22, p = 0.23$.

Electrophysiological results

Global N2pc/P_D Amplitudes (230–330 ms). The difference waves obtained by subtracting ipsi- from contralateral activity are shown in Figure 2A. The same ANOVA as above was conducted on mean difference amplitudes. A significant effect of distractor type was revealed, $F(1.24, 21.10) = 49.15, p < .001, \eta_p^2 = .74$. The voltage difference was negative to targets (-1.29 μ V), consistent with an N2pc, but it was positive to spider (2.16 μ V) and leaf (2.11 μ V) distractors, consistent with a P_D. There was no significant difference between spider and leaf distractors, $t(17) = 0.28, p = .77$. The negative (N2pc) and positive (P_D) components were significantly larger than zero, $ts(17) > 4.05, ps < .001$, Cohen's $ds > 0.95$.

Onset/Offset of distractor conditions. As depicted in Figure 2a, both the onset and offset of the P_D was shifted. The P_D to the spider distractor started and ended later than the P_D to the leaf distractor. Using the jackknife procedure, we confirmed that onset (spider vs.

leaf: 252 vs. 241 ms), $t_c(17) = 2.13$, $p = .04$, and offset (spider vs. leaf: 318 vs. 301 ms), $t_c(17) = 2.41$, $p = .028$, was delayed. In other words, suppression of the spider distractor occurred approximately 13 ms later than suppression of the leaf distractor.

Time-course of distractor suppression. We further assessed the temporal dynamics of attentional suppression of spider and leaf distractors by analyzing mean difference amplitudes (contra minus ipsi) in four 50 ms-time windows starting 150 after stimulus onset. To illustrate the time course, we subtracted the difference waves of the spider distractor from the difference wave for the leaf distractor (Figure 2D). We ran a 4 (50 ms time intervals: starting at 150, 200, 250 and 300 ms) x 2 (distractor type: spider, leaf) on the mean difference amplitudes. We found a main effect of time, $F(3, 51) = 23.91$, $p < .001$, $\eta_p^2 = .58$, but no main effect for distractor condition, $p = .319$. Critically, there was an interaction between time interval and distractor type, $F(3, 51) = 8.13$, $p < .001$, $\eta_p^2 = .32$. Post-hoc analysis revealed that the leaf distractor elicited a more positive difference amplitude than the spider distractor in the time windows from 150-200 ms (0.35 vs. -0.05 μV), $t(17) = 2.63$, $p = .018$, Cohen's $d = 0.62$, and from 200-250 ms (1.59 vs. 1.14 μV), $t(17) = 2.1$, $p = .046$, Cohen's $d = 0.51$. Conversely, in the 300-350 ms time window, the difference amplitude was more positive for the spider than the leaf distractor (1.64 μV vs. 1.17 μV , respectively), $t(17) = 2.39$, $p = .029$, Cohen's $d = 0.56$. There was no statistical difference between distractor conditions in the 250-300 ms time window, $p = .32$. The time course analysis suggests that the P_D to the spider was delayed, and this conclusion is further corroborated by one-sample t-tests against zero for each of the four time intervals. The difference amplitudes for the spider distractor were not significant from zero in the earliest time interval from 150-200 ms, $p = .82$, but were significant from 200 ms onwards, $t_s(17) > 3.57$, $p_s < .002$, Cohen's $d_s >$

0.84. For the leaf distractor, the difference amplitudes were significantly positive in all intervals, including the earliest interval, $ts(17) > 2.37$, $ps < .03$, Cohen's $ds > 0.56$.

Correlations between the onset and offset of suppression and behavior. RTs in the condition with a spider distractor did not correlate with the onset of the P_D to the spider distractor, $r(18) = -.27$, $p = .26$. The same was true for the correlation between RTs and onset of the P_D with a leaf distractor, $r(18) = -.23$, $p = .34$. However, as depicted in Figure 1E, the RTs in the condition with a spider distractor correlated with the offset of the P_D to the spider distractor, $r(18) = .47$, $p = .04$, $R^2 = .226$, which was not the case for RTs and offset of the P_D with a leaf distractor, $r(18) = 0.06$, $p = .80$.

Early positive deflection. Inspection of Figure 2A suggests that there was a positive deflection to distractor stimuli in the time range of the Ppc (100-200 ms). We ran a one-way (distractor type: no distractor, spider distractor, leaf distractor) ANOVA on the difference amplitudes between 90 and 130 ms after stimulus onset. There was a statistically significant effect, $F(2, 34) = 7.49$, $p < .002$, $\eta_p^2 = .31$. Post-hoc analysis revealed that the mean difference amplitudes occurring in the no distractor condition ($-0.17 \mu V$) were different from both distractor conditions ($0.7 \mu V$ for leaf and $0.53 \mu V$ for spider), $ts(17) > 2.49$, $ps < .023$, Cohen's $ds > 0.58$. However, the difference amplitudes for spider and leaf distractor were not statistically different, $t(17) = 1.17$, $p = .30$. Further, the difference amplitudes for spider and leaf distractors were significantly different from zero, $ts(17) > 4.85$, $ps < .001$, Cohen's $ds > 0.72$, consistent with the occurrence of a Ppc, while the difference amplitude in the no distractor condition was not significantly different from zero, $t(17) = 0.13$, $p = .89$.

Discussion

We investigated attentional suppression of threatening and non-threatening distractors (i.e., spider vs. leaf). Conditions were selected to promote the suppression of

salient-but-irrelevant stimuli. Importantly, the search task was easy because there was little similarity between target and nontargets or between target and distractor. In addition, the target stimulus was fixed because it did not swap roles with the nontarget stimuli. We found that the presence of a spider distractor increased RTs more than a leaf distractor, probably because spiders have a higher attentional priority. The electrophysiological data confirmed that both spider and leaf distractors resulted in a P_D , suggesting that both stimuli were attentionally suppressed. However, suppression of the spider distractor occurred approximately 13 ms later than suppression of the leaf. With respect to the hypervigilance-avoidance hypothesis, we did not find that attention was initially captured by threatening stimuli. That is, there was no N2pc to the spider distractor. Rather, avoidance, as indexed by the P_D , was delayed relative to neutral distractors. Thus, instead of the expected sequence of capture and suppression, we find delayed suppression for threatening stimuli. Also, the amplitude of the P_D was not different, but only the timing was, which suggests that threatening stimuli are not met with more suppression. Finally, we observed that the offset of the P_D to spider distractors correlated with RTs in the presence of spider distractors.

There is a potential caveat in Experiment 1. It is possible that visual differences between the spider and leaf distractors accounted for the delayed suppression. Despite our efforts to match visual aspects of the distractor stimuli, the remaining differences (e.g., in terms of visual spatial frequencies) might explain the electrophysiological differences (Luck & Hillyard, 1994). Further, the early positivity to both distractors, which we labelled Ppc (Positivity, posterior contralateral Fortier-Gauthier et al., 2012; Jannati et al., 2013; Leblanc, Prime, & Jolicoeur, 2008), attests to the presence of local feature discontinuities and these discontinuities may guide later attentional processes (Sawaki & Luck, 2010).

In order to rule out the possibility that imbalanced saliency between spider and leaf distractors accounts for the differential delay of suppression, we ran a second experiment using the same displays, but with a different task. In Experiment 2, participants were required to localize a missing pixel on the fixation cross. We hypothesized that low-level differences would continue to influence the lateralized ERP, even if the stimulus was mostly ignored. If the differential delay of the suppression effect were only based on stimulus characteristics, we would observe the same results as in Experiment 1.

Materials and Method

Participants. Nineteen students (2 male,) with the same characteristics as in Experiment 1 participated. One female participant's data were removed before analysis due to excessive eye movements, resulting in 18 participants for all subsequent analyses (age: $M = 22$ years, $SD = 3.25$, not significantly different from Experiment 1, $p = .54$).

Stimuli, Apparatus, Procedure, and electrophysiological recording and analysis.

Experiment 2 was similar to Experiment 1 with the following exceptions. On each trial, we removed one pixel from the vertical line of the fixation cross (50% of trials from the upper part, 50% from the lower part). Participants were required to indicate the location of the missing pixel by responding with one of two keys on a standard keyboard with their right hand. Due to technical problems, the data of four participants could not be used for the analysis of stimulus ratings. Eighteen percent of the trials were removed due to artifacts.

Results

Behavioral Results

Questionnaire. The mean level of fear in response to spiders was 46.11 (range: 18–95; SD: 24.47). The score was not significantly different from Experiment 1, $t(34) = 1.62$, $p = .113$.

Ratings. Analyses were performed on the data acquired from 14 participants. One-way, repeated-measures ANOVAs showed the expected effects of stimulus type (spider, leaf, flowers) on ratings of pleasantness, arousal, fear and disgust (see Table 2), $F_s(2, 26) > 11.48$, $ps < .001$, $\eta_p^2 > 0.469$. Post-hoc analysis indicated that spiders were rated as more unpleasant, more arousing, more frightening and more disgusting than flowers and leaves, $ts(13) > 3.3$, $ps < .005$. The ratings of leaf and flower stimuli were not significantly different concerning arousal, fear and disgust, $ts(13) > 2.01$, $ps > .07$. However, participants rated the leaf as more pleasant than the flower, $t(13) = 2.85$, $p = .014$. Spider and leaf scores were not significantly different from ratings in Experiment 1, $ts(30) < 1.48$, $ps > .16$.

Table 2. Mean ratings of the three stimuli in Experiment 2. Standard errors are given in parenthesis.

	Flower	Leaf	Spider
Pleasantness	55.6 (5.9)	68.9 (4.1)	28.3 (5.87)
Arousal	14.2 (5.2)	3.6 (1.8)	50.5 (8.2)
Fear	5.21 (2.3)	1.57 (0.7)	41.92 (9.6)
Disgust	4.35 (2.5)	0.71 (0.3)	36.1 (10.4)

Reaction Times and Accuracy. A one-way (stimulus type: no distractor, leaf distractor, spider distractor) ANOVA on RTs, $F(2, 34) = 0.71$, $p = .49$, and accuracy, $F(2, 34) =$

0.22, $p = .79$, did not find significant effects. Overall, mean RT was 506 ms and mean accuracy was .97.

Electrophysiological Results.

Global N2pc/P_D Amplitudes (230–330ms). Mean difference waves are shown in Figure 2B. The same one-way ANOVA as above on difference amplitudes (contra minus ipsilateral) during the 230–300 ms time period revealed a significant effect of distractor type, $F(2, 34) = 5.57$, $p = .008$, $\eta_p^2 = .25$. The P_D to the target in the absence of distractors (0.2 μ V) was smaller than the P_D to the leaf and flower distractors (0.63 and 0.69 μ V), $ts(17) > 2.62$, $ps < .018$, Cohen's $ds > 0.62$. However, the positivities did not differ between leaf and spider distractors (0.63 vs. 0.69 μ V), $p = .68$. The P_D was significant in both distractor conditions, $ts(17) > 2.59$, $ps < .019$, Cohen's $ds > 0.61$.

Onset/Offset of distractor conditions. There was no significant difference in onset or offset of the P_D between spider and leaf distractor conditions, $t_{cs}(17) < 0.53$, $ps > .6$.

Time-course of distractor suppression. We assessed the temporal dynamics of attentional suppression by analyzing amplitudes in 50 ms-time windows between 150 and 350 ms. We ran a 4 (50 ms time intervals: starting at 150, 200, 250 and 300 ms) x 2 (distractor type: spider, leaf) ANOVA on the mean difference amplitudes. There was no significant interaction between distractor type and time interval, $F(2, 34) = 0.45$, $p = .64$, or significant main effect of time, $F(1.3, 22.24) = .6$, $p = .55$, or distractor type, $F(1,17) = 0.03$, $p = .86$. However, one-sample t-tests revealed that the P_D in the distractor conditions were significantly positive, $ts(17) = 3.78$, $ps = .001$, Cohen's $ds > 0.89$,

Critically, by including the factor experiment in the ANOVA, we established that the temporal dynamics of attentional suppression differed significantly between Experiments 1

and 2, as evidenced by a significant three-way interaction of time interval, distractor, and experiment, $F(3, 102) = 3.22, p = .026, \eta_p^2 = .09$.

Correlations between onset and offset of suppression and behavior. There were no significant correlations between offsets of the P_D and RTs in the respective distractor conditions, $ps > .5$.

Early positive deflection. Analysis of the mean difference amplitudes in the early interval from 90 to 130 ms revealed a main effect of distractor type (none, spider distractor, leaf distractor), $F(1.45, 24.65) = 6.00, p < .013, \eta_p^2 = .43$. Post-hoc analysis revealed that mean difference amplitude to the target without distractor ($-0.04 \mu V$) was different from the distractor conditions (spider: $0.39 \mu V$; leaf: $0.61 \mu V$), $ts(17) > 2.7, ps < .013$, Cohen's $ds > 0.65$. However, there was no statistically significant difference between spider and leaf distractors, $t(17) = 1.13, p = .27$. We conducted t-tests against zero to confirm that the Ppc was present in the pooled distractor-present conditions, $t(17) = 5.04, p < .001$, Cohen's $d = 1.18$, but not in the distractor-absent condition, $t(17) = 0.31, p = .75$.

Discussion

When there was no search task and attention was focused on the fixation point, the results changed dramatically compared to Experiment 1, suggesting that low-level visual differences between spider and leaf distractors cannot account for the results observed in Experiment 1. Unlike in Experiment 1, the presence of a spider distractor did not increase RTs compared to a leaf distractor or the no distractor condition. The electrophysiological results confirmed the early positivity (Ppc) with spider and leaf distractors between 90 and 130 ms, suggesting that it is accounted for by imbalanced saliency and not related to attentional processing. Further, the Np2c to the target stimulus disappeared, suggesting that participants did not attend to it. However, both distractors continued to produce a small P_D ,

which may be caused by the sensory imbalance that already caused the Ppc. Critically, neither the latency and nor the time course of the P_D differed between spider and leaf distractors, suggesting that the delay of suppression with spider compared to leaf distractors in Experiment 1 was not accounted for by sensory processing.

General Discussion

We investigated the attentional mechanism at work when threatening distractors appear in a visual search task. Given the extant literature, we focused on salient-but-irrelevant spider stimuli. Behaviorally, we observed that RTs were longer with spider compared to neutral distractors. These results are consistent with previous studies (Devue et al., 2011; Lipp & Waters, 2007; Miltner et al., 2004; Rinck et al., 2005) and more generally with the threat capture account (Öhman & Mineka, 2001), which states that a threat-related distractor is prioritized over a neutral target. The increase in RTs in Experiment 1 with spiders compared to leaf distractors confirms the special status of threat-related stimuli in attentional selection.

The central question of the present study was whether the suppression of threatening stimuli would be different from the suppression of non-threatening stimuli. To answer this question, we created a search task that was likely to yield distractor suppression as reflected in the P_D . In particular, we selected an easy search task where target and distractor were highly discriminable and the target was fixed relative to the nontargets. We observed that the amplitude of suppression did not differ between threatening and non-threatening distractors, but the timing was different. In particular, the P_D started and ended later for the spider compared to the leaf distractor. Our results are not consistent with the hypothesis that threatening stimuli first capture attention before they are suppressed, which

we derived from the hypervigilance-avoidance hypothesis in the context of specific phobias (Mogg & Bradley, 2006). Rather, distractor suppression is delayed for threatening stimuli.

Further, we observed a correlation between the offset of the P_D to the spider and RTs in the respective distractor condition. The stronger association of the offset of suppression with behavior is consistent with a previous study on eye tracking. Gerdes, Alpers, and Pauli (2008) observed that the RTs of phobic patients increased when a suddenly appearing distractor image showed a spider compared to a neutral object. Interestingly, analyses of eye movements showed that the eyes did not move earlier to threatening than neutral images, but that they stayed longer on images of the feared objects. Thus, the offset of eye fixation on the image was related to RTs and not its onset. While the study by Gerdes et al. points to a failure to disengage attention from the feared stimulus, the underlying mechanism in our study is less clear because the P_D is related to attentional suppression, not attentional engagement or disengagement. Possibly, the time to terminate suppression determined the delay incurred by distractor processing that was visible in RTs of Experiment 1.

We did not find any difference between spider and leaf distractors in the P_{pc} interval. However, our data confirm that the spider distractor was processed differently in the P_D interval. Schematic spiders have been shown to have robust influence on attention networks and behavior (Hartikainen, Siiskonen, & Ogawa, 2012; Vuilleumier & Schwartz, 2001). It is possible that the presence of a spider delayed the active suppression due to a short-lived component linked to automatic processing of threatening stimuli. The delay in distractor suppression may reflect a reduction in the ability to engage executive control processes underlying reorienting of attention to the relevant target (Cisler & Koster, 2010). In the same vein, it has been argued that interference effects reflect delayed disengaging of attention

from fear-evoking stimuli (Gerdes et al., 2008). Task-related disengagement is likely mediated by top-down attentional control processes. It has been proposed that in situations of attentional competition, the outcome reflects the balance between top-down processing (via the prefrontal cortex) and stimulus-driven processing (via the amygdala) (Bishop, 2007). In this sense, the presence of a threat-related stimulus may disrupt top-down suppression, which slows down the behavioral response.

Finally, our data limit the scope of the threat capture account (Öhman & Mineka, 2001). The threat capture account claims that threat-related stimuli capture attention automatically, even when outside the focus of attention. However, the results of Experiment 2 do not support this claim. Although participants in Experiment 1 and Experiment 2 had similar fear of spiders and similar ratings of pleasantness, arousal, fear and disgust (see Tables 1 and 2), the P_D in Experiment 2 was insensitive to the valence of the distractors. On the one hand, this suggests that the results of Experiment 1 are not due to low-level confounds, but on the other hand, these results challenge the tenets of the threat-capture account. Specifically, they are hard to reconcile with the idea that threat-related stimuli capture attention automatically. Instead, they indicate that depending on the task, top-down control precludes attention from being captured by threatening stimuli. These results are consistent with prior research on physical saliency, which revealed the critical role of the distribution of spatial attention on attentional capture (Belopolsky & Theeuwes, 2010; Kerzel, Born, & Schonhammer, 2012)

In conclusion, our study further clarifies the interaction between top-down and bottom-up attention in the processing of irrelevant but threatening distractors. When the processing of a distractor competes with the processing of another relevant target, the active suppression of the distractor is modulated by the threat-related value conveyed by

the distractor. Concretely, a high threat value of the distractor delays the suppression of the distractor, which subsequently delays the response in the visual search task (Experiment 1). However, in contrast to some theories suggesting that threat-related distractors bias attentional selection automatically, the results of this study suggest that task demands mediate this effect. When attention is focused on the fixation point, attentional processing is unaffected by threat-related distractors (Experiment 2).

Taken together, the present results indicate that a threat-related distractor delays suppression in easy visual search task that promote attentional suppression of salient distractors. However, the same distractor did not affect performance when attention was focused on the fixation cross.

Conflict of interest statement

The authors declare no conflict of interest.

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