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Suppression history of distractor location biases attentional and oculomotor control

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ABSTRACT

Past selection experience greatly affects the deployment of attention such that targets are more readily selected if their features or locations were more frequently selected in the past. Crucially, recent studies have shown similar experience-dependent effects also for salient task irrelevant stimuli: distractors exerted less interference if they appeared at a location where they were presented more often, relatively to other possible locations. Here we investigated the effects of such *suppression history* on the immediate behavioural correlates of attentional deployment, i.e., eye movements. Participants were to make saccadic eye movements to a target stimulus, while ignoring a highly distracting irrelevant visual onset appearing abruptly on the screen in a proportion of trials. Crucially, this irrelevant onset occurred more frequently in two locations on the visual display and our results showed that, relatively to distractors elsewhere, onsets presented at these locations became easier to ignore, giving rise to reduced oculomotor capture. Consistent with the notion that experience can alter attentional deployment towards spatial locations, these findings indicate that, through learning, the priority of high frequency locations becomes suppressed, attenuating the intrinsic saliency of distractors appearing therein. Traces left by individual events of attentional suppression decrease the processing priority of coordinates within topographic maps of the visual space.

Introduction

Interacting efficiently with a crowded and ever-changing visual environment depends most critically on visual selective attention mechanisms. Among a multitude of available visual stimuli, selective attention allows the moment-to-moment focusing of limited processing resources on a restricted amount of information, aiding its access to perceptual awareness and, eventually, behavioural guidance (Chelazzi, Della Libera, Sani, & Santandrea, 2011; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004).

In the last decades a large number of studies have been dedicated to uncover the working of visual selective attention, providing substantial evidence of its impact on visual processing (Carrasco, 2011; Reynolds & Chelazzi, 2004). While the analysis of the selected pieces of information appears to be quantitatively and qualitatively enhanced (e.g., Carrasco, 2011), the un-selected stimuli may not just be "left on the background", in some cases their processing is actively suppressed (e.g., Gaspelin & Luck, 2018a, 2018b; Gaspelin, Leonard, & Luck, 2015; Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Noonan, Crittenden, Jensen, & Stokes, 2018; Suzuki & Gottlieb, 2013; Wang & Theeuwes, 2018a, 2018b, 2018c; Wyatt & Machado, 2013), so that their interference and distraction with respect to the ongoing activity is reduced. Selective attention thus seems to result from the combined, competitive action of signals capable of enhancing and/or suppressing the processing of the visual stimuli involved.

How attentional resources are deployed towards the visual stimuli in the environment was traditionally thought to derive from a balance between two classes of mechanisms, driven by different signals and relying on at least partly independent neural systems (e.g., Chica, Bartolomeo, & Lupiáñez, 2013; Theeuwes, 2010; Van der Stigchel et al., 2009). *Bottom-up* mechanisms are prompted by the physical properties of the visual inputs and prioritise stimuli that have

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conspicuous features or are unexpected (Theeuwes, 1994; Yantis & Egeth, 1999). *Top-down* mechanisms on the other hand allow the prioritisation of stimuli that, irrespectively of their physical salience, are relevant for the current internal goals (Gilbert & Li, 2013; Theeuwes, 2010).

While until very recently such bottom-up and top-down control signals were conceived to be the sole determinants of attentional control, this view has been now questioned by the discovery that selective attention is highly vulnerable to other sources of information, that access attentional control *irrespectively* of *either* current goals *or* the physical properties of the stimuli available. Indeed, the allocation of attentional resources onto visual objects or spatial locations may depend on *prior experience* with the same visual environment, a concept that however comprises a variety of phenomena (Anderson, 2016; Awh, Belopolsky, & Theeuwes, 2012; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Jiang, 2018; Todd & Manaligod, 2018). Among these are for instance the advantages found in the selection of stimuli whose location or features can be predicted on the basis of cumulative statistical contingencies (Ferrante et al., 2018; Geng & Behrmann, 2005; Sha, Remington, & Jiang, 2017). Yet, prior experience also encompasses the benefits observed in the selection of stimuli or locations whose selection in the past has been associated with rewarding outcomes (e.g., Anderson, Laurent, & Yantis, 2011a, 2011b; Chelazzi et al., 2014; Della Libera & Chelazzi, 2009; Della Libera, Perlato, & Chelazzi, 2011; Jiang, Sha, & Remington, 2015; see Failing & Theeuwes, 2018 for a review). Moreover, both types of experience-dependent sources of attentional control may exert their impact on selection at different timescales. For instance, prior experience may affect attentional processing on a trial-by-trial basis, giving rise to *intertrial priming effects* (e.g., Kristjánsson & Campana, 2010) – i.e., facilitating selection of stimuli whose features or location are repeated across consecutive trials – that can be further modulated by the concomitant delivery of reward signals (e.g., Della Libera & Chelazzi, 2006; Hickey, Chelazzi, & Theeuwes, 2010, 2014). Remarkable effects however have also been observed in the long term, leading to *systematic selection biases* with respect to stimuli or spatial locations that have acquired a relevant selection history (through pure stimulus repetition, e.g., Ferrante et al., 2018; Geng & Behrmann, 2005; Sha et al., 2017;

Wang & Theeuwes, 2018a, 2018b; 2018c; through reward delivery, e.g., Anderson et al., 2011a, 2011b; Chelazzi et al., 2014; Della Libera & Chelazzi, 2009).

The effects of prior experience are typically observed implicitly, with no need for participants to become aware of them, and it is now a matter of debate whether they should be assimilated to top-down or bottom-up forms of attentional control, or whether they should rightfully be considered as a category on their own (Awh et al., 2012; Theeuwes, 2018). Indeed, while many studies have been conducted to identify the neural correlates of top-down and bottom-up attentional control, contributing to disentangle their computational role both functionally and anatomically (e.g., Chica et al., 2013; Corbetta & Shulman, 2002; Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005), the evidence on the neural bases of the mechanisms leading and supporting experience-related plasticity of selective attention is still relatively scarce (Anderson, Laurent, & Yantis, 2014; Qi, Zeng, Ding, & Li, 2013). As a matter of fact, it might also be the case that different phenomena currently falling under this common bracket will be eventually brought back to independent sources of behavioural control, and be associated with different forms of plasticity within visual attention networks (e.g., plasticity of low-level visual representations vs. higher-order behavioural control functions; plasticity mediated by motivational levers vs. pure stimulus repetition). More evidence is now needed in order to reach a full comprehension of such adaptive features of visual selective attention (for an extensive discussion see Theeuwes, 2018, and the related commentaries: Becker, 2018; Chelazzi & Santandrea, 2018; Egeth, 2018; Gaspelin & Luck, 2018c; Kryklywy & Todd, 2018; Sisk, Remington, & Jiang, 2018; Wolfe, 2018).

Most of the evidence of experience-dependent plasticity in attentional processing has been observed with respect to the selection of behavioural targets, showing that attentional deployment is facilitated if the same visual information has been frequently selected in the past, or its selection has been associated with more positive outcomes. Such stimuli, that have therefore acquired an important *selection history*, when available in the visual environment tend to attract attention and be selected once more (e.g., Anderson et al., 2011a, 2011b; Chelazzi et al., 2014; Della Libera et al., 2011; Della Libera & Chelazzi, 2009; Jiang et al., 2015).

However, recent evidence has suggested that similar, symmetrical effects, can be observed also with respect to visual information that instead has been associated with an *history of suppression*. Considering in particular the deployment of selective attention across the visual space, the degree of interference determined by salient but irrelevant visual stimuli that appear at locations that in the past have been often associated with distracting events is reduced (Ferrante et al., 2018; Goschy, Bakos, Müller, & Zehetleitner, 2014; Leber, Gwinn, Hong, & O'Toole, 2016; Sauter, Liesefeld, & Müller, in press; Sauter, Liesefeld, Zehetleitner, & Müller, 2018; Wang & Theeuwes, 2018a, 2018b; for a recent review see Chelazzi, Marini, Pascucci, & Turatto, 2019). Depending on the specific manipulations performed, these effects have been observed for relatively wide regions of the visual field (i.e., contrasting visual hemifields with high vs. low distractor frequency, as in Goschy et al., 2014; Sauter et al., 2018; in press), but also for discrete spatial locations, emerging in a graded fashion which reflected the precise statistical contingencies applied (Ferrante et al., 2018; Wang & Theeuwes, 2018a, 2018b). Overall these studies suggest that suppression history may alter topographic maps of the visual space that code the attentional priority of the stimuli in the visual field (e.g., Todd & Manaligod, 2018). Stimuli appearing at frequently suppressed locations therefore become less capable of attracting attention, even when they happen to be task-relevant (e.g., Ferrante et al., 2018; Wang & Theeuwes, 2018a, 2018b).

Following this evidence, in this study we set out to extend our knowledge of the impact of suppression history on visual processing by probing its effects on the immediate behavioural manifestation of attentional deployment, that is the execution of eye movements (e.g., Awh, Armstrong, & Moore, 2006; Kowler, 2011). In particular, we aimed at exploring the extent to which the reduced interference determined by distractors in frequently suppressed locations would be reflected also in a change in their ability to automatically attract gaze and give rise to oculomotor capture (Theeuwes, 1994; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999).

We designed a visual search task in which participants were required, although not explicitly, to make a saccade to a colour singleton within a stimulus array and discriminate the orientation of a target bar shown inside it. In a proportion of trials, overall a bit over 50%, an additional colour singleton appeared abruptly in an otherwise empty position in the stimulus array but was completely irrelevant for the task. Importantly, while target location was equally likely in the stimulus display, the location in which distracting onsets could appear was pre-determined by design and more frequent in two out of six possible spatial locations.

Consistent with previous studies employing the oculomotor capture paradigm (e.g., Theeuwes et al., 1999; Theeuwes & Burger, 1998) we expected that the irrelevant visual onset would interfere with task performance (i.e., slower and less accurate responses). Specifically, we expected that these stimuli would yield remarkable oculomotor capture effects, such that a significant portion of eye movements would be directed towards them rather than to the task relevant item in the display (Theeuwes, 1994; Theeuwes et al., 1999; Theeuwes & Burger, 1998). Additionally, we predicted that as the frequency of distractor occurrence increased in some locations relatively to the others, the degree of interference associated with distractor presence would be gradually biased depending on its location. Crucially, we measured not only the latency and accuracy of manual responses to the main task, but also eye movements during each trial. This allowed us to examine the extent to which the expected changes in task performance would be mirrored by oculomotor performance, for instance revealing a decreased number of eye movements directed towards distractors in high frequency locations.

Unlike previous studies (Ferrante et al., 2018; Wang & Theeuwes, 2018a), we manipulated distractor probability across *two* different locations in the visual display, so that among the two lateralised distractor locations available in each hemifield one was associated with a high and the other with a low frequency bias (Figure 1). Moreover, in our paradigm the manipulations of distractor frequency were associated with spatial coordinates in the visual field that were not discretely marked in the stimulus display, and throughout the experimental session could only be occupied by salient visual onset distractors.

Methods

The study was approved by the Review Board for Research involving Human Participants (CARU) of the University of Verona. The experimental procedure
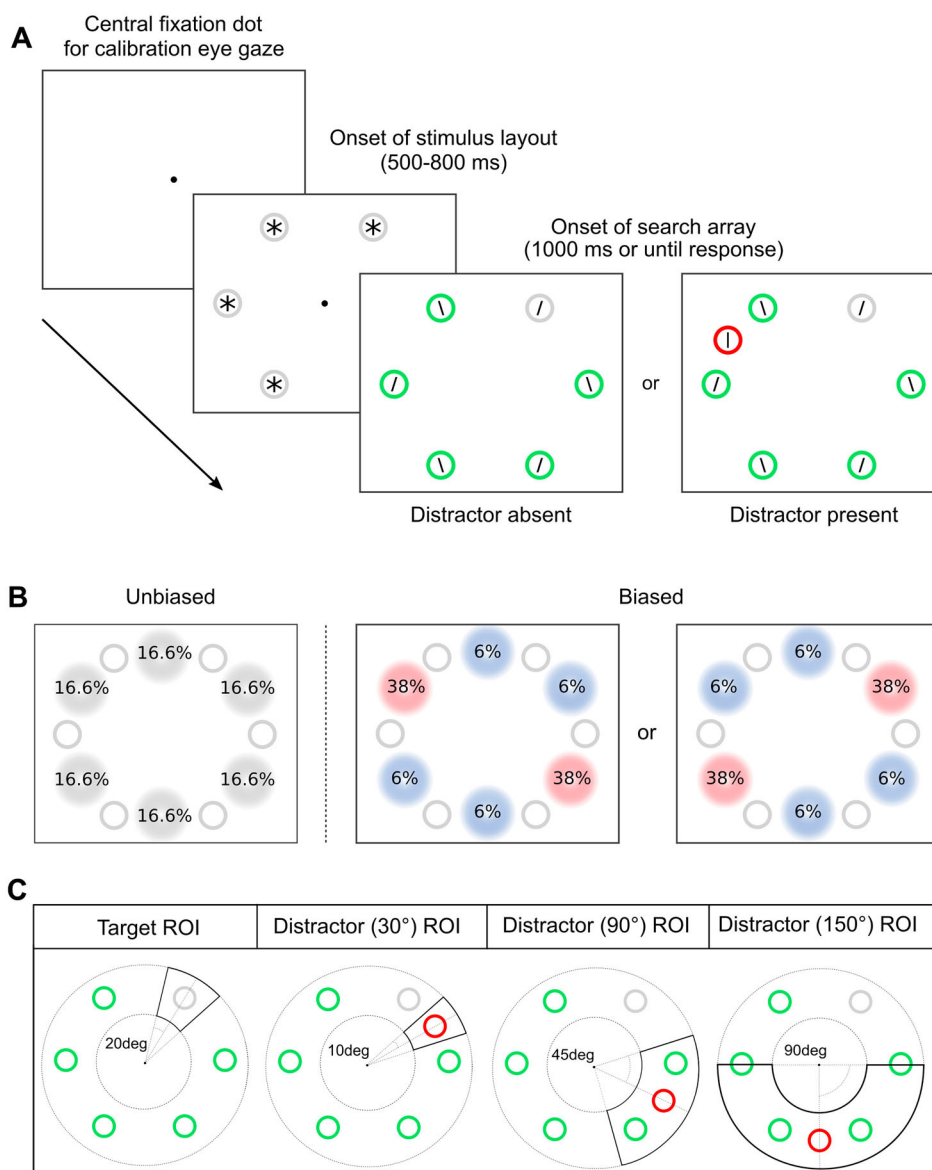
Figure 1. Illustration of the experimental procedure. **(A)** Sequence of events and time course in each trial: six placeholders forming the initial stimulus display were replaced by the search array. Here participants had to search for the task relevant circle (the only one to remain grey) and discriminate the target line located inside. The salient distractor was an additional red circle, that when present appeared abruptly in between two of the other stimuli in the array. **(B)** Distractor location probability during the Unbiased phase (left panel) and the Biased phase (right panels). The two possible assignments illustrated for the Biased phase were counterbalanced across participants. **(C)** Illustrations of the ROIs in the visual display considered to categorize saccades as directed towards the target (left panel) or towards the distractor (right panels). For distractor-directed saccades we depict three examples showing the different ROIs considered depending on the three possible distances between target and distractor, randomly occurring during the session.

was carried out in accord with the WMA Declaration of Helsinki regarding the ethical principles for research conducted on human participants and with APA ethical standards.

Participants

Thirty-two healthy volunteers were initially recruited for the study, but two of them had to be excluded from data analysis because of a very large amount of missing data due to eyeblinks and failure to maintain fixation before stimulus onset. The final sample therefore comprised 30 participants (13 males; mean age 22.3 years ± 2.5 SD). In order to determine the adequacy of this sample size, we examined the results of a pilot study ($N = 16$) with an identical experimental design, with the exception that the only responses collected were those of manual RTs. The crucial analysis,

referred to the main effect of Distractor location, indicated a very large effect size ($t(15) = 6.62$, $p < .001$, Cohen's $d = 1.66$). However, it has been proposed that the effect sizes obtained in pilot studies could be inflated, for example due to sampling biases, so that by solely relying on such effects one might end up with a main study that is still underpowered (Lakens & Albers, 2017). In order to exclude this possibility, we performed a safeguard power analysis (Perugini, Gallucci, & Costantini, 2014) which estimates the population effects size in a more conservatory way, by carrying out a power analysis on the lower limit of the 80% confidence interval of the effect size, which in our case was [1.13, 2.13]. This test suggested that 12 subjects were sufficient for obtaining a 95% power. Given the prospect of possible loss of a consistent amount of data in a study involving eye movements, we decided to increase the sample size to $N = 32$ participants, which according to the safeguard power analysis would result in a power > .999 and an effect size of $d = 1.13$.

Participants were all students at the University of Verona and naïve to the purpose of the experiment. They had normal or corrected-to-normal visual acuity. All of them signed an informed consent form prior to taking part in the study and received a fixed monetary compensation (€20) at the end of the experimental session.

Apparatus

The experiment was programmed and run by using OpenSesame 3.0 (Mathôt, Schreij, & Theeuwes, 2012) on a PC with a processor speed of 3.60 GHz. Visual stimuli were presented on a 24-inch BenQ XL2430 T LCD monitor, with a resolution of 1920×1080 pixels and a refresh rate of 144 Hz.

Eye movements were recorded by an SR Research Eyelink 1000 Plus desktop-mounted system, with a 1000 Hz temporal and 0.01° spatial resolution. Before the beginning of the experiment the gaze of each participant was calibrated with a 9-point grid. Only the right eye's position was monitored and analysed.

Participants were tested in a quiet and dimly lit room. Head movements were constrained with a chin-rest at a viewing distance of 57 cm from the display.

Stimuli and procedure

The experiment consisted of a sequence of 1044 total consecutive trials, which was interrupted about every 50 trials to allow participants to take a self-paced break. Unknown to the participants, trials were subdivided by design in two separate parts: the first 144 trials consisted of the *Unbiased phase*, and the remaining 900 were regarded as the *Biased phase*. For the purpose of data analysis, the latter was further subdivided in 3 consecutive blocks. Before the start of the experimental session, participants performed a short practice block of 16 trials that were discarded from data analysis. Overall, the experimental session lasted 1.5 h.

Participants performed an adapted version of the additional singleton paradigm, first introduced by Theeuwes (1994) (Figure 1A). Each trial started with a central fixation point (a white dot appearing at the centre of a 1.25° black disc) presented on a uniform grey background (RGB: 30, 30, 30; 14.1 cd/m^2), which also served for the purpose of drift correction on a trial-by-trial basis. Following fixation, six grey circles (RGB: 95, 95, 95; 68.6 cd/m^2; 2.5° in diameter), were presented equally spaced at the 1, 3, 5, 7, 9 and 11 o'clock positions of an imaginary circle, at 10° of eccentricity. At the centre of each grey circle a grey asterisk was also shown (39cd/m^2; 0.4° in size), which acted as a premask. Shortly after onset of this stimulus layout, randomly lasting between 500 and 800 ms, all the circles became green (RGB: 30, 120, 50; 68.2 cd/m^2), with the exception of the task relevant circle, which was the only one to remain grey. At the same time, the fixation point disappeared and the asterisks were removed from each circle unveiling a left- or right-tilted small grey line (39 cd/m^2). Participants had to discriminate the orientation of the target line located inside the grey circle by pressing the "N" or "M" key on a QWERTY keyboard with their right index or middle finger. They were encouraged to respond as quickly and accurately as possible. Although eye movements were never relevant for the main task, target lines were so small that a correct discrimination could only occur if the target was foveated (this was ensured by pilot tests). Task performance was therefore critically dependent on gaze shifts towards target location.

The search display was available until the keypress response had been recorded or for a maximum time of

1000 ms. If the discrimination response was incorrect, an error display appeared, accompanied by an 800 Hz tone for 400 ms.

In a predefined proportion of trials (see below) an additional circle was added to the display with abrupt onset. This was a red circle (RGB: 255, 0, 40; 60.8 cd/m^2), containing a small vertical grey line and since it was never relevant for the task it was regarded as a distractor to be ignored. This distractor was particularly salient not only because its features were markedly different from both the target and the remaining distractors (i.e., different colour), but – importantly – because it was an onset stimulus: it appeared abruptly in between two of the stimuli in the search array, in a location that would otherwise be left empty (Figure 1A).

Unknown to the participants, the precise location of the distractor was biased by design as follows (Figure 1B). In the Unbiased phase it appeared in 50% of the trials and when present it was shown with the same probability across the six possible locations. In the Biased phase, the distractor appeared in 64% of the trials, and with different probabilities across locations: two locations, one in each hemifield, were occupied by the onset with High Frequency (HF; overall about 76% of the distractor present trials, about 38% for each location, or 432 total trials, 216 in each location); at the remaining four it appeared with an overall Low Frequency (LF; about 24% of the distractor present trials, about 6% for each location, or 144 total trials, 72 in each location). The distractor locations associated with frequency biases were counterbalanced across participants so that for half of the participants the two HF locations were the 2 and the 8 o'clock positions in the array, and for the other half they were the 4 and 10 o'clock (Figure 1B). No frequency bias was applied to the target, whose position was randomly determined on each trial in both phases, and equally likely across the 6 possible locations in the stimulus array. At the end of the experimental session we formally assessed through a brief questionnaire whether participants had become aware of the biased probability of distractor location. They were first asked to report whether they thought they had noticed something peculiar about the spatial distribution of the distractor and, second, to report/guess the location/s where they thought it appeared most frequently.

Data analysis

Statistical analyses were performed by using R 3.4.3 (R Core Team, 2017) on different sets of dependent variables. In all cases the focus was first of all that of establishing the overall impact of the salient distractor by comparing performance in trials in which it was present to those in which it was absent. In line with our research goals we then aimed at establishing if the behavioural cost due to the distractor could be differentiated according to whether it appeared in HF vs. LF locations. Further, in order to assess whether any difference in the costs associated with distractors in HF vs. LF locations would develop within the course of the experimental session, we also compared the effects obtained in consecutive blocks of trials during the Biased phase.

With the aim of rendering as direct as possible the comparison between trials with distractors in HF and LF locations, among the four LF locations in our paradigm we selected, for each participant, the two that mirrored the HF ones on the contralateral visual field. Therefore, for participants with 2 and 8 o'clock HF locations we selected the 4 and 10 o'clock as comparable LF, and the reverse for the others. This led to the exclusion of trials in which a distractor was present but appeared on the vertical meridian (21% over the whole experimental session, considering both Unbiased and Biased phases), which therefore acted as fillers.

As already explained, performance was analysed both in terms of the manual responses to the target discrimination task, as well as in terms of the saccadic eye movements. At any rate, trials were discarded from both analyses if upon the display of the search array participants were not fixating the centre of the screen (8%) or an eyeblink had occurred (1%).

For the analyses of eye movements, we considered only the first saccades made from stimulus onset. The onset of a saccade was defined using a minimum eye velocity threshold of 35° per second and a minimum acceleration threshold of 9.5° per second. Eye movements were then assigned to different categories according to their landing position with respect to regions of interest (ROI) around target and distractor (when this was present in the array) (Figure 1C). Valid saccades were those with latencies comprised between 60 and 800 ms, that fell within an annulus between 6.5° and 13.5° from the display centre (this

criterion led to the exclusion of 16% trials in total). Within this annulus, the target ROI comprised the wedge-shaped display area within 20 deg (i.e., 20 angular degrees) from the target (vertex placed at the centre of the display, see Figure 1C, first panel). On the other side, first saccades were classified as being directed towards the distractor when their endpoint, in the given annulus, was within an ROI that was adjusted according to distractor distance from the target: 10 deg from distractors that appeared at 30 deg from the target; 45 deg from distractors appearing at 90 deg from the target; 90 deg from distractors located 150 deg away from the target (Figure 1C, second, third and fourth panels) (e.g., Theeuwes et al., 1999). Valid saccades with an endpoint that was not comprised within the ROI designated to the target or to the onset distractor (in distractor present trials) were classified as directed to one of the other non-target items in the display.

Results

Unbiased phase

First, in order to evaluate the sensitivity of our paradigm with respect to any effect of attentional and oculomotor capture, we focused on performance during the first experimental block, corresponding to the Unbiased phase and compared responses to trials in which the salient distractor was present to those in which it was absent.

Manual responses to the behavioural task

Given the very low error rate in our task (2%) statistical analyses were performed on mean Reaction Times (RTs) of correct responses, excluding trials with RTs that did not fall within 3 SD from the mean for each condition in each participant (3%).

The pairwise comparison revealed a significant effect of distractor presence ($t(29) = 10.75$, $p < 0.0001$, $d = 1.964$), reflecting slower RTs in the distractor present with respect to the distractor absent condition (802 ms vs. 760 ms) (Figure 2A).

A further test was then conducted to compare the impact of distractors appearing at the locations that in the forthcoming phase would be associated with frequency unbalances. The cost in performance due to distractor presence (i.e., the difference in RTs between the distractor-present and the distractor-absent conditions) was therefore computed and a statistical test was conducted to compare trials in which the distractor appeared in HF vs. LF locations. This comparison was very far from significance ($t(29) = 0.12$, $p = 0.91$, $d = 0.022$, Bayes Factor = 0.195), suggesting that a priori, before the start of any manipulation of distractor frequency, the different distractor locations led to comparable effects (42 ms vs. 43 ms for HF and LF) (Figure 3B).
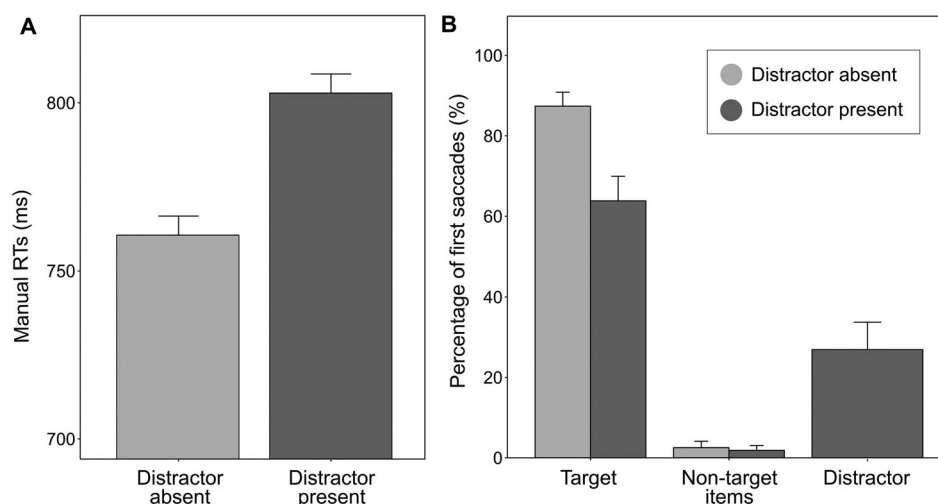
Figure 2. Manual responses and oculomotor performance as a function of distractor presence in the Unbiased phase. **(A)** Mean of correct manual Reaction Time (RTs), plotted separately for distractor absent and present trials. **(B)** Percentage of first saccades directed towards each of the possible items in the array, i.e., Target, Non-target items (the green circles) and salient Distractor, separately for each distractor presence condition. In these and in all other graphs, error bars depict the within-subject confidence intervals (Cousineau, 2005, corrected according to Morey, 2008).

Eye movements

As described above, although our behavioural task required participants to deliver manual responses, eye movements were also recorded and analysed according to the same steps adopted for the analysis of manual RTs. The saccades considered were those associated with a correct response at the main task.

First saccades to the target. Consistently with what emerged from the analysis of manual RTs, salient distractors had also a strong impact on oculomotor behaviour, markedly affecting the destination of first saccades from the onset of the search array. During the Unbiased phase the percentage of first saccades directed to the target was very high when the distractor was absent (87%), but it dropped significantly when it was present (64%), $t(29) = 11.01$, $p < 0.0001$, $d = 2.011$. No difference emerged during the Unbiased phase between the impact of distractors appearing at locations that would become HF vs. those that would be associated with LF (64% vs. 63% respectively; $t(29) = 0.32$, $p = 0.74$, $d = 0.059$, Bayes Factor = 0.204).

Oculomotor capture. Even within trials leading to correct target discrimination, the salient distractor in the display exerted a strong oculomotor capture effect. During the Unbiased phase the percentage of first saccades directed to the onset distractor was much higher (26%) with respect to those directed to the other non-target stimuli in the array (average per item 1%), $t(29) = 8.70$, $p < 0.0001$, $d = 1.590$ (Figure 2B). No differences were found between oculomotor capture events associated with distractors appearing at locations that would become HF vs. LF (27% vs. 25% respectively; $t(29) = 1.02$, $p = 0.31$, Bayes Factor = 0.315).
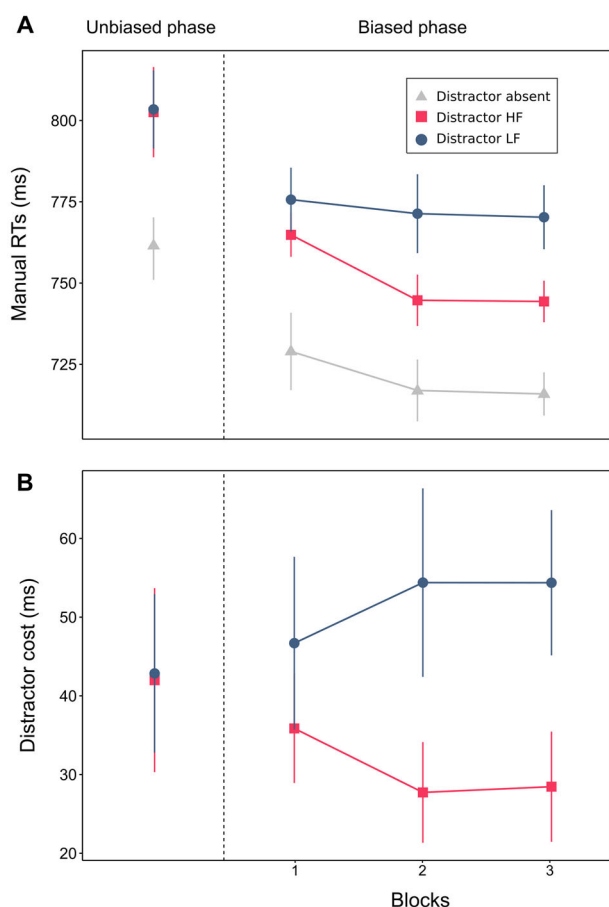
Biased phase

After having established that our experimental task gave rise to robust costs in performance due to the presence of a salient visual distractor, and after verifying that a priori the locations that would become associated with different distractor frequencies led to comparable costs, we moved to evaluate the effects of the key manipulations operated during the Biased phase.

As it is always the case in studies manipulating the overall frequency of distractor location, the fact that during the Biased phase irrelevant onsets were more likely to occur in HF locations increased also the probability that a distractor appeared in the same HF location across consecutive trials. Intertrial contingencies associated with the repetition of distractor properties are known to give rise to significant priming effects, facilitating responses in trials in which a distractor appears at the same location as in the previous trial (e.g., Kristjánsson & Campana, 2010). In principle therefore it is possible that, when examining the impact of frequency-related manipulations at a general level, intertrial priming may act as a confounder for the effects of interest. Previous studies have already shown that the effects associated with unbalances in distractor location can be found independently from any intertrial contingencies (see for instance Ferrante et al., 2018). However, to ensure that our findings derived from the overall frequency manipulation of distractor location, all statistical analyses relative to the Biased phase were replicated after removing all trials in which distractor location was the same as to the immediately preceding trial (about 20% of the original data). All the results were in perfect agreement with those obtained from the analyses conducted on the complete dataset.

Manual responses to the behavioural task

We computed the costs in manual RTs associated with distractor presence as the difference between mean RTs in distractor present and absent conditions, separately for trials with irrelevant onsets in HF and LF locations (raw mean data are shown in Figure 3A). These values were then submitted to a 2×3 repeated-measures analysis of variance (ANOVA), with Distractor Location (HF: High Frequency; LF: Low Frequency) and Block (3 consecutive blocks in the Biased phase) as within-subjects factors. This ANOVA revealed a significant main effect of Distractor Location ($F(1,29) = 29.57$, $p < 0.0001$, $\eta_p^2 = 0.504$), reflecting a lower overall distractor cost when it appeared at the HF locations (31 ms) compared to the LF (53 ms) (Figure 3B). The overall increase in RTs at the target discrimination task due to distractor presence was significantly lower when it appeared in high frequency locations. This finding is consistent with previous studies showing than the attentional capture exerted by visual distractors is reduced if they appear at locations more frequently occupied by salient nonrelevant stimuli (e.g., Ferrante et al.,

Figure 3. Manual responses as a function of Distractor Location for the Unbiased and Biased phases. For the sake of comparison, in this and in the subsequent figures each graph depicts performance in both Unbiased and Biased phases, separated by a vertical dotted line. Ticks on the *x*-axis refer to the consecutive blocks within the Biased phase. **(A)** Mean of correct manual RTs plotted separately for Distractor absent trials and for trials with Distractor present in HF or LF locations. **(B)** Mean cost in manual RTs associated with distractors in HF and LF locations.

2018; Wang & Theeuwes, 2018a, 2018b). The main effect of Block was non significant ($F(2,58) = 0.002$, $p = 0.99$, $\eta_p^2 = 0.00008$), suggesting that overall the cost due to distractor filtering remained constant across the whole experimental session.

Interestingly however, the interaction between Distractor Location and Block approached significance ($F(2,58) = 3.13$, $p = 0.05$, $\eta_p^2 = 0.097$). The pairwise comparisons (Holm corrected) revealed than the main effect of Distractor Location tended to develop throughout the experimental session: whereas in the first block of the Biased phase the difference between HF and LF distractor costs was not reliable ($t(29) = 1.9$, $p = 0.06$), in the following blocks it became larger and robust (Block 2: $t(29) = 4.42$, $p = 0.0002$; Block 3: $t(29) = 4.9$, $p < 0.0001$) (Figure 3B).

Interestingly, besides the difference in interference caused by distractors in HF vs. LF locations, the cost associated with distractors in HF locations, despite being relatively small, remained significant throughout the whole experimental session (Block 3, $t(29) = 8.56$, $p < .0001$, $d = 1.564$).

Given that in our task two locations in the display were associated with high distractor frequency, and that for each participant they were positioned in different hemifields, we asked whether the overall impact of learning would have differed across the two hemifields. In order to do this, we ran an ANOVA that was similar to the one described above, with Side (left or right) as an additional factor, focusing our interest on the interaction between Side and Distractor location possibly modulated by block. Neither of these effects was significant (Side by Distractor location, $F(1,29) < 0.0001$, $p = 0.99$, $\eta_p^2 = 0$; Side by Distractor location by Block, $F(2,58) < 0.145$, $p = 0.87$, $\eta_p^2 = 0.004$), clearly indicating that in both hemifields, the HF and LF locations were undergoing similar effects due to the biases in distractor frequency.

Eye movements
First saccades to the target. In order to reveal more directly the impact of HF and LF distractors on eye movements, we computed the difference between the percentage of first saccades directed toward the target in distractor present and absent conditions, and submitted this value to a 2 × 3 ANOVA, with Distractor Location (HF vs. LF) and Block (1–3) as main factors (raw mean data are shown in Figure 4A). This ANOVA revealed a significant main effect of Distractor Location ($F(1,29) = 61.89$, $p < 0.0001$, $\eta_p^2 = 0.680$), suggesting that the decrease in the number of target-directed saccades due to distractor presence was much larger when it appeared in a LF location (distractors in LF locations lowered the number of target-directed saccades by 11%). The main effect of Block instead was non significant ($F(2,58) = 1.19$, $p = 0.31$, $\eta_p^2 = 0.039$), suggesting that overall the detrimental effect of distractor presence remained constant across blocks (Figure 4B).

The interaction between Distractor Location and Block was nearly significant ($F(2,58) = 2.90$; $p = 0.06$, $\eta_p^2 = 0.090$), indicating that even though the difference between trials with distractors in HF and LF locations tended to become larger as the session proceeded, it was already robust during the first block. Indeed,
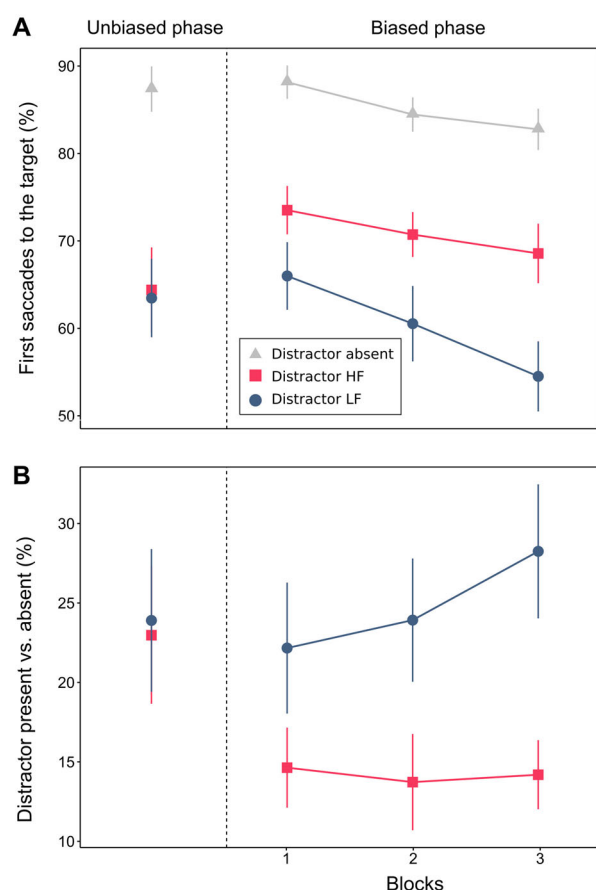
Figure 4. Percentage of first saccades to the Target as a function of Distractor Location for the Unbiased and Biased phases. **(A)** Percentage of first saccades directed to the Target plotted separately for Distractor absent trials and for trials with Distractor present in HF or LF locations. **(B)** Mean difference in percentage of first saccades to the target between the distractor absent and the distractor present condition, plotted separately for HF and LF locations.

as can be readily appreciated in Figure 4A, the number of saccades directed to the target during Block 1 was significantly higher in trials with a distractor in HF locations (73%), and it further increased even with respect to the Unbiased block, which could be regarded as a baseline (Distractor HF: percentage of saccades directed to the target in Block 1 vs. Unbiased phase, $t(29) = 3.47$, $p = 0.003$, $d = 0.635$).

Nevertheless, despite this tendency, the impact of distractors appearing in HF locations remained significant even in the last block, with respect to distractor absent trials (Block 3: $t(29) = 7.59$, $p < 0.0001$, $d = 1.386$).

Again, we asked whether there were any differences in the effects associated with the two HF locations considered, however in the ANOVA which comprised Side as an additional factor, neither the

interaction between Side and Distractor location ($F(1,29) < 2.16$, $p = 0.15$, $\eta_p^2 = 0.069$), or the triple interaction between Side, Distractor location and Block ($F(2,58) < 0.197$, $p = 0.82$, $\eta_p^2 = 0.006$) were significant.

First saccades to the target: time course. Saccades directed to singletons in the visual display are thought to be driven by basic stimulus properties in an automatic manner. Within the distribution of such automatic gaze shifts it is typically found that the vast majority of responses lay on the side of the curve with the fastest saccades (e.g., Mulckhuyse, van Zoest, & Theeuwes, 2008). Given that in our experimental paradigm the circle containing the target was also a singleton with respect to the remaining objects in the search array, we asked whether the presence of a salient distractor in HF vs. LF locations would affect the *distribution* of eye movements elicited by, or directed to, the target. The percentage of target-directed saccades in distractor present conditions (either in HF or LF locations) was therefore analysed as a function of their latency by applying a Vincentizing procedure (Ratcliff, 1979).

For each participant and each distractor location we considered the distribution of the latencies of first saccades and divided it in Quartiles. For each Quartile, associated with a given mean latency, we computed the percentage of saccades directed to the target, separately for trials in which the distractor appeared in HF or LF locations. An ANOVA was then carried out on mean percentages for each Quartile, with Quartile (1–4) and Distractor Location (HF vs. LF) as factors. The main effect of Distractor Location was significant ($F(1,29) = 41.01$, $p < 0.0001$, $\eta_p^2 = 0.585$) and so was the main effect of Quartile ($F(3,87) = 22.06$, $p < 0.0001$, $\eta_p^2 = 0.432$) (Figure 5A). Their interaction however was not reliable ($F(3,87) = 1.38$, $p = 0.25$, $\eta_p^2 = 0.045$), suggesting that, when a distracting onset appeared in the display, if it occurred at LF locations it had a generalised detrimental effect on target-directed saccades, reducing their occurrence throughout the whole latency distribution.

Oculomotor capture. In order to assess whether the effect of suppression history would also emerge in oculomotor capture, an ANOVA was conducted on the percentage of first saccades directed toward the distractor, with Distractor Location (HF vs. LF) and Block (1–3) as main factors. The analysis revealed a
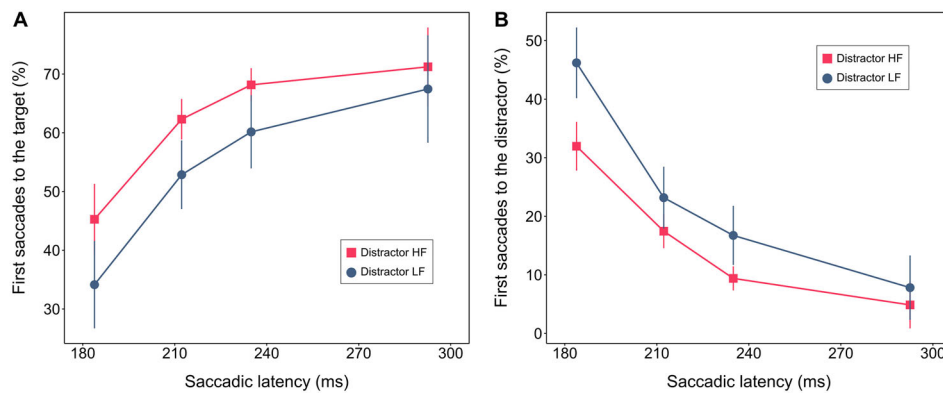
Figure 5. Time course of oculomotor performance. **(A)** Percentage of first saccades directed to the target and mean saccadic latency in each Quartile, plotted separately for trials with distractor in HF vs. LF locations. **(B)** Percentage of first saccades directed to the salient distractor and mean saccadic latency in each Quartile, plotted separately for trials with distractor in HF vs. LF locations.

significant main effect of Distractor Location ($F(1,29) = 39.59$, $p < 0.0001$, $\eta_p^2 = 0.577$) and a nearly significant main effect of Block ($F(2,58) = 3.07$, $p = 0.05$, $\eta_p^2 = 0.095$). The interaction between Distractor Location and Block however was not significant ($F(2,58) = 0.56$, $p = 0.5$, $\eta_p^2 = 0.019$) (Figure 6). Hence, the salient distractor, if present, attracted overall more first saccades when it appeared at LF (28%) compared to HF locations (18%) and this effect appeared very early after the introduction of biases in the spatial probability of the distractor, remaining constant thereafter. Indeed, the percentage of saccades to distractors in HF locations during the first block was significantly lower even with respect to the Unbiased phase (Block 1 vs. Unbiased phase, $t(29) = 5.31$, $p = 0.0001$, $d = 0.970$) (Figure 6).

Interestingly, although the oculomotor capture associated with distractors in HF locations was
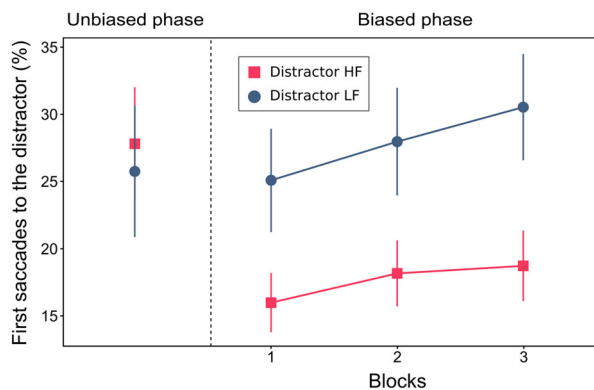
extremely reduced, it remained statistically significant until the very last block (Block 3: $t(29) = 8.38$, $p < 0.0001$, $d = 1.530$).

In order to assess whether the history acquired by HF and LF locations would also affect the time needed to disengage from the distractors that appeared there (prior to reorienting towards the task relevant item), a similar analysis was conducted on the duration of the fixations following oculomotor capture events. Interestingly, none of the main effects was significant (Distractor Location: $F(1,29) = 1.11$, $p = 0.29$, $\eta_p^2 = 0.037$; Block: $F(2,58) = 0.78$, $p = 0.45$, $\eta_p^2 = 0.026$), nor was the interaction between the two (Distractor Location by Block: $F(2,58) = .69$, $p = 0.50$, $\eta_p^2 = 0.023$), suggesting that the impact of suppression history revolved crucially on processes taking place during saccadic planning.

In the ANOVA which included Side (left or right) as a factor, neither the interaction between Side and Distractor location ($F(1,29) = 0.058$, $p = 0.81$, $\eta_p^2 = 0.001$) nor the three way interaction were statistically significant ($F(2,58) = 0.522$, $p = 0.60$, $\eta_p^2 = 0.017$).

Oculomotor capture: time course. Saccades indexing oculomotor capture by the salient distractor were also submitted to a Vincentizing procedure, following the same criterion described above for target-directed saccades. An ANOVA was carried out on the mean percentage of saccades towards the distracting onset, with saccadic latency Quartile and Distractor Location as main factors. The effect of Distractor Location was significant ($F(1,29) = 25.80$, $p < 0.0001$, $\eta_p^2 = 0.470$), in line with the overall finding of reduced oculomotor capture elicited by distractors in HF locations, and so

Figure 6. Oculomotor capture as a function of Distractor Location for the Unbiased and Biased phases. Percentage of first saccades directed to the Distractor are plotted separately for HF and LF Distractor Location.

was the main effect of Quartile ($F(3,87) = 52.90$, $p <$ 0.0001, $\eta_p^2 = 0.645$), reflecting that oculomotor capture saccades decreased as a function of saccadic latency (Figure 5B). Crucially however the interaction between Distractor Location and Quartile was significant ($F(3,87) = 4.86$, $p = 0.003$, $\eta_p^2 = 0.143$). Paired comparisons showed that the effect of suppression history was modulated by saccadic latency.

Overall the HF vs. LF difference was statistically significant only in the first and third Quartiles (Quartile 1, $t(29) = 6.09$, $p < 0.0001$, $d = 1.112$; Quartile 2: $t(29) = 2.12$, $p = 0.08$, $d = 0.388$; Quartile 3: $t(29) = 2.66$, $p = 0.03$, $d = 0.486$; Quartile 4: $t(29) = 1.75$, $p = 0.08$, $d = 0.321$). However, comparisons of this effect across Quartiles indicated that the difference found in the first quartile, with the shortest latencies, tended to differ significantly from those observed in slower saccades (Quartile 1 vs. Quartile 2: $t(29) = 2.53$, $p = 0.08$, $d = 0.463$; Quartile 1 vs. Quartile 3: $t(29) = 1.95$, $p = 0.24$, $d = 0.356$; Quartile 1 vs. Quartile 4: $t(29) = 3.79$, $p = 0.004$, $d = 0.693$; Quartile 2 vs. Quartile 3: $t(29) = 0.57$, $p = 0.57$, $d = 0.104$; Quartile 2 vs. Quartile 4: $t(29) = 1.08$, $p = 0.57$, $d = 0.197$; Quartile 3 vs. Quartile 4: $t(29) = 1.39$, $p = 0.52$, $d = 0.254$; Holmes corrected comparisons).

Awareness of distractor frequency biases

Twenty-four out of the thirty participants involved in the study reported to have had the impression that the salient distractor did not appear with the same probability across the different locations in the display, responding positively to a yes/no questionnaire. However, only four of these reported the two locations actually associated with the HF bias. When these four participants were excluded from the analyses, all the relevant results were replicated, suggesting that awareness did not have a role in how these effects became manifest in behavioural performance.

Discussion

In this study we explored how the overt deployment of selective attention (i.e., saccadic eye movements) was affected by systematic unbalances in the frequency with which given spatial locations are associated with the presence of non relevant, distracting events.

In a visual search task, participants were asked to discriminate a small target that needed to be foveated, and in a proportion of trials the target display was accompanied by the onset of a salient but irrelevant distractor. As expected, based on previous research (e.g., Theeuwes et al., 1999), distractor presence led to a significant increase in the manual RT to respond to the target as well as affecting the endpoint of saccadic eye movements (Figure 2).

However, the introduction of biases in the frequency with which the distractor appeared at different locations in the stimulus array led to dramatic changes in the level of interference associated with it (Figure 3), in line with recent evidence (Ferrante et al., 2018; Wang & Theeuwes, 2018a, 2018b). Irrelevant onsets appearing in locations frequently associated with distraction gradually reduced their interference with the main task, so that they gave rise to lower costs in performance. Indeed, participants became better able to ignore distraction occurring at spatial locations that in the past had been repeatedly associated with salient irrelevant events, that had to be actively suppressed in order to allow for an efficient performance at the main task. In line with previous studies (e.g., Ferrante et al., 2018; Wang & Theeuwes, 2018a, 2018b, 2018c), we propose that these phenomena reflect changes in the level of activation within *spatial priority maps*, or neural representations of the visual field, within parietal brain areas, encoding spatial coordinates in terms of their processing priority (i.e., LIP, Bisley & Goldberg, 2010).

The spatial orienting of attention and gaze is thought to depend upon the degree of activity of nodes within these maps, so that locations with higher activity will have higher priority, and a greater probability of attracting attention and saccades (e.g., Gottlieb, 2007; Serences & Yantis, 2007). Within such maps, priority can be assigned on the basis of difference signals, which reflect either the basic properties of the stimuli appearing at the given locations (e.g., Arcizet, Mirpour, & Bisley, 2011) or task goals (e.g., Zelinsky & Bisley, 2015). However, many studies have recently described behavioural advantages, probably due to changes in spatial priority maps, triggered by prior experience. As a consequence, for instance specific spatial locations can be prioritised if in the past they have been more often occupied by target stimuli (Ferrante et al., 2018; Geng & Behrmann, 2005; Wang & Theeuwes, 2018a, 2018b, 2018c), or if

the selection of target information therein has led to more rewarding consequences (Chelazzi et al., 2014).

Our study focused specifically on the role of past experience in terms of the accumulation of evidence relative to distractor filtering. Salient irrelevant onsets such as those appearing in our experimental paradigm are associated with vigorous increases in their representation within priority maps, via bottom-up, and trigger attentional and oculomotor capture. Under these circumstances, an efficient deployment of attention towards the task relevant information is accompanied by a *decrease* in the activation of distractor location within priority maps affecting attentional orienting and saccades (as in LIP, Ipata et al., 2006), mainly driven by inhibitory signals originating within the frontal lobe (i.e., DLPC, Suzuki & Gottlieb, 2013).

Within this framework, our data suggest that the suppression of distractor-related activation occurring on a trial-by-trial basis might leave enduring traces which eventually shape priority maps and affect the basic representation of stimulus locations in the visual display. As a consequence, the representation of locations that have accumulated inhibitory traces following an history of suppression becomes weaker, so that salient distractors – that normally exert a powerful attentional and oculomotor capture – become very easy to disregard when they appear at these positions in the display.

Interestingly, recent studies proposed that at least part of the behavioural effects associated with distractor frequency manipulations may derive from a very basic and widespread form of learning, that is *habituation* (Bonetti & Turatto, 2019; Turatto & Pascucci, 2016; Turatto, Bonetti, & Pascucci, 2018). Habituation is a central learning process which mediates the progressive reduction of a reflexive response to a stimulus, when this occurs repeatedly (Thompson, 2009). In line with this hypothesis, it was shown that attentional capture – as a correlate of the orienting response towards a salient and unexpected event – can be virtually extinguished when salient distractors appear systematically (Turatto & Pascucci, 2016; Turatto et al., 2018), and that the crucial features of these effects are reminiscent of classic habituation phenomena (Bonetti & Turatto, 2019).

Indeed, habituation may underlie many instances in which, with repeated exposure, the responses elicited by salient distractors are reduced or even extinguished. In their recent work for instance Bonetti and Turatto (2019) have shown that the oculomotor capture triggered by an irrelevant visual onset is subject to habituation and the extent to which this reflexive response is reduced depends on the overall onset probability, being more marked when they appear more frequently. As it is generally the case for experimental approaches aiming at revealing the effects of habituation in attentional learning, this study implied the adoption of manipulations and data analysis procedures that do not allow a straightforward comparison with other works which – like ours – focus on the effects of suppression history (but see Turatto, Bonetti, Pascucci, & Chelazzi, 2018 for a recent attempt in this direction). At any rate, more evidence is needed in order to understand the extent to which this generalised central learning process interacts with other cognitive mechanisms that, similarly sensitive to the statistical regularities of environmental stimuli, map specifically the processing priority of locations in the visual space (see for instance Chelazzi et al., 2019, for an extensive review).

Notably, in our study eye movements were already affected during the first block in which the statistical regularities were introduced, suggesting that it does not take long before participants learn (implicitly) these contingencies. Indeed, when the irrelevant onset appeared in a location with high distractor frequency, the number of saccades directed to the target was significantly higher even with respect to the Unbiased phase, which could be regarded as a baseline (Figure 4A). The oculomotor capture exerted by distractors in high frequency locations was also significantly reduced with respect to the Unbiased phase (Figure 6). It is interesting to note however that despite the extensive training and the additional effects of suppression history, the salient distractor in HF locations remained highly distracting until the end of the experimental session, so that even in the very last block of trials the costs associated with its presence were still significant for all of the dependent variables considered.

Interestingly, even though the effects of such suppression history were already found early immediately following the introduction of the regularities, it took until Block 2 for the effects to be found on manual RTs (Figure 3), which then persisted until the end of the experiment. Relatively to manual RTs, the analysis of saccadic eye movement behaviour provides

therefore a more sensitive measure of the attentional plasticity due to statistical learning, with the effects emerging as statistically significant from Block 1. Moreover, by analyzing the latency distribution of saccades we were also able to observe a differential impact of suppression history on eye movements directed towards the target and those captured by the distractor. While target-directed saccades exhibited a generalised effect of suppression history, which was independent of latency, saccades due to oculomotor capture revealed that the effect of suppression history was stronger for the eye movements with the shortest latencies (Figure 5). In line with previous reports (Ferrante et al., 2018; Jiang, 2018; Todd & Manaligod, 2018; Wang & Theeuwes, 2018a, 2018b, 2018c), this suggests that the suppression history associated with the HF locations was able to lower their basic activation within priority maps of the visual space, reducing the possibility that irrelevant onsets appearing at those coordinates would elicit automatic, reflexive orienting responses (Mulckhuyse et al., 2008).

Our data also allowed to explore whether statistical learning due to suppression history develops differently within the left or right visual hemifield, since for each participant there were two high frequency locations, one in each hemifield (Figure 1B). Previous reports have suggested that the efficiency of distractor filtering might be asymmetric across hemifields (e.g., Carlei & Kerzel, 2018). Hemifield differences might therefore have emerged also with respect to the statistical learning of distractor filtering. Inconsistent with this idea, all tests conducted indicated that learning affected the high and low frequency locations placed in the right or left hemifield very similarly, showing no overall advantage of one hemifield over the other.

The present study reveals the impact of prior experience on the overt deployment of selective attention by directly investigating eye movements. In particular, we provide substantial evidence of how even reflexive, automatic orienting responses elicited by the abrupt onset of (yet) irrelevant visual stimuli are affected by the history associated with their spatial location, above and beyond their physical salience. The accumulation of traces left by individual events of distractor inhibition decrease the priority of locations within a topographic map of the visual space, so that attentional filtering becomes more efficient at locations that have acquired a significant "suppression history", i.e., where distraction – and its suppression – has occurred more frequently.

While future studies will need to reveal the mechanisms supporting such experience-dependent attentional plasticity, our data suggest that the processes involved can adjust simultaneously the priority of different spatial locations at once, and they are not lateralised, as similar effects can be observed in both hemifields.

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