

# UNIVERSITA' DEGLI STUDI DI VERONA

DEPARTMENT OF NEUROSCIENCES, BIOMEDICINE AND MOVEMENT SCIENCES

GRADUATE SCHOOL OF LIFE AND HEALTH SCIENCES

DOCTORAL PROGRAM IN NEUROSCIENCE, PSYCHOLOGICAL AND PSYCHIATRY SCIENCES

32<sup>nd</sup> Cycle/year 2016

#### TITLE OF THE DOCTORAL THESIS

### "Dealing with distractor interference: the impact of suppression history on attentional and oculomotor capture"

S.S.D. BIO/09

Coordinator: Prof. Gianluigi Zanusso

Tutor: Dr. Chiara Della Libera

Doctoral Student: Valeria Di Caro

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivs 3.0 Unported License, Italy. To read a copy of the licence, visit the web page:  $\checkmark$ 

http://creativecommons.org/licenses/by-nc-nd/3.0/



Attribution — You must give appropriate credit, provide a link to the license, and indicate if changes were made. You may do so in any reasonable manner, but not in any way that suggests the licensor endorses you or your use.



**NonCommercial** — You may not use the material for commercial purposes.

**NoDerivatives** — If you remix, transform, or build upon the material, you may not distribute the modified material.

Dealing with distractor interference: the impact of suppression history on attentional and oculomotor capture – Valeria Di Caro PhD thesis Verona, April 24,2020

# ABSTRACT

Salient distractors appearing in the visual field trigger an involuntary oculomotor capture, so being able to ignore them is paramount for an efficient attentional selection. Recent findings have revealed that past experience of distractor filtering greatly affects the deployment of attention such that it can reduce the priority of locations frequently associated with irrelevant information and, accordingly, weaken the interference of distractor appearing therein. Such benefit associated with suppression history suggests that selective attention has adaptive experience-dependent features. There are still gaps however in the knowledge of the mechanisms underlying these phenomena, that need to be more clearly identified and detailed.

In a series of experiments, we addressed this topic by exploring the effect of suppression history on the immediate behavioral measures of attentional deployment - i.e. eye-movements - and on their neural correlates. Using variants of a visual search task, we manipulated the probability of occurrence of a salient distractor such that it occurred more frequently at two locations on the visual display, unbeknown to the participants (High Frequency locations - HF). The results showed that the amount of oculomotor capture triggered by the distractors appearing at HF locations was dramatically reduced relative to distractors appearing at other locations, consistently with the improvement also shown on task performance. Testing the permanence over time of these benefits, we found that some residual effects of suppression history were still detectable after the frequency unbalances were no longer in place, but their traces lingered for a very short time, vanishing definitively 24-hours later. Importantly, the bias induced by suppression history was accomplished by changes in neural activity at a relatively early stage of cortical visual processing. Indeed, the distractor-related cortical activities explored at posterior-occipital areas showed a reduced neural activation for distractors appearing at HF locations as indexed by a smaller N2pc, hence providing evidence of a decreased deployment of selective attention towards these stimuli, prior to saccadic planning.

In summary, this work provides compelling evidence that suppression history affects attentional spatial priority by dynamically down-weighting the representation of spatial locations that have been more frequently associated with distraction, and whose selection has been therefore inhibited. Our data suggest that such plasticity, within topographic maps of the visual space, is transient and functional, and supported by neural changes in cortical visual processing that sustains ongoing oculomotor control.

# **TABLE OF CONTENTS**

### CHAPTER 1: ATTENTIONAL CONTROL AND DISTRACTOR FILTERING

1.1 INTRODUCTION	
1.2 DISTRACTOR CAPTURE	
<b>1.3 DEALING WITH DISTRACTOR CAPTURE</b>	
1.3.1 Matter of strategy	17
1.2.2 Matter of learning	
1.3 CONCLUSION	

### CHAPTER 2: DISTRACTOR FILTERING VIA SUPPRESSION HISTORY

2.1 INTRODUCTION	
2.2 METHOD	
2.2.1 Participants	
2.2.2 Apparatus	
2.2.3 Stimuli and procedure	
2.2.4 Data analysis	
2.3 RESULTS	
2.3.1 Unbiased phase	
2.3.2 Biased phase	
2.4 CONCLUSION	

### CHAPTER 3: SHORT AND LONG-TERM EFFECTS OF SUPPRESSION HISTORY

3.1 INTRODUCTION	55
3.2 GENERAL METHOD	60
3.2.1 Apparatus	60
3.2.2 Stimuli	60
3.2.3 Design	62
3.2.4 Data analysis	62
3.3 EXPERIMENT 1: LONG-TERM EFFECTS	63
3.3.1 Participants	63

3.3.2 Experimental procedure	64
3.3.3 Results	65
3.3.4. Conclusion Experiment 1	71
3.4 EXPERIMENT 2: SHORT-TERM EFFECTS	73
3.4.1 Participants	73
3.4.2 Experimental procedure	73
3.4.3 Results	74
3.4.4 Conclusion Experiment 2	78
3.5 CONCLUSION	79

### CHAPTER 4: NEURAL CORRELATES OF DISTRACTOR FILTERING VIA SUPPRESSION HISTORY

4.1 INTRODUCTION	
4.2 METHOD	
4.2.1 Participants	
4.2.2 Apparatus	
4.4.3 Stimuli and procedure	
4.2.4 Data analysis	
4.3 RESULTS	
4.3.1 Manual RTs	
4.3.2 Eye movements	
4.3.3 EEG results	
4.4 CONCLUSION	

<b>CHAPTER 5: GENERAL DISCUSSION</b>	I 115
REFERENCES	

# PREFACE

At first glance, explaining *What Attention is* may seem the easier and foregone starting point to introduce this thesis, after all, as William James wrote in 1890, *"Everyone knows what attention is (...) It implies a withdrawal from some things in order to deal effectively with others".* 

In spite of this clear and traditional definition, the domain of attention is actually nowadays a field of heated debates.

For centuries researchers have tried to explain how the control of attention works, especially by focusing on the mechanisms driving the selection of the relevant information. In the last few years, many new studies have been focalized on the "coin's flipside" of attention, which is the inhibition of irrelevant information. Hence, the so-called "distractor filtering" has been recognized to be pivotal to refrain the limited cognitive resources from the expensive elaboration of salient but irrelevant stimuli that constantly compete to get our attention and be processed. Indeed, the ability of dealing with distracting stimuli is crucial in everyday life, allowing us to prevent interferences on the task in which we are involved and, therefore, carry out goal-direct behavior.

So far, research suggested that distractor filtering seems to be vulnerable to the influence of many types of information and thus may be driven by different mechanisms. There are however still several open questions that need to be addressed in order to reach a complete understanding of their contribution and their functioning. The investigation of how distractor filtering works is a key step to improve the knowledge of how goal-directed deployment of attention takes place, as well as to increase the overall knowledge with respect to attentional control.

The studies presented in this thesis will treat the filtering of visual distractors within the framework of experience-depended learning.

The general aim of this work is to explore whether and how the repeated experience of distractor filtering -i.e. suppression history - could bias the ability to attend to relevant information and suppress the salient but irrelevant one.

**Chapter 1** is dedicated to outlining the theoretical background of this topic by providing evidence of different sources guiding attentional deployment in attentional capture paradigms.

**Chapter 2** presents the first study which has investigated the influence of prior experience on distractor filtering. Specifically, the experiment reported explores whether and how attentional and oculomotor capture elicited by distractors appearing more often at specific locations can be attenuated.

**Chapter 3** debates the maintenance of the benefit due to suppression history. Through two experiments we investigated the permanence of this effect in time. Experiment 1 explored long-term effects, while Experiment 2 explored short-term effects.

**Chapter 4** is dedicated to unveiling the neural underpinnings of suppression history. In a co-recording EEG/Eye-tracker experiment we monitored the neural response and the oculomotor capture elicited by distractors appearing at locations with a significant suppression history.



# ATTENTIONAL CONTROL AND DISTRACTOR FILTERING



### **1.1 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-tomoment focusing of limited processing resources on a restricted amount of information, aiding its access to perceptual awareness and, eventually, behavioral guidance (Chelazzi, Della Libera, Sani, & Santandrea, 2011; Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004).

So far, a large number of studies have been dedicated to uncovering the working of visual selective attention. While many of these have been mostly focused on the selection of behavioral targets, in the last decades growing interest has been dedicated to the un-selection of disrupting non-target items, that is *distractor filtering*. Recent evidence has shown that distractors may not just be "left on the background", rather they must be inhibited and, in some cases, their processing must be 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).

Indeed, in spite of the fact that *goal-directed behavior* should address, by definition, the target information, it is not unusual in everyday life to encounter disrupting, unforeseen events, which lead to swerving from the "right road".

Such "attentional capture" elicited by salient stimuli is a robust finding across different experimental settings, however there is still an open and heated dispute on how the visual and attentional systems handle these stimuli. For a long time, this dispute was between two opposite theories, namely the top-down model on one side, and the bottom-up model on the other one. Both theories were amply experimentally supported, but none prevailed until now, suggesting that in order to overcome this theoretical impasse a new approach might be necessary.

The next paragraphs will explain both the traditional and the newest theories of attentional capture, mainly focusing on the factors aiding the attentional system in preventing and/or shielding from distractor interference.

### **1.2 DISTRACTOR CAPTURE**

According to the salience model of attention, the degree of distinctness of an item with respect to the surrounding environment is well known to be perceptually salient because it stands out among neighboring stimuli (Itti, Koch, & Niebur, 1998; Parkhurst, Law, & Niebur, 2002). This is the case of the so-called *singleton*, which is a stimulus having a unique feature value compared to the scene, which is instead relatively homogeneous (Duncan & Humpreys, 1989; Todd & Kramer, 1994). Several studies have demonstrated that a singleton item "pops out" from the rest of the environment, and even when it is irrelevant with respect to the task at hand, it can capture attention.

Experimentally, the first evidence of attentional capture by a singleton distractor has come from the "additional singleton paradigm" introduced by Theeuwes in 1992, which revealed the behavioral interference induced by the presence of a singleton distractor in a visual search task (Theeuwes, 1992). Traditionally, in this task observers had to look for a target singleton (e.g. the unique green diamond among green circles) and to report by key-press the orientation of a bar shown inside it (Fig. 1.1).



# Figure 1.1. Adapted illustration of the "additional singleton paradigm" and the typical task performance. From Theeuwes, 1992.

(A)<u>Task</u>. Participants searched for the shape-singleton (i.e. the green square). In the distractor condition a colorsingleton distractor was also shown. (B) <u>Task performance</u>. Mean reaction time for distractor absent vs. distractor present condition. Interestingly, despite the relative ease of the task, it was found that the target discrimination was significantly delayed in the presence of an additional color singleton distractor (e.g. the unique red circle among green circles) as revealed by the longer manual reaction times (RTs) on the main task.

This cost in performance was interpreted as proof of the automatic misallocation of attention on the most salient item in the array (i.e., the distractor), which is, therefore, the first one selected. The longer RTs observed should indicate the extra time needed to shift attention from the distractor to the target (Theeuwes, 1992; 2010).

In the debate on attentional control the idea argued by Theeuwes stands among those claiming the so-called *bottom-up* model of attention, which predicts that that attention is crucially driven toward those stimuli that are perceptually salient. Therefore, this model argues an automatic inevitable attentional capture by salient stimuli, that happens even when they are irrelevant (Theeuwes, 1994; Yantis & Egeth, 1999).

This idea has found supporting evidence in studies investigating electrocortical responses (i.e. Event-Related Potential components - ERPs). Specifically, in 1990, a component was discovered which appeared when a target was selected, which was thereafter considered an index of attentional allocation. This component, termed N2pc, is a negative-going deflection observable at the posterior scalp sites (PO7/PO8, i.e. over visual cortex) at ~200ms after the stimulus onset and is commonly greater in amplitude contralaterally to the attended hemifield (Hickey, McDonald, & Theeuwes, 2006; Luck, 2012; Luck & Hillyard, 1990, 1994a, 1994b).

Hickey and colleagues, in a typical attentional capture task, have demonstrated that when a target was shown at the vertical meridian and a salient but irrelevant distractor was presented in the right or in the left visual field, a clear N2pc contralateral to the distractor was triggered, thus demonstrating that attention was covertly (in the absence of eye-movements) misallocated toward the salient distractor (Fig.1.2) (Hickey, et al., 2006).



Figure 1.2. Visual search task and data from Hickey et al. (2006).

Participants searched for the shape singleton (the diamond), while maintaining fixation on the centre. The dotted circle indicates the color distractor when present. (A) The lateralized target elicited a posterior ERP negativity in the latency of the N2pc at electrodes contralateral to the target when the distractor was absent. (B)Vertical target and lateral distractor elicited a posterior ERP negativity in the latency of N2pc that is contralateral to the distractor.

When a salient stimulus captures attention, it also tends to capture eye gaze, a phenomenon known as *oculomotor capture* (e.g., Ludwig & Gilchrist, 2002; Theeuwes, De Vries, & Godjin, 2003).

In an oculomotor paradigm investigating eye movements during a visual search task, Theeuwes and colleagues (Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999) have shown that the eyes were often automatically directed toward the more salient item in the array even when this was a distractor (Fig.1.3). In their experiment, participants had to look for the unique gray circle in a circular visual

14

array and discriminate whether the target contained a 'c' or a reversed 'c'. The authors found that, when an additional item appeared abruptly in the array (i.e. an *onset*), the eyes went toward it before going to the target on about 40% of the trials. This oculomotor capture determined by the distractor was prominent only for the shorter saccades, providing evidence of the reflexive nature of bottom-up capture.



Figure 1.3. Oculomotor capture paradigm. From Theeuwes et al., 1999.

(A) <u>Task.</u> Dashed lines indicate gray circles, while solid lines indicate red circles. Participants searched for the unique gray singleton (the Target), while ignoring an onset distractor.

With respect to the previous findings, which used RTs in a target discrimination task as indirect measures to infer the attentional capture determined by the distractor, oculomotor capture paradigms have the advantage to provide a direct index of what is attended in the visual array, resulting in behavioural guidance. In particular, an onset stimulus appearing in a visual array was shown to be particularly efficient in investigating oculomotor capture, due to its intrinsic capability to elicit oculomotor orienting with respect to singletons which are salient only on the basis of color or brightness (Irwin, Colcombe, Kramer, & Hahn, 2000; Jonides & Yantis, 1988).

<sup>(</sup>B) <u>Oculomotor capture</u>. Eye movement trajectories for distractor onset absent (left panels) and onset present (right panels) conditions.

The studies reported here are only a little part of the vast evidence concerning stimulus-driven attentional capture that was collected in the last decades. In sum, bottom-up models predict an inevitable capture by a salient distractor, a point of view which tends to reduce selective attention systems at the mercy of perceptual saliency, even when the more salient item is disruptive with respect to the ongoing goal. Although this reflexive phenomenon has, intuitively, an evolutionary value, because it allows noticing salient events which might signal imminent danger, when the stimulus attended doesn't fit with the goal of the moment, overriding such distraction is crucial in order to deal efficiently with an environment rich of competing stimuli.

As a matter of fact, regardless of theoretical standpoints, that in everyday life, we constantly face distractors and do ignore them somehow. With this respect, it was experimentally shown that attentional capture is not inevitable, rather it can be drastically reduced in many situations: when the specific task requirements help in target discrimination (e.g. Bacon & Egeth, 1994), or prior knowledge about stimulus features and/or locations can be strategically used (e.g. Arita, Carlisle, & Woodman, 2012), or, finally, when the repeated exposure to a distractor lead a form of habituation (e.g. Turatto & Pascucci, 2016).

Therefore, the physical salience of a stimulus does not tell the whole story of attentional deployment, but instead it must be reckoned that the working of selective attention can adapt and make good use of factors and strategies that crucially underlie the ability to prevent the "unavoidable" capture due to distractors. The following paragraphs will provide evidence of factors implicated in dealing with distractor interference, which have proved to support and/or boost distractor filtering.

### **1.3 DEALING WITH DISTRACTOR CAPTURE**

#### 1.3.1 Matter of strategy

Theorists of attention have challenged the bottom-up model of attentional capture, sustaining that the presence of a physical salient item is not enough to automatically capture attention. According to their view, it should be considered that in the computation of visual salience other factors, linked to the task, may play a key role as, for example, the search strategy adopted by the subject and the relationship between the perceptual features defining target vs. distractors, i.e., the dimensional set (Bacon & Egeth, 1994; Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994; Nothdurft, 2002).

These theories are framed into the top-down model of attentional control, which sustains that attentional allocation is heavily under "voluntary" control, which leads to select the items fitting with our expectations and goals. In this respect, a distractor can be strategically inhibited under conditions that optimize target selection. For instance, Bacon and Egeth, in 1994, claimed that attentional capture is dependent on the search strategy adopted. According to this view, the interference due to the distractor found in the additional singleton paradigm is closely related to the fact that both target and distractor were singletons, with respect to the remaining homogeneous items in the visual array. Given that participants were implicitly encouraged to search for a stimulus bearing a "unique" feature (i.e. the only square), this might have promoted the adoption of a "singleton search mode" which could implicitly increase the task relevance of both the target, which was a singleton because of its shape, and the distractor, which was a singleton because of its color, thus increasing their reciprocal competition for attentional selection. To provide support for their hypothesis, the authors carried out a modified version of the additional singleton paradigm in which the array comprised several different shapes, so that the target was no longer a singleton and could be detected only on the basis of its defining feature

Attentional control and distractor filtering

(i.e. using a "feature search mode"). Their results have shown that the color singleton distractor could capture attention only when the adoption of a singleton search mode was possible, whereas when subjects were engaged in a feature search mode it didn't interfere anymore. These findings demonstrated that attentional capture can be strategically reduced in a top-down fashion, based on the search set adopted (Bacon and Egeth, 1994).

In cases like this, the reduction of distractor interference can be envisioned as an indirect effect of the benefit associated with target selection, which was precisely guided by its feature-based definition. However, studies have shown that overcoming the distractor is a process can be accomplished directly, namely by implementing active inhibition mechanisms. These, under specific circumstances, can operate preventively, even before the distractor occurs (Sawaki, Geng, & Luck, 2012; Gaspar & McDonald, 2014; Serences, Yantis, Culberson, & Awh, 2004; Arita et al. 2012), or can be engaged reactively, leading to a fast and powerful rejection of the distractor after the inevitable misallocation of attention (Geng & DiQuattro, 2010; Gaspar & McDonald, 2014; see Geng, 2014 for a review).

For instance, prior knowledge of the distractors' features can be used to preventively inhibit distractor interference. Arita and colleagues (2012) have shown that when observers knew the color of the upcoming distractors, they were better able to avoid their interference on the main task. In the visual search task that they adopted, a color cue (positive, negative or neutral cue) was shown prior to the search display (Fig. 1.4). The authors have found that the presentation of a cue indicating the color of the upcoming distractor (i.e., negative cue), led to faster RTs in the target-discrimination task just like the presentation of a cue indicating the color of the upcoming target (i.e., the positive cue), compared to a neutral condition. Thus, they argued that the information about distractor features (that they defined "template for rejection") was used to preventively bias attention away from the task-irrelevant information (Arita et al., 2012).

18



#### Figure 1.4. Experimental paradigm from Arita et al. 2012.

Participants had to discriminate the position of the gap in the red target (upper or lower). Prior to the search display onset a cue was shown that could be "positive" (i.e. a colored square indicating the color of the target), "negative" (i.e. a colored square indicating the color of distractors), or "neutral" (i.e. a colored square different from both target and distractors).

However, there are some situations in which the knowledge of the distractor feature does not help in handling it. According to the assumption postulated by the Dimension-Weighting Account (DWA), our attentional control is modulated by the dynamic adjustment of saliency signals coming from the perceptual dimensions (i.e., shape, color, brightness, etc.) defining the stimuli with which we are dealing. In the case of the saliency signal coming from the distractor, the foreknowledge of its defining dimension could lead to adjustments that down-weight the processing of this dimension and, thus, reduce attentional capture. Nevertheless, while this can be true for distractors that are defined by a different dimension from the one that defines the target (different-dimension distractors), when the distractor is defined by the same dimension that defines the target such down-weighting becomes unsuitable because while deprioritizing distractors it would also impact on the processing of the target (Liesefeld, & Müller, 2019). With this respect, Sauter and colleagues directly provided compelling evidence of the influence of the dimensional-weighting in determining the attentional capture (Sauter, Liesefeld, Zehetleitned, & Müller, 2018). In their study participants searched for an orientation singleton target (12° tilted bar) and, while one group had to ignore a red distractor (i.e. different dimension distractor), the other one group had to ignore a 90° tilted distractor (i.e. same-dimension distractor). They have shown that the interference due to distractor presence was significantly higher in the same-dimension distractor group (RTs cost: 94 ms) than in the different-dimension distractor group (RTs cost: 14 ms), therefore demonstrating the differential magnitude of interference based on the target-dimension and distractor-dimension similarity (see also: Müller, Geyer, Zehetleitner, & Krummenacher, 2009; Liesefeld, Liesefeld, Töllner, & Müller, 2017 for ERPs evidence).

It seems evident that, in dealing with distractor interference, the experimental paradigm adopted has a crucial impact on the strategy employed by subjects during task performance, and the deployment of attentional resources seems to adapt accordingly.

When proactive suppression mechanisms are used, these seem to involve specific areas in the prefrontal cortex that critically set top-down attentional priority (Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Lega, Ferrante, Marini, Santandrea, Cattaneo, & Chelazzi, 2019). While these adjustments may be particularly useful in order to deal with distractors, their engagement is cognitively expensive and in some situations may also lead to costs in performance, for instance when a distractor is expected but does not actually appear (Marini et al., 2016).

In other situations instead, the stimuli involved are so salient that attentional capture is much more difficult to avoid, and in order to limit their interference with the task they must be actively suppressed after the initial capture.

Evidence of active suppression mechanisms comes from ERPs studies (e.g. Carlisle & Woodman, 2011; Gaspelin & Luck, 2018a; Sawaki et al., 2012). Specifically, these have focused on the so-called *Distractor positivity* (Pd), which is a cortical response which has been putatively associated with distractor suppression (Hickey, Di Lollo, & McDonald, 2009). This component is a positive-going deflection occurring at ~150-250 ms after stimulus onset which is wider at contralateral scalp sites relative to the side of the "suppressed" item.

When a distractor was shown on the visual display simultaneously with the target, a contralateral Pd component was clearly observable on trials with faster RTs, suggesting that the faster and more efficient detection of the target could be associated with the interplay of active distractor suppression mechanisms (Fig. 1.5) (Sawaki et al., 2012; Gaspar & McDonald, 2014; Gaspelin & Luck, 2018a).

Interestingly, a recent study employing an oculomotor capture paradigm revealed that a Pd appeared contralaterally to the distractor shown only when participants made a saccade away from it, whereas it was absent in the trials in which the distractor triggered attentional capture (Weaver, van Zoest, & Hickey, 2017).





On trials with short RTs, the contralateral-ipsilateral difference was dominated by a Pd component. In contrast, the contralateral-ipsilateral difference for trials with long RTs was dominated by an N2pc component.

In sum, the studies reported above indicate that the inhibition of distractor interference is viable under specific circumstances in which top-down control can come into play. Specifically, previous knowledge about the target features (information to attend) or the distractor features (information to avoid) allows the setting of a search strategy that leads to preventing, in a proactive way, attentional capture by the distractor. In cases in which the distractor captures attention anyway, it is actively inhibited by the attentional system, which suppresses its processing.

#### 1.2.2 Matter of learning

Facing distractor interference sometimes leverages the capability of the attentional system to implicitly learn from the experience obtained in the past.

Indeed, the allocation of attentional resources may depend on prior experience with the same visual environment, a concept that overall comprises a variety of phenomena (Anderson, 2016; Awh, Belopolsky, & Theeuwes, 2012; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Jiang, 2018; Todd & Manaligod, 2018).

For example, in paradigms in which rewards are delivered in turn for task responses, distractor filtering was improved for trials in which the item appearing as a distractor was a stimulus whose attentional selection in the past had been systematically followed by lower rewards. The attentional system, therefore, biases its propensity to be captured by a distractor on the basis of previous disincentives (Della Libera, & Chelazzi, 2009).

A determining factor in aiding distractor filtering consists in the "practice" acquired in dealing with irrelevant information and, thus, with its suppression. Previous studies have shown that the repeated experience with the attentional selection of specific stimuli and/or stimulus features can greatly benefit from practice so that it becomes progressively easier to select a target or a target feature that has been selected more frequently in the past (e.g. Geng & Behrmann, 2005; Sha, Remington, & Jiang, 2018). Similarly to attentional selection, which can benefit from repeated practice, a recent and growing literature is providing evidence that it is easier to ignore distractors that are encountered more frequently. This phenomenon, termed "Suppression History", is attributed to the capability of the attentional system to catch and exploit the statistical regularities present in the environment, thus exhibiting a form of statistical learning. This kind of learning can interest the repetition of the distractor features (e.g. Vatterott & Vecera, 2012), the frequent occurrence of the distractor in given spatial locations or areas in the visual

field (e.g. Ferrante, Patacca, Di Caro, Della Libera, Santandrea, & Chelazzi 2018; Goschy, Bakos, Müller, & Zehetleitner; 2014; Wang, & Theeuwes, 2018a; Sauter, Liesefeld, & Müller, 2019; Sauter, et al., 2018) or their overall display probability (e.g. Neo & Chua, 2006; Sayim, Grubert, Herzog, & Krummenacher, 2010).

In the experiment carried out by Vatterott and Vecera, the distractor cost typically encountered in the additional singleton paradigm was virtually eliminated if the distractor's singleton color was constant across trials, but it was recovered when it changed across blocks (Vatterott & Vecera, 2012). Such results suggest that attentional priority may be tuned on the basis of learned experience with distractor properties.

Another interesting phenomenon leverages on distractor probability, which can include both the overall distractor display probability (Marini, Chelazzi, & Maravita, 2013; Geyer, Muller, & Krummenacher, 2008; Sayim et al., 2010) and, crucially, its occurrence across given positions in the visual field.

In situations in which the probability of encountering a distractor is high, the costs due to its filtering can be drastically reduced thanks to the contribute of topdown proactive inhibition mechanisms. These, as discussed above, are costly in terms of the processing resources they require and reveal the strategic contribution of executive functions in dealing with irrelevant material that is expected (Marini et al., 2016).

The de-prioritization of distractors due to previous experience, however, has also proved to occur on the basis of their spatial location, leading to forms of suppression history that is space-specific. More specifically, recent studies have shown that the systematic occurrence of a distractor at a given location is implicitly learned and used to subsequently bias attention away from this location, degrading the processing of any item occurring therein (Wang, & Theeuwes, 2018a; Ferrante et al., 2018). In one of the experiments conducted by Ferrante and colleagues, participants had to discriminate the target by manual response while a salient distractor was also shown on 50% of the trials. Distractor probability was biased such that one stimulus location in the visual array was occupied by the distractor with a higher probability with respect to the others. The results obtained have shown that the unbalanced appearance of a distractor across locations significantly affects attentional deployment, inducing the attentional system to deprioritize the location more frequently associated with it. Indeed, when the distractor appeared at the "high-probability" location the RTs on the main task were faster than when it appeared at other "low-frequency" locations. Conversely, when at the highprobability location a target appeared, RTs were delayed, as proof of the fact that the de-prioritization due to learning was specific for that location, and did not depend on distractor features.



**Figure 1.6. Distractor filtering via statistical learning from Ferrante et al., 2018 (Exp.2).** (A) Task illustration: participants had to discriminate the pointing direction of the double arrow target, while a color-singleton distractor was shown.

(B) Distractor cost on manual RTs as a function of distractor location (LDPL = low distractor probability location; IDPL = intermediate distractor probability location; HDPL = high distractor probability location).

These results were interpreted as proof that statistical learning phenomena can shape spatial priority maps of attention, by reducing the processing priority of the locations experienced as less relevant.

However, while on the one hand statistical learning of distractor location is able to reduce its interference, it was shown that this information is efficiently used only under specific circumstances. For instance, Sauter and colleagues have tested the effect of distractor probability unbalances in a spatial probability cueing paradigm, in which one area of the visual display contained the distractor on 90% of trials. Crucially, the authors showed that the probability cueing effect was closely dependent on distractor-dimension. Indeed, when the distractor was in a differentdimension with respect to the target, the mechanism adopted to overcome its interference was the down-weighting of the distractor dimension, while the unbalances in distractor frequency didn't impact on performance. Thus, in cases like this, other sources of attentional control are preferentially employed in order to handle distractor interference. Conversely, when the distractor was in the same-dimension and the down-weighting was no more adoptable, participants significantly benefited from the frequency unbalances, by better ignoring distractors appearing at the frequent area. Therefore, these findings show that the benefit due to implicit learned unbalances of distractor location is dimensional-weighting constrained (Sauter, et al., 2018).

### **1.3 CONCLUSION**

The studies reported in this chapter provide a brief framework of the current theoretical landscape on the alleged mechanisms engaged in distractor filtering. While on one side the complete filtering of salient distractors is perhaps not feasible, due to biological reasons, on the other side reducing the impact of distraction is pivotal to allow goal-directed behavior, therefore it is crucial to find the best way to deal with it.

Some of the studies proposed have debated the role of the physical salience of the distractor, which has been traditionally recognized as a crucial factor driving the automatic capture of attention. According to this view, we are involuntarily captured by the more salient item in the environment. However, is attentional control really at the mercy of physical salience or can we develop skills to defend ourselves against distraction?

Several theorists have questioned the assumption of an inevitable attentional capture, providing evidence of the contribution of several factors in overcoming distractor interference. However, attentional capture seems to be preventable via the engagement of top-down selection strategies and/or proactive distractor filtering mechanisms, and even when capture has been triggered its detrimental impact on

performance seems to be further limited by implementing active post-selection suppression mechanisms.

However, although these forms of distractor inhibition and/or suppression can be both efficient, the active engagement of suppression resources may pose a heavy cognitive load, which may eventually result in overall costs in performance. Recent studies have demonstrated that distractor inhibition may be efficiently accomplished even through forms of implicit learning that may be cognitively less expensive. One of these concerns the repeated experience of distractor filtering, which builds up suppression history. The studies reported in this line of research provided evidence that this form of experience-dependent learning gives rise to robust benefits in distractor filtering. Overall this evidence suggests that the attentional priority can be shaped upon previous experience and driven, implicitly, toward the relevant information and away from the irrelevant ones (e.g. Ferrante et al., 2018; Wang & Theeuwes, 2018a).

It is important to note however that independently of the theoretical account considered, the implementation of inhibitory processes can heavily depend on the experimental paradigms employed, making it necessary to carry out further explorations to disambiguate among different possible explanations. With respect to the effects of suppression history, so far the studies carried out have revealed that it can affect behavior and its effects on selective attention have been estimated indirectly, by exploring their impact on manual RTs to a given task.

The studies described in this thesis investigated the effects of suppression history on a direct measure of attentional deployment, by analyzing its impact on eye movements towards items in the visual display. The evidence reported recounts the overall consequences of suppression history on the overt deployment of attention (Chapter 2), their impact over time (Chapter 3) and their possible neural underpinnings (Chapter 4).



# DISTRACTOR FILTERING VIA SUPPRESSION HISTORY\*

<sup>\*</sup> Parts of this section have been published in the paper: Di Caro, V., Theeuwes, J., & Della Libera, C. (2019). Suppression History of distractor location biases attentional and oculomotor control. *Visual Cognition*, 27(2), 142-157.

### **2.1 INTRODUCTION**

Most of the evidence of experience-dependent plasticity in attentional processing has been observed with respect to the selection of behavioral 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 a 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, et al., 2014; Leber, Gwinn, Hong, & O'Toole, 2016; Sauter, et al., 2019; Sauter, et al., 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; 2019), 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 behavioral 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, et al., 1999).

We designed a visual search task in which participants were required, although not explicitly, to make a saccade to a color 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 color 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 lateralized distractor locations available in each

hemifield one was associated with a high and the other with a low frequency bias. 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.

### **2.2 METHOD**

The study was approved by the Review Board for Research involving Human Participants (CARU) of the University of Verona. The experimental procedure 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.

#### 2.2.1 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  $\pm$  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<0.001, 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 > 0.999 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 ( $\in$ 20) at the end of the experimental session.

#### 2.2.2 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  $1920 \times 1080$  pixels and a refresh rate of 144 Hz.

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

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.

#### 2.2.3 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 2.1A). Each trial started with a central fixation point (a white dot appearing at the center of a 1.25° black disc) presented on a uniform grey background (RGB: 30, 30, 30; 14.1 cd/m2), 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/m2; 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 center of each grey circle a grey asterisk was also shown (39cd/m2; 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/m2), 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/m2). 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/m2), 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 color), 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 2.1A).

Unknown to the participants, the precise location of the distractor was biased by design as follows (Figure 2.1B). 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 2.1B). 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.



#### Figure 2.1. 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.

#### 2.2.4 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 behavioral 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 analyzed 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 center 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  $35^{\circ}$  per second and a minimum acceleration threshold of  $9.5^{\circ}$ 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 2.1C). Valid saccades were those with latencies comprised between 60 and 800 ms, that fell within an annulus between  $6.5^{\circ}$  and  $13.5^{\circ}$  from the display center (this criterion led to the exclusion
of 16% trials in total). Within this annulus, the target ROI comprised the wedgeshaped display area within 20 deg (i.e., 20 angular degrees) from the target (vertex placed at the center of the display, see Figure 2.1C, 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 2.1C, 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.

### **2.3 RESULTS**

#### 2.3.1 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

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 2.2A).

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 2.3B).



# Figure 2.2. 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 behavioral task required participants to deliver manual responses, eye movements were also recorded and analyzed 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 behavior, 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 2.2B). 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).

#### 2.3.2 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

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 2.3A). These values were then submitted to a 2 × 3 repeatedmeasures 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 2.3B). 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 non-relevant stimuli (e.g., Ferrante et al., 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.



**Figure 2. 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.

Interestingly however, the interaction between Distractor Location and Block approached significance (F (2,58) = 3.13, p = 0.05,  $\eta^2_p$  = 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 < 0.0001, 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  $2 \times 3$  ANOVA, with Distractor Location (HF vs. LF) and Block (1–3) as main factors (raw mean data are shown in Figure 2.4A). 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 2.4B).



Figure 2.4. 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.

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, 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 analyzed 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 2.5A). 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 generalized detrimental effect on target-directed saccades, reducing their occurrence throughout the whole latency distribution.



Figure 2.5. 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.

**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

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 2.6). 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 2.6).



Figure 2.6. 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.

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 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 2.5B). 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 behavioral performance.

## **2.4 CONCLUSION**

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.

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, 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 may 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 behavioral advantages, probably due to changes in spatial priority maps, triggered by prior experience. As a consequence, for instance specific spatial locations can be prioritized 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 distractorrelated 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 behavioral 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 straight- forward 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 generalized 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. The oculomotor capture exerted by distractors in high frequency locations was also significantly reduced with respect to the Unbiased phase. 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, which then persisted until the end of the experiment. Relatively to manual RTs, the analysis of saccadic eye movement behavior 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 generalized 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. 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

51

participant there were two high frequency locations, one in each hemifield. 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 decreases 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 lateralized, as similar effects can be observed in both hemifields.



# SHORT AND LONG-TERM EFFECTS OF SUPPRESSION HISTORY



# **3.1 INTRODUCTION**

As discussed in Chapters 1 and 2, a growing number of studies have shown that attentional deployment can be remarkably adjusted on the basis of prior experience. The Experiment described in Chapter 2 showed that distractor filtering can become increasingly facilitated if the salient distractor appears at a spatial location that has been more frequently ignored, thus suggesting that the attentional priority of spatial locations in the visual field can be adjusted following forms of statistical learning.

Previous studies, concerned with learning-based adjustments of attentional selection had shown that the previous experience of target selection across the visual space elicits an attentional bias toward locations that were selected more frequently in the past (i.e. selection history), thus leading to a benefit in the subsequent target selection (e.g. Ferrante, Patacca, Di Caro, Della Libera, Santandrea, & Chelazzi, 2018; Wang, & Theeuwes, 2018a; Geng, & Behrmann, 2005; Jiang, Li, & Remington, 2015; Jiang, Swallow, & Rosenbaum, 2013a; Sha, Remington, & Jiang, 2017). Interestingly, this advantage gained in target selection was found to be so strong that it was maintained over time, suggesting that selection history was capable of leading to lasting changes in attentional priority similarly to other forms of implicit learning.

Evidence bearing on this point was, for instance, provided by Jiang and colleagues. In a visual search study they manipulated target probability across the visual display and showed not only the emergence of an attentional bias for the region in the visual field frequently associated with target presence, but also the long-term persistence of this effect which was still found even until a week after the training (Jiang, Swallow, Rosenbaum, & Herzig, 2013b).

Considering these premises, the question arises whether the persistence of the symmetrical effects of suppression history, that have been described now in many different studies, will be similarly prolonged. The pieces of evidence obtained concerning distractor filtering seem to suggest that the effects of prior history are similar to those affecting target selection and this could lead to envision the involvement of similar or shared mechanisms underlying both these forms of experience-dependent learning.

In this regard, a concept that has acquired a great importance for this discussion is that of spatial priority maps, which consist of neuro-cognitive representations of the visual space that guide attentional deployment towards locations whose overall priority – coded on the basis of top-down and bottom-up control signals – is the highest (Zelinsky, & Bisley, 2015). For example, among the studies cited above, both Ferrante et al. (2018) and Wang & Theeuwes (2018) argued that statistical learning could affect attentional deployment by inducing plastic changes in the priority maps of the visual space. Specifically, the locations more frequently associated with the target could boost their priority in these maps consistently with the selection history acquired, eventually biasing attentional deployment toward these, more relevant, locations.

Reversely, the priority of locations that have acquired substantial evidence of suppression should be reduced in these maps, and thus supporting the ongoing filtering process.

Since the first gathering of clear evidence that suppression history strongly impacts on the immediate deployment of visual-spatial attention, it still remains to be clarified whether these effects are supported by processing biases which dynamically to adjust the underlying priority maps or whether the traces accumulated are stored in memory and give rise to lasting effects like it seems to occur with respect to selection history.

Given the previous findings of lasting effects due to selection history, it should be not surprising to find that suppression history could successfully shape longterm attentional deployment as well. However, the evidence obtained so far is unclear, leaving still several gaps not only in order to understand the degree of persistence of these learned bias, but most importantly in understanding whether the mechanisms underlying selection and suppression history are shared and similarly subject to the influence of learning.

Some indication of differences in the lasting effects due to selection and suppression history comes from the studies reported by Ferrante and colleagues (Ferrante et al., 2018). In one experiment exploring the statistical learning of both target selection and distractor suppression, they had shown that, differently from the benefit acquired in target selection, that persisted during an extinction regimen (i.e. after the probability biases were removed), the effects of statistical learning associated with distractor location were no longer observed. Indeed, although the authors found a significant effect during the training (i.e. a performance benefit in trials with a distractor at a high-frequency location), in the subsequent extinction phase only a trend was found in the expected direction that could suggest a slight attenuation of the initial effect which was however not persistent.

Within a different approach, very recently Sauter and colleagues have conducted some interesting experiments to test the effects of unbalances in distractor location probability and their carry-over effect (Sauter, Liesefeld, & Müller, 2019). In particular, the authors tested this effect in experiments in which the distractor saliency was determined by manipulating the defining-dimension of the distractor with respect to the target (see Chapter 1). In their visual search task, the distractor appeared in 90% of cases within a given area, and the benefits in target discrimination were only found when the distractor was defined by the same dimension which also defined the target (i.e., both target and distractor were different with respect to other items in the array because of their orientation). As discussed in Chapter 1, relatively to a situation in which target and distractor are defined by different dimensions (i.e., the target is defined by orientation and the distractor by color), this condition is more challenging for attentional selection, because generic mechanisms that contribute to down-weighting a whole perceptual dimension are not eligible to inhibit the distractor (i.e., an overall reduction in the priority of "orientation signals" would also reduce the priority of the target, because it is also defined by this perceptual property). In contrast, when the distractor was defined by a different perceptual dimension with respect to the target, the benefit determined by the frequency biases applied to distractor location was virtually non observable. This finding suggested that if distractors can be filtered out on the basis of higher-level descriptions, their filtering will not be influenced by statistical manipulations acting at a lower-level feature such as their spatial location.

Following this initial evidence, these authors also found that during a test session in which the unbalances in distractor location probability were removed the lasting effect of such implicit cueing of distractor probability was found only when the learning occurred with the same-dimension distractor, and it was maintained both 5 min and 24 hours later (Sauter, Liesefeld, & Müller, 2019). Incidentally, this finding perhaps explains the absence of lasting effects in the experiment by Ferrante et al. (2018), in which the distractor was a color singleton and thus was defined by a different dimension with respect to the target, which was defined on the basis of its shape. The authors argued that the implicit cuing effects of distractor probability can be maintained in time, but, because the filtering of distractors defined by same vs. different dimensions is mediated by different types of attentional mechanisms, these are also affected differently by prior history. Only the mechanisms involved in distractor filtering at the level of its specific features will be sensitive to frequency-based unbalances of distractor location, leading to durable changes in the representation of spatial priority.

On a different theoretical line, Turatto and colleagues have recently proposed an alternative perspective that is grounded in the phenomenon of habituation. As discussed in Chapter 2, according to this notion, benefits in distractor filtering can be explained as a consequence of the automatic decrement in response due to mere habituation of a reflexive orienting response toward a salient stimulus, triggered by repeated exposure to it (Bonetti, & Turatto, 2019). Following this view, they have shown that the oculomotor capture elicited by an onset distractor was progressively attenuated over the course of a task requiring to make a saccade toward the target, and that this effect had the typical characteristics of habituation as, for instance, its short- and long-term components. Indeed, it was shown that the benefit in the reduction of distractor interference due to repeated exposure was maintained from several minutes to days (Turatto, & Pascucci, 2016).

Evidently, the amount of evidence on the permanence of the effects due to suppression history is still scarce, and the results described are sometimes conflicting. This leaves open the way to further investigations, to try to ascribe this phenomenon to specific cognitive mechanisms.

Here, we describe two eye-tracking experiments aimed to clarify whether suppression history could lead to lasting learning-induced plasticity or whether it improves distractor filtering through ongoing adjustments of spatial priority. We employed the same visual search task used in our previous study (see Chapter 2), which was able to induce clear suppression history effects on both manual responses and oculomotor behavior. In both experiments the participants performed a training session, in which they had to discriminate manually by key-press a singleton target while ignoring a sudden onset distractor which, when present, could appear more frequently at two locations. Differently from other studies conducted so far on the permanence of prior experience effects, here we crucially focused on a direct index of attentional deployment using distractors that fall outside of a strict "dimension-based". Specifically, given that the task didn't explicitly require to make eye-movements, oculomotor data would mirror spontaneous saccades that can be considered a more valid ecologic measure of overt attention, thus avoiding an overestimation of top-down inhibitory control. Furthermore, the choice to employ an onset stimulus, allowed us to go beyond the dimension-dependent definition of distractor salience, that in previous studies was a "relative" feature insomuch as defined by the matching with respect to the target dimension. Here the distractor is associated with a singleton color, like the target, but at the same time, it is uniquely salient because it is a new stimulus appearing in the visual field, which is known to automatically captures exogenous attention more strongly than other stimuli, independently from the target features (Folk, & Remington, 2015; Jonides, & Yantis, 1988; Irwin, Colcombe, Kramer, & Hahn, 2000). After an extensive training, we investigated the maintenance of learned-induced suppression in a Test phase performed 24 hours later (Experiment 1) or immediately after the end of the Training session (Experiment 2), by probing both the manual RT to the task and the oculomotor behavior. Firstly, we expected to replicate the findings in previous reports regarding the change in spatial priority while the imbalances in distractor location were in place, during the Training phase. Thereafter, consistently with findings reported with respect to selection history, we expected to observe that the accumulation of suppression traces associated with the high frequency distractor locations would lead to lasting changes in their attentional priority.

## **3.2 GENERAL METHOD**

Both experiments were carried out in accord with the WMA Declaration of Helsinki and with APA ethical standards, and they were approved by the Review Board for Research involving Human Participants (CARU) of the University of Verona.

The task and the stimuli employed were the same for each experiment, whereas some changes regarded the temporal unfolding of the experimental sessions and the number of trials involved in each session. For better clarity, in the following sections we are going to firstly illustrate the general method and then detail the substantial changes in the sections relating to each experiment.

#### 3.2.1 Apparatus

The experiments were programmed and run by using OpenSesame 3.0 (Mathôt, Schreij, & Theeuwes, 2012) on a PC with a processor speed of 3.60 GHz. We presented visual stimuli on a 24-inch BenQ XL2430T LCD monitor, with a resolution of 1920 x 1080 pixels and a refresh rate of 144 Hz.

In each experiment, the eye-movements of the right eye only were collected and recorded by the SR Research Eyelink 1000 Plus desktop-mounted system, with a 1000 Hz temporal and 0.01° spatial resolution. 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. A 9-point calibration of the gaze of each participant was performed before the beginning of the experiments.

#### <u>3.2.2 Stimuli</u>

The task employed for each experiment was the same previously used for the study described in Chapter 2 (see. Fig.2.1, panel A for the task illustration). All trials began with an eye drift correction trial in which participants had to fix a central white dot  $(1.25^{\circ} \text{ in diameter})$  presented on a uniform gray background (RGB: 30,30,30; 14.1 cd/m<sup>2</sup>). Following fixation, upon the onset of the stimulus

display, participants were free to move their eyes elsewhere. Six grey circles (RGB:95, 95, 95; 68.6 cd/m<sup>2</sup>; 2.5° in diameter), with a pre-mask consisting of a grey asterisk located inside (39cd/m<sup>2</sup>; 0.4° in size), were simultaneously presented at 10° of eccentricity, equally spaced at the 1, 3, 5, 7, 9 and 11 o'clock positions of an imaginary circle. After a random variable interval of 500-800 ms, the fixation dot was removed and all the circles changed color, becoming green (RGB: 30,120,50; 68.2 cd/m<sup>2</sup>), with the exception of the singleton stimulus acting as target, which was the only one remaining grey. At the same time, all the asterisks inside the circles were removed so unveiling a left- or right-tilted small grey line (39 cd/m<sup>2</sup>). This search display was available until response or for 1000 ms. The task demand was to perform a manual response, reporting whether the target line was left- or right-tilted by pressing the "N" or "M" key on a QWERTY keyboard. Participants were encouraged to be as fast and accurate as possible. If the discrimination response was incorrect, it was signaled to participants by an error display and an 800 Hz tone.

Importantly, we designed the target line so small and so eccentric, that correct discrimination could only occur if the target was in fovea (as revealed by previous pilot tests). Given that, although the participants didn't receive explicit instructions about eye-movements (indeed after fixation the were free to move their eyes), the task implicitly required to make a saccade toward the target. This is crucial for our paradigm, by allowing to explore more naturally the oculomotor behavior, with respect to a purely saccadic task (i.e., which would require subjects to make an eye movement towards the target and thus exert an extraordinarily higher degree of top-down control over their oculomotor behavior).

Despite the fact that the target was a singleton, and so it was physically salient, to tap the mechanisms associated with distractor filtering we introduced a more salient item in the array which appeared in a proportion of trials (established specifically by design; see below for each experiment). It was an additional red circle (RGB: 255, 0, 40; 60.8 cd/m<sup>2</sup>) that abruptly appeared in the display at one of the empty locations between the other circles. This stimulus stood out and was particularly salient – and distracting - since just like all new and unexpected items

in the environment it had the intrinsic ability to strongly grab eye gaze (and therefore spatial attention).

#### 3.2.3 Design

Each experiment was designed following the same procedure, and consisted of three phases. First of all, the participants performed a short practice block, followed by a Baseline phase, in which the distractor, present in the 50% of the trials, appeared randomly and equally across the six possible distractor locations. After a while (see below for details), at the beginning of the Training phase, unbeknown to the participants, the overall distractor presence changed to 64% and its distribution across locations was unbalanced by design as follows. Two locations, one for each hemifield and counterbalanced across participants, were occupied by the distractor with High Frequency (HF; overall 76% of the distractor present trials, 38% for each location); at the remaining four it appeared with Low Frequency (LF; 24% of the distractor present trials, 6% for each location) (Chapter 2, Fig. 2.1, Panel B). The last phase consisted of the Test phase, in which the distractor probability was reestablished and balanced across locations (as in the Baseline phase): the distractor, now present in 50% of the trials, appeared at each location with the same probability. Importantly, no frequency bias was applied to the target, the position of which was balanced and randomly determined among the six possible locations over the course of the whole experiment.

#### 3.2.4 Data analysis

Statistical analyses on eye-movements and manual reaction times (RTs) were both performed by using R 3.4.3 (R Core Team, 2017). Manual RTs were analyzed only on correct responses excluding trials in which the RT was not comprised within 3 SD from the mean for each condition in each participant (excluded data: Exp.1=2.9% of trials; Exp.2=2.73%). Accuracy was very high (Exp.1=98%; Exp.2=98%) and was not affected by the variables manipulated, therefore the results of these preliminary analyses are not reported here. All the analyses on manual RTs were performed by considering distractor cost as the dependent measure, i.e. the difference in RTs between the distractor-present and the distractorabsent conditions.

Eye-movements were computed by considering a saccade when the eye velocity exceeded the threshold of 35°/s whit a minimum acceleration of 9.5°/s. For analysis, we considered only the first saccades made from the stimulus onset with latencies comprised between 60 ms and 800 ms (this criterion led to the exclusion of 3.3% of trials in Exp.1 and of 2% of trials in Exp.2). Saccade latency was defined as the interval between the onset of the stimuli and the beginning of the first saccade. Eye-movements were analyzed in terms of direction of the first saccade leaving the center point. Specifically, we considered valid saccades those that fell within the slice-shaped display area within 20 deg (i.e., 20 angular degrees) from the target (vertex placed at the center of the display). On the other side, first saccades were classified as being directed towards the distractor when their endpoint fell within a slice area 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 (e.g., like in Theeuwes et al., 1999).

## **3.3 EXPERIMENT 1: LONG-TERM EFFECTS**

Experiment 1 aimed to explore the permanence of suppression history effects in the long-term, thus investigating whether the benefit observed in the filtering of distractors at high frequency locations could persist even after the removal of the frequency biases, 24-hours after the training was last performed.

#### 3.3.1 Participants

Twenty-one healthy participants were initially recruited for the study, but three 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 18 participants (6 males; mean age 22 years  $\pm$  3.2 SD).

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 ( $\in$ 20) at the end of the experimental session.

#### 3.3.2 Experimental procedure

The Experiment was performed on two consecutive days and consisted of three phases designed as follows. On the first day, after a brief practice block, participants performed an initial balanced phase, the Baseline phase, followed by the Training phase, in which, crucially, the frequency of the distractor was unbalanced by design unbeknown to the participants. This first session (day 1) comprised overall 1060 trials (practice: 16 trials; baseline: 144 trials; training: 900 trials) and lasted approximately 1.5 hours. During the whole session participants could take a short break after every ~50 trials.



#### Figure 3.1. Sequence of the experimental phases.

Percentages indicate the distractor location probability during each phase. High Frequency locations are shown in red, Low Frequency in blue, whereas gray is used to indicate the even distribution. The two possible assignments illustrated for the Training phase were counterbalanced across participants. The Test phase was performed 24-hours after the Training.

On the second day, participants performed exactly the same visual search task, but without frequency unbalances of distractor locations, so that, exactly as in the Baseline phase of the first day, the distractor could appear with the same probability across locations. This session, acting as Test phase, lasted approximately 45 minutes and comprised 504 trials overall, with short breaks interspersed on every  $\sim$ 50 trials (Fig. 3.1).

#### 3.3.3 Results

#### 3.3.3.1 Manual RTs

Data analyses were computed on the means of correct manual RTs to the discrimination task and conducted by considering as dependent variable the mean distractor cost (ms).

**Baseline phase**. To verify that in the Baseline phase different distractor locations led to comparable effects, and so discarding any possible a priori effects, we conducted a test to compare the impact of distractors appearing at locations that in the Training phase would become associated with frequency unbalances. This comparison was not significant (t(17)=0.164, p = 0.87, d= 0.03), suggesting that before the frequency manipulations the distractor led to a similar attentional cost independent of the location occupied (Fig.3.2, panel A).

**Training phase.** Data analyses on the Training phase were computed separately for trials with irrelevant onsets at High frequency and at Low Frequency locations. We conducted a 2 x 3 repeated-measures analysis of variance (ANOVA), with Distractor Location (HF: High Frequency; LF: Low Frequency) and Block (3 consecutive blocks in the Training phase) as within-subjects factors. As expected by previous finding, the distractor cost was lower when the onset appeared at the HF locations (~31ms) compared to LF locations (~51ms), as shown by the significant main effect of Distractor Location (F(1,17)=10.88, p= 0.004,  $\eta_p^2$ =0.39). The main effect of Block was not significant (F(2,34)= 0.83, p= 0.44,  $\eta_p^2$ = 0.09), however the interaction between Distractor Location and Block was significant

(F(2,34)=4.64, p=0.01,  $\eta_p^2$ =0.35)(Fig.3.2, panel A). This result revealed that the difference between trials with distractors appearing at HF and LF locations tended to become larger throughout the Training phase, with the incremental accumulation of suppression history. Indeed, the post-hoc pairwise comparison comparing the difference in cost between HF and LF in the first block with respect to the last block confirmed that the main effect of Distractor Location became larger in the last block (Block1 vs. Block3: t(17)= 3.04, p=0.007, d=0.71).



**Figure 3.2.** Manual responses as a function of Distractor Location and Phase. Mean cost in manual RTs associated with distractor in HF (in red) and LF (in blue) locations, during the Baseline, the Training (Panel A) and the Test (Panel B) phases. Error bars depict the within-subject confidence intervals (Cousineau, 2005, corrected according to Morey, 2008).

**Test phase.** A 2x3 ANOVA similar to the one performed on the data from the Training phase was employed to analyze the Test phase. Despite the large and robust effect of Distractor Location found in the Training phase, none of the main factors considered, nor their interaction, was significant in the Test phase (Distractor location: F(1,17)=0.11, p=0.73,  $\eta_p^2=0.006$ ; Block: (2,34)=0.30, p=0.73,  $\eta_p^2=0.02$ ; Distractor Location x Block: F(2,34)=0.80, p= 0.45,  $\eta_p^2=0.10$ ). Distractors induced the same cost on RTs independently of the locations they occupied. The distractor cost in RTs was nevertheless overall reduced with respect to the Baseline phase, so revealing a generalized improvement in task performance (Distractor cost: Baseline= ~50 ms, Test=~33ms; t(17)=2.91, p=0.009, d= 0.69). However, despite this significant reduction, the cost was, in any case, robust until

the end of the Test session (one-sample test: t(17)=9.05, p<0.0001)(Fig.3.2, panel B).

Training vs. Test. To directly compare the Training and the Test phase we conducted an ANOVA with Phase (Training vs. Test) and Distractor Location (High frequency vs. Low frequency) as main factors. The data showed a significant interaction between Distractor frequency and Phase (F(1,17)=11.14, p=0.003, p=0.003) $\eta_p^2 = 0.39$ ). To explore whether the changes in Distractor Location through phases were due to a general resettlement that involved both High and Low frequency location in a similar fashion, we performed pairwise comparisons (Holm corrected) between the last block of the Training and the first block of the Test, separately for each condition. This analysis revealed that while the reduction in attentional capture found in the Training phase for distractors appearing in High frequency location was maintained also in the Test phase (t(17)=1.03, p=0.313, d=0.24), distractors at Low Frequency locations that in the Training phase elicited a strong attentional capture, seemed to have lost their strength with respect to the last block of the Training phase (t(17)=4.058, p=0.001, d=0.95). Thus, the changes found in the Test phase seem due mainly to changes involving distractor filtering at locations that had acquired a weaker suppression history, which -24 hours after the training - seemed to have become as easy to ignore as those which were associated with a more significant suppression history.

**Bin analysis.** Considering the possibility that some residual effect could be maintained in the very first trials of the Test phase, we additionally subdivided it into 21 bins containing each ~ 16 trials for each subject. The pairwise comparison conducted between High and Low Frequency locations in the first bin of the Test phase showed that no residual effect was maintained, not even in the earliest trials (t(17)=0.749, p=0.463, d=0.17).

#### 3.3.3.2 Eye-movements

For the eye-movements analyses we considered as dependent variable the percentage of first saccades that upon stimulus onset were directed "correctly" toward the target (hereafter called "valid saccades"), and the percentage of first saccades "wrongly" directed toward the onset distractor ("captured saccades").

**Baseline phase.** As for the case of RT data, firstly we discarded possible a priori effects of Distractor location. The pairwise comparison between locations that in the Training phase would become HF and LF was not significant for valid saccades (t(17)=0412, p=0.685, d= 0.09))(Fig.3.3, panel A). Curiously, for captured saccades a significant effect was found, but as shown in the graph, this possible a priori effect is in the opposite direction with respect to what will be expected to happen over the course of the training phase (t(17)=2.291, p=0.035, d= 0.540))(Fig.3.4, panel A).

**Training phase.** Saccades directed toward the target were analyzed by computing the difference between the percentage of first valid saccades in the distractor present and absent trials. These data were submitted to a 2 x 3 ANOVA with Distractor Location (HF vs. LF) and Block (1 to 3) as within-subjects factors. The analysis had shown a significant and robust main effect of Distractor Location (F(1,17)=43.056, p<0.0001,  $\eta_p^2$ =0.71). Neither Block nor Distractor Location x Block were significant (Block: F(2,34)=0.848, p= 0.437,  $\eta_p^2$ =0.07; Distractor Location x Block: F(2,34)=1.845, p=0.175,  $\eta_p^2=0.16$ ) (Fig.3.3, panel A). A similar ANOVA was conducted on the mean percentages of first saccades landed on the distractor. Also in this case, we found a significant main effect of Distractor location  $(F(1,17)=22.423, p=0.00019, \eta_p^2=0.56)$ , but no significant effects of Block or its interaction with Distractor location (Block: F(2,34)= 0.362, p= 0.698,  $\eta_p^2$ =0.03; Block x Distractor Location: F(2,34) = 0.021, p = 0.978,  $\eta_p^2 = 0.002$ ), suggesting that the differences between trials with distractors at HF and LF locations was already observable during the first block and remained constant across the Training (Fig.3.4, panel A).



**Figure 3.3.** Percentage of valid saccades as a function of Distractor location and Phase. (A) Percentage of first saccades directed to the target (upper graph) and mean difference in this percentage between the distractor absent and the distractor present condition (lower graph), plotted separately for HF and LF locations, for the Baseline and the Training phases. (B) Percentage of first saccades directed to the target (upper graph) and mean difference in this percentage between the distractor absent and the distractor present condition (lower graph), plotted separately for HF and LF locations, for the Baseline and the Training phases. (B) Percentage of first saccades directed to the target (upper graph) and mean difference in this percentage between the distractor absent and the distractor present condition (lower graph), plotted separately for HF and LF locations, for the Test phase.

**Test phase.** The ANOVA conducted on the differences between the percentage of first valid saccades in the distractor present and absent trials revealed that none of the effects found in the Training phase was maintained during the Test phase (Distractor location: F(1,17)=0.408, p=0.5311,  $\eta_p^2=0.02$ ; Block: F(2,34)=0.364, p=0.697,  $\eta_p^2=0.04$ , Distractor location x Block: F(2,34)=0.059, p=0.942,  $\eta_p^2=0.008$ )) (Fig.3.3, panel B). Also with respect to the analyses on the captured saccades, the ANOVA with Distractor Location and Block as main factors, revealed no effects for each of the factors considered (Distractor Location: F(1,17)=1.46, p=0.24,  $\eta_p^2=0.07$ ; Block: F(2,34)=0.43, p=0.64,  $\eta_p^2=0.04$ ; Distractor Location x Block: F(2,34)=0.07, p=0.92,  $\eta_p^2=0.006$ ) (Fig.3.4, panel B).

Therefore, during the Test distractors induced the same interference on oculomotor behavior independently of the locations they occupied. However, similarly to the findings on manual RTs, their interference was overall reduced with respect to the Baseline phase, again revealing a generalized improvement in distractor filtering (overall captured saccades: Baseline=~29%, Test=~19%; t(17)=2.45, p=0.02, d=0.58). Interestingly, despite the extensive practice and the significant overall reduction of distractor costs observed during the Test phase, the impact of distractors was still however highly significant (one-sample test: t(17)=7.41, p<0.0001).



**Figure 3.4.** Oculomotor capture as a function of Distractor location and Phase. Percentage of first saccades directed to the distractor, plotted separately for HF and LF locations, during the Baseline and the Training phases (**A**), and during the Test phase (**B**).

**Training vs. Test.** We directly compared Training and Test phases by performing an ANOVA with Phase (Training vs. Test) and Distractor Location (High frequency vs. Low frequency) as main factors. For valid saccades, data showed a significant interaction between Distractor Location and Phase (F(1,17)=17.67, p=0.0005,  $\eta_p^2=0.51$ ). The pairwise comparisons (Holm corrected) between the last block of the Training and the first block of the Test, separately for each distractor condition (HF and LF), showed that the higher number of valid saccades found during the Training phase when the distractor appeared at High Frequency locations was maintained in the first block of the Test phase (Block 3 vs. Block 4: t(17)= 0.91, p= 0.37, d=0.21). Differently, the interference due to distractor appearing at Low Frequency in the Training phase was significantly

reduced in the Test phase, in which the cost in the percentage of valid saccades became comparable to the one due to distractors at HF locations (Block 3 vs. Block 4: t(17)=2.95, p=0.01, d=0.69). The ANOVA performed on captured saccades data showed a similar significant interaction between Distractor Location and Phase (F(1,17)=16.31, p=0.0008,  $\eta_p^2=0.48$ ). The pairwise comparisons (Holm corrected) between the last block of the Training and the first block of the Test revealed that the reduced oculomotor capture elicited by distractors appearing at High frequency locations in the Training phase was maintained in the first block of the Test phase (Block 3 vs. Block 4: t(17)=0.11, p=0.906, d=0.02). Instead, the strong oculomotor capture elicited by distractors was significantly reduced already in the first block of the Test phase (Block 3 vs. Block 4: t(17)=2.96, p=0.01, d=0.69).

Again, these findings seem to indicate that the absence of Distractor location differences found in the Test phase may result from changes in the ability to filter out distractors even at locations that had acquired a weaker suppression history.

**Bin analysis.** On the percentage of first valid saccades, the pairwise comparison conducted between High and Low Frequency locations in the first bin of the Test phase showed that no residual effect was maintained, not even in the very first trials (t(17)= 1.766, p= 0.095, d=0.41). Consistently, the analysis performed on the percentage of saccades directed toward the distractor showed that distractors appearing at the previous High and Low-frequency locations elicited the same degree of oculomotor capture already in the very first trials (t(17)= 0.483, p= 0.634, d=0.11).

#### 3.3.4. Conclusion Experiment 1

Experiment 1 aimed to explore the permanence of the suppression history effects in the long-term.

First of all, importantly, the results obtained during the first day have confirmed our previous results (Di Caro et, al. 2019). Suppression history significantly affected both attentional and oculomotor control, indeed distractors appearing at locations where distraction had occurred more often (i.e. High frequency locations) were better ignored, as revealed by the faster RTs on the discrimination task and the weaker oculomotor capture. This benefit developed quickly, appearing early after the introduction of frequency biases, and was strongly maintained over the course of the Training, until the very last trials.

However, despite the strong benefit acquired, no effects were maintained in the following day, not even in the very first trials performed. The results obtained in the Test phase revealed a generalized improvement in distractor filtering, perhaps due to the mere practice with the visual search task and the filtering of visual onsets, which was independent of the history associated with the locations in which the distractors appeared.

Nevertheless, in spite of the long training performed and of the additional practice during the Test phase, the onset distractor continued to elicit a relevant interference which could still be appreciated notwithstanding the general benefit, confirming the intrinsic, and hard to shield, salience of this kind of stimulus.

These findings confirmed that suppression history can be efficient in contrasting salient distractors by affecting attentional and oculomotor control while frequency biases are in action. However, the history associated with specific locations seems to determine a transient benefit that is not maintained in the long-term, vanishing already 24-hours after the training. It is thus possible that the effects of suppression history on attentional deployment are sustained by dynamic and transient adjustments of spatial priority, rather than by long-lasting changes settled through learning in the spatial priority maps involved.
# **3.4 EXPERIMENT 2: SHORT-TERM EFFECTS**

In light of the results obtained in Experiment 1, the following experiment was designed to investigate for how long the effects due to suppression history could be maintained after the frequency bias is removed, and therefore after distractor probability is reset to an even distribution across locations. With this aim, differently from the previous procedure, here the Training and the Test phases were performed consecutively, <u>on</u> the same day.

## 3.4.1 Participants

Twenty-four healthy participants were initially recruited for the study, but four 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 20 participants (10 males; mean age 22 years  $\pm$  3.2 SD).

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 ( $\in$ 15) at the end of the experimental session.

### 3.4.2 Experimental procedure

The experiment consisted of three phases that were performed on the same day. These phases took place seamlessly, and the whole trial sequence was only interrupted after every ~50 trials to allow for a short break. At first, participants performed a brief practice block, followed by the Baseline phase, the Training phase and, finally, the Test phase. The experiment comprised overall 1054 trials (Practice: 16; Baseline: 72; Training: 750; Test: 216) and lasted approximately 2 hours. The frequency of the distractor across locations was biased exactly as in Experiment 1, thus the distractor appeared with the same frequency in Practice, Baseline and Test phases, while it appeared with different frequencies during the Training phase (High frequency: overall 76%; Low frequency: overall 24%).

#### 3.4.3 Results

All statistical analyses conducted were the same as in Experiment 1.

3.4.3.1 Manual RTs

**Baseline phase.** Again, we confirmed the absence of *a priori* effects. The pairwise comparison between locations that in the Training phase would become HF and LF showed that distractors elicited the same cost on manual RT independently of the location occupied in the Baseline phase (t19)= 1.12, p= 0.276, d= 0.25)(Fig.3.5).

**Training phase.** Consistently with the main results found in Experiment 1, the analysis of variance (ANOVA) computed on the distractor cost in the manual responses showed a main effect of Distractor location (F(1,19)= 25.501, p< 0.0001,  $\eta_p^2$ =0.57). The main effect of Block and the interaction between Block and Distractor location were not significant (Block: F(2,38)= 0.531, p= 0.592,  $\eta_p^2$ =0.02; Block x Distractor location: F(2,38)= 0.953, p= 0.394,  $\eta_p^2$ =0.04) (Fig.3.5). With respect to the previous experiment, here the absence of a significant interaction revealed that the difference in distractor cost associated with high and low frequency locations was maintained constant over the course of the training.



**Figure 3.5. Manual responses as a function of Distractor Location and Phase.** Mean cost in manual RTs associated with distractors in HF (in red) and LF (in blue) locations, during the Baseline, the Training, and the Test phase.

**Test phase.** The analysis of variance (ANOVA) with Distractor Location and Block as main factors, revealed that, once again, the main effect of Distractor Location was not maintained in the Test phase, although this time it was performed immediately after the Training (F(1,19)= 2.16, p=0.158,  $\eta_p^2$ =0.10). Also the main effect of Block and the interaction between Block and Distractor location were not significant (Block: F(2,38)= 1.972, p=0.153,  $\eta_p^2$ =0.09; Block x Distractor location: F(2,38)= 0.205, p= 0.814,  $\eta_p^2$ =0.01)(Fig. 3.5).

**Training vs. Test.** The ANOVA with Phase (Training vs. Test) and Distractor Location (High frequency vs. Low frequency) as main factors showed that the interaction between Distractor location and Phase approached to significance  $(F(1,19) = 3.344, p=0.08, \eta_p^2 = 0.14)$ . We performed explorative pairwise comparisons (Holm corrected) between the last block of the training and the first block of the test, separately for each condition (HF and LF).

Analyses revealed that the reduction in attentional capture found in the Training phase for distractor appearing in High Frequency location was maintained also in the Test phase (t(19)= 0.457, p=0.652, d=0.10). The comparison between Training and Test for distractors appearing at LF location instead approached to significance (t(19)= 2.307, p= 0.06, d= 0.51).

**Bin analysis.** In order to individuate possible residual effects of suppression history at the beginning of the Test phase, we divided it into 9 bins containing  $\sim 15$  trials for each subject and condition.

The pairwise comparison conducted between the High and the Low Frequency locations in the first bin of the Test phase revealed that no residual effects on manual RTs were detectable, not even in the very first trials following the Training phase (t(19)=0.627, p=0.538, d=0.14).

#### 3.4.3.2 Eye-movements

**Baseline phase.** The pairwise comparison between locations that in the Training phase would become associated with HF and LF was not significant for both valid saccades (t(19)=0.585, p=0.565, d=0.13) and captured saccades

(t(29)=0.694, p= 0.495, d= 0.15), confirming the absence of a priori effects (Fig.3.6).

**Training phase.** Saccades directed toward the target were analyzed by computing the difference between the percentage of first valid saccades in the distractor present and absent trials.

The analysis of the variance (ANOVA) with main factors Distractor location and Block, revealed a significant main effect of Distractor location (F(1,19)= 53.26, p<0.0001,  $\eta_p^2=0.73$ ). The effect of Block approached to significance (F(2,38)= 2.99, p= 0.06,  $\eta_p^2=0.13$ ). The interaction between Block and Distractor location was significant (F(2,38)=5.44, p=0.008,  $\eta_p^2=0.22$ ) (Fig.3.6). Therefore, the pattern of results concerning the development of this effect through the Training session seemed to differ from that observed in manual RTs; here the differential effect of distractor location on the percentages of valid saccades seems indeed to grow as the training proceeded.



**Figure 3.6.** Percentage of valid saccades as a function of Distractor location and Phase. Percentage of first saccades directed to the target (upper graph) and mean difference in this percentage between the distractor absent and the distractor present condition (lower graph), plotted separately for HF and LF locations, for the Baseline, the Training, and the Test phase.

A similar ANOVA was conducted on the percentage of the first saccades landed on the distractor (i.e. captured saccades). The analysis showed a significant main effect of Distractor location (F(1,19)= 34.13, p< 0.0001,  $\eta_p^2$ =0.64). The main effect of Block and the interaction between Block and Distractor location were not significant (Block: F(2,38)= 1.55, p= 0.22,  $\eta_p^2$ =0.07; Block x Distractor location: F(2,38)= 0.81, p= 0.44,  $\eta_p^2$ =0.04) (Fig.3.7).

**Test phase.** The ANOVA on correct saccades highlighted a significant main effect of Distractor location (F(1,19)= 7.004, p= 0.016,  $\eta_p^2$ =0.26). The main effect of Block and the interaction between Block and Distractor Location were not significant (Block: F(2,38)= 0.12, p= 0.88,  $\eta_p^2$ =0.006; Block x Distractor location: F(2,38)= 1.35, p= 0.27,  $\eta_p^2$ =0.06) (Fig.3.6).

The ANOVA on the captured saccades with Distractor Location and Block as main factors, revealed a main effect of Distractor location (F(1,19)= 14.72, p= 0.001,  $\eta_p^2$ =0.43). The effect of Block and the interaction between Block and Distractor Location were not significant (Block: F(2,38)= 1.91, p= 0.16,  $\eta_p^2$ =0.09; Block x Distractor location: F(2,38)= 1.85, p= 0.17,  $\eta_p^2$ =0.08) (Fig.3.7).



Figure 3.7. Oculomotor capture as a function of Distractor location and Phase. Percentage of first saccades directed to the distractor, plotted separately for HF and LF locations for the Baseline, the Training, and the Test phase.

Taken together, these data on both valid and captured saccades depict the permanence of residual effects of suppression history in the short-term, which – crucially - is only revealed by eye movements. After the removal of frequency biases, distractors appearing at locations that were previously associated with a significant history of suppression continued to be ignored more efficiently, giving rise on one hand to lower oculomotor capture, and on the other to benefits on the saccades directed to the target.

**Training vs. Test.** The ANOVA on valid saccades with Phase (Training vs. Test) and Distractor Location (High frequency vs. Low frequency) as factors showed a significant main effect of Distractor location (F(1,19)= 30.36, p<0.0001,  $\eta_p^2$ =0.61). The main effect of Phase and the interaction between Phase and Distractor location were not significant (Phase: F(1,19)= 1.68, p= 0.21,  $\eta_p^2$ =0.08; Phase x Distractor location: F(1,19)= 2.62, p=0.12,  $\eta_p^2$ =0.12). Therefore, in the Test phase the effects of suppression history matured during the Training phase seemed to continue to affect the percentage of valid saccades.

A similar ANOVA was performed on the percentage of captured saccades, showing a significant main effect of Distractor location (F(1,19)= 37,19, p< 0.0001,  $\eta_p^2=0.66$ ). Both the main effect of Phase and its interaction with Distractor location were not significant (Phase: F(1,19)=1.11, p=0.30,  $\eta_p^2=0.05$ ; Phase x Distractor location: F(1,19)= 0.41, p= 0.52,  $\eta_p^2=0.02$ ).

#### 3.4.4 Conclusion Experiment 2

Experiment 2 aimed to explore the permanence of suppression history effects in the short-term, in order to estimate for how long the benefits acquired could be maintained after the removal of the frequency bias.

Once more, we replicated our previous results, so confirming that suppression history significantly affects both attentional and oculomotor capture due to onset distractors.

Differently from Experiment 1, the removal of frequency bias here happened immediately following the Training phase in a seamless fashion. This design allowed the detection of some residual effects, thus revealing that the benefit acquired during the frequency unbalances was actually maintained and continued to affect performance, although only for a short time. Interestingly, these residual effects were only observable with respect to oculomotor behaviour, whereas the impact of distractors appearing at locations associated with different suppression histories was no longer evident on manual responses to the discrimination task in the Test phase. In our paradigm manual RTs seemed to provide a less sensitive measure for the detection of experience-dependent biases. Given that our task allowed subjects to explore freely the display upon delivering the manual response to the target, the tracking of spontaneous saccades not only allowed to explore a more straightforward index of attentional selection, but also provided a more sensitive and reliable detector of changes in attentional spatial priority.

## **3.5 CONCLUSION**

In this study, we explored the impact of the suppression history associated with given spatial locations in order to detect the permanence of its effect on attentional deployment after the removal of frequency biases, to establish whether and to what extent residual effects could be observed, both in the long- and in the short-term.

So far, it was shown that suppression history significantly biases attentional deployment across the visual space in a dynamic fashion, that is while distractor frequency unbalances are in action. Specifically, when a given location often contains distractors, this location seems to keep track of the inhibition applied to such irrelevant information, so that its priority will be coherently lowered, due to its higher probability of being a source of distraction. This bias was clearly shown by recent evidence coming from studies which explored both RTs in target responses and oculomotor behavior in visual search tasks, and revealed how suppression history has an important impact not only on task performance but also directly on attentional orienting, by influencing the guidance of eye-movements.

These findings suggested that the baseline weights of priority maps, which guide the deployment of spatial attention, may be shaped by gaining or losing priority due to the prior experience accumulated during the attentional processing of stimuli at specific locations, which has led to the selection or to the inhibition of visual information. Such baseline changes in priority maps would thus affect attentional deployment accordingly, making it easier to attend locations that are already coded with a higher priority (based on their selection history), or easier to ignore, or not attend, locations that are coded with a lower priority from the beginning (based on their suppression history).

Even considering the possibility that these experience-dependent changes involve plasticity at the level of spatial priority maps, whether these adjustments may be lasting or transient is still unclear. In fact, while studies in the field of target selection are more consistent in observing long-term effects of prior experience, the findings concerning distractor filtering and suppression history are mixed.

Considering that the overall effects of selection and suppression history observed while the frequency unbalances are ongoing are often symmetrical, our prediction was that the benefits acquired in distractor filtering should be maintained after the removal of the biases, exactly like it happens for selection history. After all, other forms of implicit learning in the perceptual and attentional domain have also shown permanent effects over time, presumably due to the accumulation of memory traces that eventually drive attention accordingly (e.g. Jiang, Swallow, Rosenbaum, & Herzig, 2013b refs.).

Therefore, above and beyond the mere development of a skilled expertise involving the filtering of distracting stimuli, peculiar benefits were found in the processing of stimuli appearing at spatial locations that have been previously associated with a marked suppression history. The two experiments described in this Chapter tried to elucidate the permanence of such suppression history effects at different delays from the training sessions, and under an extinction regimen (i.e. when all frequency biases were removed).

Our findings revealed a progressively stronger benefit in task performance when dealing with distractors that appeared at locations that had been suppressed more frequently, and these results were directly supported by oculomotor measures. Indeed, despite the fact that it was never required to make "valid saccades" towards the relevant item, the spontaneous eye movements were more likely directed toward the target when the concurrent distractor appeared at a location with a significant suppression history. That location seemed thus to have accumulated traces of suppression that allowed the attentional system to label it as "unimportant", and therefore avoid its selection. On the other side, distractors appearing at unexpected locations, with a relatively lower suppression history, continued to grab a significant number of first saccades, reflecting the fact that the weaker experience of distractor filtering at this location did not allow to deprioritize its coordinates in the corresponding attentional maps.

These results provide additional evidence of robust attentional biases due to prior experience, suggesting that attentional deployment is driven by mechanisms that adjust spatial priority moment by moment on the basis of the ongoing frequency unbalances.

However, quite surprisingly, looking at the maintenance of such suppression effects over time, it seems that this phenomenon does not determine significant lingering effects. Indeed, once the frequency biases are removed, the traces left by prior experience affect attentional deployment only for a short time, so that 24hours later the specific history of suppression associated with given locations seems lost.

Interestingly, while task performance doesn't seem to benefit from these residual effects, not even in the short term, oculomotor behavior was significantly biased even after the training, showing clear benefits in the filtering of distractor at high frequency locations during the test phase. This finding suggests a prominent reliability of oculomotor measures in the investigation of attentional implicit biases, since they can reflect even the slightest changes in attentional deployment due to past experience.

The discrepancy between our results and the findings concerning target selection may suggest that the possibility of observing long-term attentional biases following statistical learning may depend on the type of resources engaged. While the relevance of the target alone triggers the deployment of a great amount of attentional resources, dedicated to its processing, distractor filtering is critically dependent on its saliency and closely related to the occurrence of other factors, so that the amount of resources required to deal with may vary. For example, in the study reported by Sauter and colleagues the distractor dimension (same/different to target dimension) played a key role in defining the salience of the distractor and, thus, the resources needed to overcome it. Indeed, long-term effects in distractor filtering were found only within the condition "same-dimension distractor", so when the competition between target and distractor was higher, and more cognitive engagement was needed (Sauter, et al., 2019).

In our study, although onsets are powerful distractors per se, the absence of additional competition with the target could have determined the engagement of a lower amount of processing resources and, thus, lower need to maintain in memory the information concerning the "irrelevant" occurrence.

Moreover, in our paradigm targets and salient distractors never shared their spatial locations: irrelevant visual onsets appeared at locations that could never be occupied by a target or a nonsalient distractor, and vice-versa. This fact could have determined an additional reason for a lower target-distractor competition, and consequently a lower amount of resources involved in sorting out relevant and irrelevant information which may have eventually acted as a deterrent for the maintenance of suppression history information over time. Further investigations will be certainly necessary to disambiguate the role of target-distractor competition in the permanence of suppression history benefits. However, our results provide new knowledge concerning the possible mechanisms underlying suppression history, suggesting the involvement of dynamic adjustments of attentional priority rather than lasting experience-dependent plasticity. Additionally, the findings here provided would claim the independence of suppression history from the habituation phenomenon. Differently from habits, that require many repetitions to be formed and are usually gradually acquired (Graybiel, 2008; Seger & Spiering, 2011), suppression history effects emerge quickly after the introduction of biases in distractor presence at specific locations. Additionally, differently by habituation paradigms, in which the benefits in distractor suppression usually persist for many days even after relatively short training sessions (~45 min), the extensive training adopted in our study ( $\sim 2$  hours) was still not sufficient to allow the persistence of residual effects in the long term, further corroborating the dissimilarity between suppression history effects and habituation learning.

Future directions should try to disambiguate the mechanisms involved in distractor filtering via suppression history. In light of the evidence reported here, one direction could focus on deepening the role of target-distractor competition and the length of training, in order to unveil possible additional influences that could lead to development long-term traces of the benefits acquired.



# NEURAL CORRELATES OF DISTRACTOR FILTERING VIA SUPPRESSION HISTORY



## **4.1 INTRODUCTION**

The bulk of research in visual-spatial attention has been amply relying on response time measurement in visual search tasks. In the last decades, the employment of physiological measures, such as electroencephalography (EEG), has become widespread, allowing to monitor brain activity on a high-resolution time scale, and thus contributing to the understanding of the mechanisms underlying visual search.

Specifically, several studies have focused on Event-Related Potentials (ERPs), a methodology that allows to track, within the EEG signal, the allocation of attentional resources millisecond by millisecond. In line with behavioral studies on attentional capture, studies employing ERPs methodology have provided several pieces of evidence of the neural signatures of attentional selection and distractor capture, by revealing different patterns of cortical activity associated with the selection of both relevant and irrelevant items in visual search tasks.

The first to observe an event-related potential component specifically triggered by attended stimuli were Luck and Hillyard in 1990. This component is the Negative Posterior Contralateral deflection in the N2 latency range (N2pc), namely the negative-going deflection occurring at 200 ms after stimulus onset, that shows an enhanced amplitude at the site of the posterior scalp (PO7/PO8) that is contralateral to the stimulus attended in the visual display (Luck, 2012; Luck & Hillyard, 1990, 1994a, 1994b). Several ERPs studies have provided converging evidence of its association with attentional selection, and this component is thus considered a sensitive marker to measure the allocation of visual-spatial attention and attentional selection (Luck, Girelli, McDermott & Ford, 1997).

Interestingly, given its relationship with attentional selection, this component can be also adopted as a sensitive index of distractor capture, i.e. revealing that selective attention was deployed towards the distractor. Indeed, many studies have shown that in a visual search task for a target located on the vertical meridian (therefore non lateralized), if a salient distractor was also shown in the right or left visual field, a contralateral N2pc was evident, thus clearly triggered by the involuntary shift of attention toward the irrelevant distractor (Hickey, McDonald, & Theeuwes, 2006; Liesefeld, Liesefeld, Töllner, & Müller, 2017).

Investigating the N2pc elicited by a salient distractor allows not only to track the covert shift of attention to such irrelevant but salient information (in cases in which eye gaze must be maintained on central fixation) but also provides substantial information on "when" the interference due to a distractor disrupts attentional control. Indeed, the N2pc is an acknowledged temporal marker for the connection between the pre-attentive perceptual processing and the selective attentional processing of the attended stimuli (e.g. Woodman and Luck, 1999; 2003).

In the previous chapters, we argued the need to further explore the dynamics underlying experience-dependent attentional learning processes, in order to understand which mechanisms support changes in attentional priority related to these forms of learning. Understanding how these effects influence the temporal dynamics of visual attention could provide additional and robust information with respect to the neural underpinnings of experience-dependent attentional biases, perhaps revealing the processing levels at which the learning mechanisms involved could take place.

In this regard, for instance, it was shown that the N2pc is sensitive to the changes in attentional priority produced by gratifying prior experiences. This is the case, for example, of the successful learning of high-reward contingencies, which was found to be associated with increased N2pc amplitude upon the onset of target information previously associated with higher rewarding values and higher efficiency in task performance (e.g., Kiss, Driver & Eimer, 2009; Feldmann-Wüstefeld, Brandhofer, & Schubö, 2016; Sawaki, Luck, & Raymond, 2015). In a similar fashion, when stimuli previously associated with high-reward selection history appear as distractors they trigger a larger N2pc, thus revealing that prior experience had changed the priority of these stimuli which had become more salient (because they acquired a reward value) and that this change could be tracked by this component (Qi, et al., 2013). In cases like this, the more powerful distractor capture was therefore generated by the modulation in the neural activity originating from sensory-perceptual regions of the visual cortex.

Considering other forms of implicit learning, as for instance those associated with the statistical contingencies of distractors (i.e. suppression history), whether and how the N2pc associated with a distractor could reflect changes in attentional priority due to the suppression history acquired by its location it has yet to be determined.

In this respect, Wang and colleagues have recently explored the interaction between prior-experience and attentional deployment by investigating the ERPs components (Wang, van Driel, & Theeuwes, 2019). In their study, the effect of unbalances in distractor appearance across locations was explored in an additional singleton paradigm in which participants had to search for a singleton target while a salient distractor could also appear. They recorded ERPs, mainly focusing their interest on a positive contralateral wave, namely the Distractor positivity (Pd) component, which usually begins 150-250 ms after the stimuli onset and is hypothesized to reflect the engagement of active attentional suppression mechanisms (Gaspelin & Luck, 2018a; Gaspar, Christie, Prime, Jolicoeur, & McDonald, 2016; Gaspar & McDonald, 2014; Sawaki & Luck, 2013; Hickey, Di Lollo, & McDonald, 2009). These authors found that distractors appearing more often at a given high-probability location elicited a prominent Pd, which, conversely, was not triggered by distractors at the low-probability location. This data suggests an active spatial suppression for locations frequently containing irrelevant information. However, whether the frequency bias could also lead to changes in the attentional selection of the distractor (signaled by the N2pc), rather than only promote its active suppression, was not clear.

Therefore, while this benefit in overcoming distractors at high-probability locations seems due to the engagement of an active suppression mechanism, on the other hand, it is still unclear whether it could reflect also changes in stored attentional priority maps, resulting from proactive inhibition processes. It would be interesting to clarify at which level of processing the interference due to a distractor is fought and overcome by the prior-experience bias: is it only a matter of reactive suppression or also of prospective inhibition and, thus, of un-selection?

As a matter of fact, in some situations a good way to make use of priorexperience could consist of biasing attentional selection rather than suppressive mechanisms per se, thus providing "implicit triggers" to avoid distractor ("let's not select it"), as an alternative to employing resources to actively suppress it.

A way to orient among these possibilities could be provided by the concurrent recording of ERPs and eye-movements, which could provide information not only concerning the neural activity of selection and/or suppression but at the same time reveal the corresponding behaviour, thus providing an ecologic measure of the related attentional biases.

For a long time, ERPs paradigms precluded the investigation of eye-movements because rotations of eye-balls are known to affect the EEG signal (Plöchl, Ossandón, & König, 2012), and the studies in the field of attention have prevalently investigated covert shifts of attention, with subjects maintaining fixation on a central point and paying attention to stimuli at the periphery of their visual field (e.g., Hickey, et al., 2009; Luck & Hillyard, 1990, 1994). Conversely, studies employing eye-tracking methodology allowed to investigate overt attentional deployment but without being able to track the related brain activity. New advances in both eye-tracking technology and EEG methods of analysis have recently offered the promising opportunity to investigate the neural correlates of visual-spatial attention directly connected to natural viewing behavior.

Therefore, in the following study, we investigated whether and how suppression history may cause changes in both cortical activity and overt attention, by simultaneously investigating ERPs components and eye-movements in a visual search task.

Given our previous behavioral and eye-movements findings, we expected that the benefits in distractor filtering specifically associated with high frequency distractor locations, could be mirrored in reduced cortical components associated with attentional selection, which might also be predictive of a reduction in the degree of the amount of oculomotor capture they determined. This possibility would be in line with the idea of changes in spatial priority maps of attention, that should induce to deprioritize the irrelevant locations under specific circumstances.

With this aim, we analysed in particular two cortical event-related potentials that are commonly thought to index attention selection and distractor suppression respectively: the N2pc and the Pd.

Specifically, we investigated whether the amplitude of N2pc triggered by salient distractors could depend on the history associated with the locations in which they appear, so that distractors appearing at locations with a significant suppression history would lead to reduced N2pc amplitudes as well as a reduced oculomotor capture. In order to clarify the role of active distractor suppression and/or distractor proactive inhibition, we expected to find coherence between cortical responses and oculomotor behaviour that could be in line with one or both of these possibilities. Therefore, a reduced attentional selection of the distractor (i.e. smaller N2pc) might correspond to a lower number of first saccades directed toward it. Similarly, the cortical response indexing active suppression (larger Pd) should be reflected in differences in the amount of time the distractor was fixated after having captured attention. Fixation duration of a distractor, in fact, is a measure usually taken to assess the time needed to disengage attention from a stimulus that has been attended, and to subsequently suppress it, prior to a shift of attention towards a new object (Posner, 1980).

We designed a visual search task in which participants had to provide a manual response to a tilted target line while ignoring a salient more-tilted distractor, both shown among an array of other non-tilted items. Distractor saliency was defined by the dimensional relationship of the distractor relative to the target. Following the theory termed Dimension-Weighting Account, when both target and distractor are defined by the same dimension (i.e. the orientation) they are highly competitive, and the inhibition of this kind of distractors is particularly arduous (see Liesefeld, & Müller, 2019). To investigate the effect due to suppression history, distractor probability across locations was biased so that distractors were more likely at two specific locations in the visual array. Spontaneous eye-movements and EEG were concurrently recorded in order to determine (1) whether changes in the neural representation of distractor location revealed a loss of distractor salience within the visual system and/or reflect its active suppression; (2) whether such neural changes fostered efficient eye-movement behavior.

We predicted that distractor filtering mechanisms could be differently implemented in occipito-parietal cortex depending on the amount of resources engaged. Thus, the condition in which the distractor appears at a location where it is very frequent – and perhaps expected - should induce lower neural activation, mirroring the lower conflict on both task performance and oculomotor control.

Moreover, concurrent EEG and eye-movements recording could also provide additional information on the selectivity of the N2pc component to attended stimuli. Given that N2pc is quantified as the difference in amplitude between contralateral versus ipsilateral activity, it should reflect the preferential allocation of attentional selection towards a side, rather than to a specific item or location. The concurrent oculomotor data would allow going beyond this confounding possibility, by directly revealing "what", within a visual hemifield, is actually attended.

## **4.2 METHOD**

#### 4.2.1 Participants

Eighteen students at the Ludwing-Maximilians-Universität München were recruited for this study, for which they received monetary compensation. They were all naïve to the investigated aims and had normal or corrected-to-normal visual acuity and color vision. Data from two participants were excluded given a large amount of missing data due to eye blinks and EGG artifacts. The final sample included sixteen participants (7 males, mean age  $26 \pm 5$  SD). The experiment was carried out according to the WMA Declaration of Helsinki. All participants signed the informed consent before taking part in the experiment.

#### 4.2.2 Apparatus

The experiment was programmed and run in MATLAB (MathWorks, Natick, MA). Participants were seated in a sound-reduced and dimly lit room, with the head positioned on a chin-rest in front of a CRT monitor (1024 x 768) at a viewing distance of 70 cm. The eye movements and the electroencephalogram (EEG) were simultaneously recorded.

The position of the right eye was recorded by an SR Research Eyelink 1000, with a 1000 Hz temporal and 0.01° spatial resolution. A 9-point grid calibration was run at the beginning of the experiment and when the participant moved the head from the chin-rest.

The EEG was recorded continuously a BrainAmp amplifier (BrainProducts, Munich, Germany).

We used a 58-channel cap, with Ag/AgCl electrodes positioned according to the international 10-10 system. Two additional electrodes were placed on both mastoids, while the other two were positioned at the outer canthi of both eyes to monitored ocular artifacts. The signal was referenced online to the left mastoid and re-referenced offline to the average of both mastoids. All impedances were kept below 10 k $\Omega$ .

#### 4.4.3 Stimuli and procedure

Participants performed a visual search task for a right tilted bar presented as a target among an array of vertical bars. The experiment consisted of a first practice block of 48 trials (not included in the analyses) and 7 blocks of 216 trials each, separated by short breaks every 54 trials. Overall, the experiment comprised 1512 trials and lasted  $\sim$  2 hours.

Each trial started with a gray fixation point (RGB: 120, 120, 120; size: 0.5° in diameter) shown on a dark gray background (RGB: 30,30,30), that was used for the drift correction of the eye gaze on a trial-by-trial basis. Once the fixation point was foveated by the participant the stimulus display was shown. The stimuli consisted of 54 light gray bars (RGB: 255, 255, 255; size: 1.8°) arranged on three imaginary concentric circles, with a radius of 5.2°, 7.8°, and 10.4° respectively. Each bar contained a small hole (3% of the bar's height), located in the upper or in the lower part. All stimuli were vertical bars, with the exception of the target and the distractor (Figure 4.1). The target was the bar defined by its off-vertical orientation (15°), tilted to the right. The task demand was to discriminate whether the hole in the target bar was located in the upper or lower part, by clicking as fast and accurately as possible the designated key on the mouse controller. The search display was

shown for 2 seconds, and the manual response had to be given within 4 seconds. If the answer was incorrect, a red disc appeared in the center of the screen. The intertrial interval was jittered between 200 and 1,000 ms. At the end of each block, participants received feedback about the average number of correct responses.





The target is the  $15^{\circ}$  tilted bar while the distractor is the more inclined bar ( $45^{\circ}$ ), always tilted in the opposite orientation with respect to the target.

This figure shows one of the possible stimulus displays, which is the Midline-target/Lateral Distractor condition, suitable to elicit the N2pc to a lateral distractor.

In ~ 78% of trials, a distractor was also shown, consisting of a more inclined bar (45°), always tilted in the opposite direction with respect to the target<sup>\*</sup>.

<sup>\*</sup> Differently with respect to the other experiments reported in this thesis, here we didn't use an onset distractor because we needed to use visual displays with an equal number of items on each side.

Both target and distractor were located on the second ring in the visual display (7.8° of eccentricity). The target bar could appear at the 2, 4, 6, 8, 10 and 12 o'clock positions. The distractor could appear at the 1,5,6,7,11 and 12 o'clock positions.

In order to trigger the N2pc and the Pd components, we varied target and distractor locations to obtain five different configurations (Fig.4.2) according to the displays previously used by Liesefeld and colleagues (Liesefeld et al., 2017). Specifically, the *Lateral Target/Distractor Absent* configuration would have allowed to extract the pure target-N2pc when the target appeared at one of the lateralized locations.



Figure 4.2. Schematic sample displays from each stimulus configuration.

The effect of distractor interference could be appreciated on the target N2pc by means of the *Lateral Target/Midline Distractor* configuration, in which the distractor is present but because it falls on the midline cannot elicit a lateralized component. In the *Midline Target/Lateral Distractor* configuration the distractor

appeared at one of the lateralized locations, while the target was shown in the midline, so the elicited N2pc contralaterally to the distractor should represent the correlate of distractor selection, while the Pd may have indicated the engagement of distractor suppression. Finally, in the *Contralateral-Distractor* configuration, target and distractor were presented on the opposite sides of the display, while in the *Ipsilateral-distractor* configuration they were shown on the same side.

Crucially, the spatial distribution of salient distractors was biased in frequency in order to obtain unbalances across locations, so that each of the possible distractor locations would acquire a different suppression history.

Therefore, while target locations were assigned randomly and equally across the possible locations, distractor locations were pre-determined by design, unbeknown to the participants. Specifically, the distractor appeared with High Frequency at two out of six locations (HF; ~ 72% of the distractor present trials, ~ 36% for each location; overall 840 trials) and with Low Frequency in the remaining four locations (LF; ~ 28% of distractor present trials, ~ 7% for each location; overall 168 trials).



#### Figure 4.3. Spatial probabilities of Target and Distractor.

Illustration of the spatial distribution of both Target (grey) and Distractor. The target appeared with the same probability across locations. Two locations contained the Distractor with High Frequency (HFD locations, shown in red), whereas the remaining four were occupied by a Distractor with Low Frequency (LFD locations, in blue). The locations in the midline were the only shared between targets and distractors, and were regarded as fillers. The figure shows one of two possible assignments counterbalanced across participants, in which the HFD locations were at 1 and 7 o'clock positions. For the other group of participants, the HFD locations where at 5 and 11 o'clock positions.

The two HF locations were established one for each hemifield and counterbalanced across participants, hence they could be the 1 and the 7 o'clock positions, or the 5 and the 11 o'clock positions (Figure 4.3).

For behavioral analyses, we didn't include the trials in which the distractor appeared at 6 and 12 o'clock locations (~11%), which were those on the vertical meridian and the only ones that could also be occupied by a target over the course of the experiment. Hence, we compared the behavioral and EEG measures obtained with respect to HF locations and the two specular LF locations.

#### 4.2.4 Data analysis

Statistical analyses were performed by using R 3.43 (R Core Team, 2017) for manual RT and eye-movements data, and Matlab (MathWorks, Natick, MA) and the EEGLAB toolbox (Delorme and Makeig, 2004) for EEG data.

**Manual RT analysis.** The performance on the discrimination task was evaluated in terms of means of manual reaction times (RTs) of the trials with accurate responses (~97%). Specifically, we considered as dependent variable the cost in performance due to distractor presence (i.e. the difference in RTs between the distractor-present and the distractor-absent trials).

**Eye-movements analysis.** We discarded trials in which upon the display of the search array the participants were not fixating the center of the screen or an eyeblink had occurred. Furthermore, we included in all statistical analyses only the trials in which the saccadic latency was comprised between 60 ms and 800 ms and the fixation duration was below 800 ms. Overall, we discarded from statistical analysis  $\sim$ 12% of the trials.

The eye-movements were identified as saccades when they reached a minimum velocity of  $35^{\circ}$ /s and a minimum acceleration of  $9.5^{\circ}$ /s. For eye-movement analyses, we considered only the first saccades made since the onset of the visual stimuli that traveled a minimum distance of  $1^{\circ}$ . To classify these saccades as being

toward the target or toward the distractor we considered the portion of space within a slice-shaped region of interest (ROI) specifically designed for both the target and the distractor. More in detail, the first saccades were classified as being directedtowards a specific item when they landed within the slice defined by the 20° angle centered on the stimulus (with the vertex located at the center of the display). All first saccades that fell outside of these regions were classified as directed toward any of the other non-target stimuli in the visual array.

**EEG analysis.** Continuous EEG signal was pre-processed and filtered by applying 0.5-Hz high-pass and 40-Hz low-pass FIR filters (EEGLAB default). The typically-distributed oculomotor artifacts were extracted and rejected by using an independent component analysis (ICA; EEGLAB, extended mode).

We excluded trials with artifacts in the channels of interest (PO7/PO8; voltage steps larger than 50 V per sampling point, activity changes less than 0.5 V within a 500-ms time window, or absolute amplitude exceeding  $\pm$  30 V).

Data were segmented into epochs from -200 ms to 700 ms relative to the stimuli onset, and the pre-stimulus interval was used to baseline correct the ERPs.

In order to extract ERPs, EEG epochs from each condition were averaged separately for contralateral and ipsilateral electrodes, and the lateralized components of interests were measured from contralateral-minus-ipsilateral difference waves at the PO7/PO8 electrode sites.

Specifically, we measured the N2pc and the Pd components obtained from the following display configurations: Midline Target/Distractor Absent, Midline Target/Lateral Distractor, and Lateral Target/Midline Distractor. The component latency was estimated by using 50%-area latency (Luck, 2005), and the component area was determined as the region defined by the ERP, a threshold set at 30% of the component's amplitude, and the two time points where the ERP crossed the threshold (on- and offset of the respective component). The analysis windows for amplitudes of the components of interest were defined detecting the 50%-area latency on the strongest component of the respective polarity in the respective grand-average difference wave and defining amplitudes as the mean activity in a 30-ms window centered on these time points.

## **4.3 RESULTS**

#### 4.3.1 Manual RTs

Overall, manual RTs were slower when the distractor was present compared to the distractor absent condition (t(15)=11.54, p<.0001, d= 2.88), therefore distractor presence induced a significant cost in performance. Consistently with previous studies (Ferrante et. al, 2018; Wang & Theeuwes, 2018), we expected to find a reduction of this interference when the distractor appeared at HF locations compared to the LF locations, revealing that the suppression history acquired by HF locations allowed to ignore these stimuli more easily. As predicted, the analysis of variance (ANOVA) conducted on the mean of distractor cost, with Distractor Location (HF vs. LF) and Block (7 blocks) as within-subject factors, showed a main effect of Distractor location (F(1,15)= 33.94, p<.0001,  $\eta_p^2$ =0.69).



**Figure 4.4. Manual responses as a function of Distractor location and Block.** Mean cost in manual RTs (i.e. the difference in RTs between the distractor-present and the distractor-absent conditions) associated with distractors in HF and LF locations, across blocks. Error bars depict the within-subject confidence intervals (Cousineau, 2005, corrected according to Morey, 2008).

Neither the main effect of Block nor the interaction between Distractor location and Block were significant (Block: F(6,90)=0.48, p=0.81,  $\eta_p^2$ = 0.03; Distractor location x Block: F(6,90)=1.41, p=0.21,  $\eta_p^2 = 0.07$ ) (Fig. 4.4). The benefit acquired appeared very early after the bias was introduced, indeed a further pairwise comparison showed that the difference between HF and LF was already significant during the first block (t(15)=2.30, p<.05, d=0.57).

#### 4.3.2 Eye movements

Very recent studies had shown that suppression history can strongly bias eye movements by reducing the automatic oculomotor capture elicited by salient distractors (both onsets and singletons) appearing at locations where distraction had been more frequent (Di Caro et al., 2019; Wang, Samara, & Theeuwes, 2019). Consistently with these findings, we explored whether a distractor defined within the same dimension of the target could elicit an oculomotor capture and whether the suppression history applied to its location could prevent their interference with the current task. In particular, we focused on different measures of eye-movements, in order to discriminate at which level of the saccadic programming and implementation this experience-dependent bias may act.

**Landing position.** The landing position of the first saccade made upon stimulus onset was evaluated as a measure of oculomotor capture. Overall, distractors elicited a strong oculomotor capture, indeed ~ 39% of first saccades in distractor present trials were directed to the distractor, and this percentage was significantly different from the percentage of saccades directed toward the any of the other non-target items, thus indicating a strong oculomotor capture (t(15)=8.62, p<.0001, d=2.15) (Fig.4.6). Consistently, the first saccades directed toward the target were also affected by distractor presence, and the percentage of saccades was drastically reduced in the distractor present condition compared to when it was absent (distractor present: ~19% vs. distractor absent ~51%; t(15)=7.65, p<.0001, d=1.91) (Fig.4.5).



**Figure 4.5. Oculomotor performance as a function of distractor presence.** Percentage of first saccades directed toward each of the possible items in the visual array, separately for each distractor present condition. The percentage of first saccades directed toward non-target items was averaged per item in the array.

In order to assess how the suppression history of specific locations could bias oculomotor behavior and whether this effect differed across blocks, we conducted an ANOVA on the percentage of first saccades directed toward the distractor, with Distractor location (HF vs. LF) and Block (1-7) as main factors. The analysis revealed a significant main effect of Distractor location (F(1,15)= 28.87, p<.0001,  $\eta_p^2 = 0.65$ ), hence the distractor grabbed less first saccades when it appeared at HF locations (~37% of distractor present trials) compared to the LF locations (~54% of distractor present trials). This effect appeared very early, indeed the difference in oculomotor capture elicited by distractors at HF and LF locations was significant already in the first block (t(15)=3.73, p<.01, d=0.93). Neither the main effect of Block nor the interaction between Distractor location and Block were significant (Block: F(6,90)= 1.39, p=.22,  $\eta_p^2$ = 0.08; Distractor location x Block: F(6,90)= 1.64, p= .14,  $\eta_p^2$ = 0.09) (Fig.4.6A).



Figure 4.6. Saccade landing position as a function of Distractor location. (A) Mean percentage of first saccades directed toward the distractor and (B) mean percentage of first saccades directed toward the target in the distractor present trials, plotted separately for HF and LF distractor location, across Blocks.

A similar ANOVA was also conducted on the percentage of first saccades directed toward the target in the distractor present trials. This analysis revealed similar but specular results, showing a main effect of Distractor frequency in the form of a lower number of first saccades correctly directed toward the target when the distractor was present and appeared at LF locations (~11%) compared to the HF (~21%) (F(1,15) = 40.02, p<.0001,  $\eta_p^2$ =0.72). The main effect of Block was also significant (F(6,90)=2.84, p<.05,  $\eta_p^2$ = 0.15), reflecting that, overall, the number of first saccades correctly directed toward the target tended to increase throughout the experiment (Fig.4.6B). The interaction between Distractor location and Block was far from being significant (F(6,90)=1.43, p=.21,  $\eta_p^2$ = 0.08).

**Saccadic accuracy.** In order to better characterize oculomotor behavior in a crowded visual display such as the one adopted in this study, here we considered an additional eye-movement parameter, that allows quantifying the accuracy of the implemented saccade. Saccadic accuracy was determined by its amplitude, specifically by the "gain", that is the ratio between the distance traveled by the eye and the distance of the target from the starting point of the saccade (expected saccade amplitude). Thus, values closer to 1 are an index of higher saccadic

accuracy. Under normal conditions, in a visual search task for the target, the saccade falls close to its center, and the gain is near 0.9-0.95 (Becker, 1989).

We investigated whether the target-saccade accuracy was differently affected by the presence of the distractor and whether the changes in accuracy were related to distractor location. The pairwise comparison revealed that target-saccades were more accurate when the distractor was absent (gain:~0.90) compared to when it was present (gain:~0.88) (t(15)=2.74, p=0.015, d=0.69). Moreover, distractors that appeared at HF and LF locations biased saccadic accuracy in a different fashion. Data showed a lower gain when the distractor appeared at LF location (~0.83) compared to the HF (~0.88), so the saccades were more accurate in the latter case (t(15)=2.69, p<.05, d= 0.67) (Fig.4.7A). These data indicate that saccadic programming under interference – while a distractor is also present in the display – is affected by the suppression history associated with distractor location.

The same analysis was conducted on saccades directed toward the distractor. Although the result didn't reach significance, it revealed a tendency for saccades to land closer to the distractor when it appeared at LF locations (gain: ~0.92) compared to the HF (gain: ~0.83) (t(15)=2.10, p=.053, d=0.53), suggesting that distractors at LF locations were indeed more likely to be selected by attention and become the intended targets of saccadic eye movements (Fig.4.7B).



Figure 4.7. Saccadic accuracy of target-directed saccades and captured saccades as a function of Distractor location.

(A)The mean gain in the saccadic amplitude of saccades directed toward the target plotted separately for HF an LF distractor location in distractor present trials. (B) The mean gain in saccadic amplitude of saccades directed toward the distractor was plotted separately for HF an LF.

**Fixation duration.** The duration of the first fixation following a saccade which landed on the distractor was analyzed in order to evaluate whether suppression history affected the time needed to disengage and reorient attention from the distractor toward other stimuli in the visual array. For this analysis, we considered a more restricted ROI, which was defined not only by the region within the visual angle centered on the stimuli (20°) as for previous analyses, but also by the distance from the center, i.e. only the saccades landing in the portion of this region between 5° and 10.6° of eccentricity were included in this analysis.

The pairwise comparison conducted to compare trials in which first saccades landed at HF vs. LF locations revealed a significant difference in the mean fixation duration (t(15)= 3.10, p=0.007, d= 0.77), reflecting longer fixations for distractors appearing at LF location (~188 ms) compared to distractors appearing at HF location (~ 177 ms) (Fig. 4.8).



**Figure 4.8. Fixation duration as a function of distractor location.** Mean fixation time following saccades which landed on the distractor, plotted separately for HF and LF conditions.

Taking into consideration these overall results, these findings indicate that the distractor appearing at the less predictable location not only captures more first

saccades, but these saccades tend to bring this stimulus closer to the fovea and lead to longer fixations, before it can be successfully rejected.

Considering the fact that these saccades were also those which fell closer to the center of the stimulus (shown by the higher gain), we wondered whether the differences found in fixation time could be related to saccadic accuracy. In fact, the longer time needed to reject a stimulus that has been selected by mistake could be determined to the need to better discriminate this stimulus, rather than its location, given that the less precise saccades, more frequent in the HF condition, had a higher probability of falling on one of the other non salient distractors, that were vertical and easier to be rejected.

To disambiguate this possibility, we performed a linear regression using the mean gain as a predictor variable of the mean fixation time for distractor-captured saccades. Data showed that the fixation times were positively related to the magnitude of saccadic accuracy (R=0.348, p=0.009) (Fig. 4.9), therefore longer time was required to disengage from the distractor when it was foveated with more precision.



**Figure 4.9.** Correlation between saccadic accuracy and fixation time. The mean fixation time of captured-saccades shown as a function of the mean gain. Lower gain values indicate lower saccadic accuracy, with saccades ending farther from the center of the stimulus.

#### 4.3.3 EEG results

**ERPs of distractor capture and distractor suppression.** First of all, in order to evaluate the sensitivity of the paradigm with respect to the cortical response to a salient distractor, we tested whether the contralateral distractor captured attention independently of the history associated with its location.

We replicated findings of previous studies, indeed a significant distractor N2pc was elicited in the Midline Target/Lateral Distractor condition (-0.79  $\mu$ V; t(15) =-3.772, p=0.0018, d =0.94) so indicating a strong distractor capture. A prominent Pd also emerged in the same condition (0.89  $\mu$ V; t(15) =4.970, p=0.00016, d = 1.24) and, crucially, it appeared later (~81 ms) than the distractor N2pc (t(15)=10.18, p<0.0001, d= 2.54). Therefore, after its selection, the contralateral distractor was actively suppressed.

**ERPs and suppression history.** We analyzed the distractor N2pc and Pd in the Midline Target/Lateral Distractor condition, separately for HF and LF locations.

Both distractors appearing at LF locations and those appearing at HF locations elicited a prominent N2pc (LF: -1.31  $\mu$ V; t(15) =-3,743, p= 0.0019, d = 0.93; HF: -0.70  $\mu$ V; t(15)=-3,064, p= 0.0078, d = 0.76), importantly however, these components were significantly different in amplitude. Indeed, when the distractor appeared at LF locations the N2pc was larger (-1.12  $\mu$ V) (Fig. 4.10B) compared to distractors appearing at HF locations (-0.49  $\mu$ V) (t(15) =-1.88, p= 0.03, d = 0.47) (Fig. 4.10A). This result indicates stronger attentional capture for distractor appearing at the less predictable location.

No differences in distractor N2pc latencies were found with respect to the different distractor frequency locations (HF= 240 ms vs. LF=235 ms; t(15)= 0.55, p=0.59, d = 0.13).

Concerning the component indexing distractor suppression, namely the Pd, ttests against zero showed that distractors elicited a reliable Pd at all locations (HF:  $0.72 \,\mu\text{V}$ , t(15)=3.20, p=0.005; LF: 0.97  $\mu\text{V}$ , t(15)=2.74, p=0.01), and the difference between Pds associated with distractors at HF and LF locations was not significant (t(15)=0.58, p=0.28, d = 0.14). This result indicates that a strong distractor suppression occurred in a similar fashion, independently of the history associated with its spatial location.



**Figure 4.10.** Lateralized event-related potentials for the Midline Target/Lateral Distractor display, presented in separated panels according to the suppression history of distractor location: High Frequency (panel A) and Low Frequency (panel B). Difference waves were obtained by subtracting ipsilateral from contralateral waveforms, and N2pc was analysed in these difference waves at electrode sites (PO7/PO8). Shadings indicate the mean-amplitude windows applied for the N2pc and the Pd sequentially. The vertical dashed line indicates the onset of the search display.

**ERPs and eye-movements.** We explored the ERPs data in light of the oculomotor data, so using the information concerning the landing position of the first saccade upon stimulus onset.

These analyses had to be performed on a sub-sample of 12 participants, due to the additional reduction of trials included in the conditions considered here, which had led to a high number of missing trials for four subjects.

Preliminary results had shown that the N2pc to a contralateral distractor is significantly observable for captured saccades, so when eye gaze was effectively directed toward the distractor (-0.73  $\mu$ V; t(11)=-2.64, p=0.02, d= 0.76)(4.11A). In the absence of oculomotor capture (i.e. trials in which the distractor was contralateral, but the eyes went elsewhere), the N2pc was no longer observable (-0.29  $\mu$ V, contrast with respect to zero: t(11)=1.37, p=0.19), and the amplitude of the negative-going wave within the N2pc time-window was significantly smaller than in captured-saccades trials (t(11)=1.91, p=0.04, d=0.55)(Fig.4.11B).



**Figure 4.11. N2pc to distractor as a function of oculomotor behaviour.** The distractor N2pc for the Midline Target/Lateral Distractor display is presented in separated panels according to the landing position of the eye-movement: captured-saccades (panel **A**) and non-captured saccades (panel **B**).

This result may indicate that the pattern of neural activity is, in fact, predictive of oculomotor capture, however, this result has to be interpreted with caution, because of the relatively lower sample size considered. For the same reason, the same analysis considering target-directed saccades could not be performed, because there were no trials enough to perform a reliable analysis on Pd component for captured-saccades.
## **4.4 CONCLUSION**

In this study, we explored the neural changes and the behavioral responses associated with distractor filtering in conditions of high- and low- predictability of distractor occurrence in the visual space.

Beyond the traditional theories on top-down and bottom-up control of attentional selection, it was recently pointed out that prior experience has an important role in attentional guidance. New studies have shown changes in attentional spatial priority due to the likelihood of occurrence of a target or a distractor at given spatial locations. Indeed, statistical contingencies are (implicitly) learned and used to improve target selection at locations frequently associated with relevant items and to prevent distractor interference at locations often containing salient but irrelevant information (e.g. Di Caro et al., 2019; Ferrante et. al, 2018; Goschy et al., 2014; Sauter et al., 2018; Wang, & Theeuwes, 2018a).

Visual search studies measuring manual RTs and oculomotor behavior revealed a marked flexibility which allows making good use of statistical contingencies in order to deal with distractor interference, however it remains still unclear whether this "skill", which is implicitly acquired, acts to proactively prevent distractor capture, or to reactively speed-up suppression mechanisms after an involuntary attentional capture.

Behavioral findings on RTs of task responses led to hypothesise that these effects are supported by plastic changes in attentional priority, however, they can only provide an indirect evidence of the mechanisms behind this improvement in distractor filtering. On the other hand, the use of ERP components allowed to infer the putative control processes activated before, during and after the (covert) shifts of spatial attention, but without the direct behavioral evidence of overt attentional deployment.

In this study, we employed concurrent EEG/eye-movements recording in order to obtain more information about the mechanisms responsible for the improvements in distractor filtering determined by prior experience. By means of an experimental paradigm tapping the effect of suppression history on attentional and oculomotor capture, we recorded ERPs to monitor cortical activation in conditions of distractor capture and inhibition respectively. Specifically, we focused on two ERP components: the N2pc, which is commonly interpreted as an index of attentional selection, and the Pd, usually associated with the active suppression of salient distractors.

Our results are in line with previous findings of distractor capture, indeed we found both neural and behavioral evidence of the involuntary attentional capture elicited by a salient distractor. Specifically, the distractor elicited a prominent N2pc in the Midline-Target/Lateral Distractor condition, and this finding was corroborated by the significant distractor cost on RTs and by the strong oculomotor capture associated with it. This distractor-N2pc was followed by a remarkable Pd, which suggested that after the misallocation of attentional selection, the irrelevant information was actively suppressed.

After establishing that our distractors elicited a strong attentional capture, we explored the effect of the suppression history associated with their spatial location. Our hypothesis was that, in line with previous behavioral studies, distractors appearing more often at specific locations (HF locations) could be easier to ignore. Additionally, we expected that this improvement could be mirrored by coherent neural changes, triggering a weaker attentional selection and a stronger suppression at HF distractor locations.

The analysis of the neural correlates revealed that distractors appearing at LF locations triggered a greater N2pc compared to distractors at HF locations, thus indicating that the latter elicited a lower attentional capture.

Again, both the RTs and the oculomotor data were in line with these phenomena, indeed, when a distractor appeared at an HF location, participants ignored it more easily, as shown by faster RTs in the discrimination task and lower oculomotor capture. Such reduced distractor capture corresponded to more targetdirected saccades, which were also more precisely directed toward the target item in the HF condition, therefore showing that processes involved in saccadic programming were directly affected by suppression history, by adjusting the saccadic implementation on the basis of prior experience. This finding may indicate that the bias induced by suppression history could act before the implementation of a saccade, at a pre-attentive processing level. This hypothesis could explain the effect of suppression history on the amplitude of the N2pc and the absence of any effects concerning the Pd component. Indeed, while a Pd component was clearly observable following the attentional capture due to a distractor, this suppression was independent of the suppression history associated with its location, so indicating that the learned bias didn't impact on post-capture suppression processes.

Therefore, our findings suggest that the suppression history of spatial locations affected distractor attentional capture, by reducing the selection of distractors appearing at locations that had acquired a higher probability of being a source of irrelevant information. However, when attention was misallocated toward a distractor, the employment of suppression mechanisms to discard it was inevitable. However, the effort required by this mechanism was independent of the suppression history accumulated by distractor location, suggesting that the attentional mechanisms reflecting experience-dependent adjustments may not comprise postselection suppression processes.

The absence of any differences in the Pd components elicited by distractors at locations with a different suppression history is in contrast with previous recent findings reported by Wang and colleagues (Wang et al., 2019). In their study, they found that distractors appearing at high-frequency locations were associated with wider Pd, while no differences were found concerning the N2pc.

However, these opposite findings could find a possible explanation by considering some crucial differences between the experimental manipulations employed in their study and in ours. Previous studies had shown, that a variable that is crucially predictive of the need for post-selection suppression is the degree of target-distractor interference so that a distractor's perceptual salience cannot alone affect the amplitude of a Pd component (Hickey, et al, 2009). As a matter of fact, in our study, we found a significant Pd which, although un-affected by the frequency bias introduced, was presumably due to the strong interference triggered by this particular distractor, which shared its defining dimension with the target and, therefore, was highly competitive for the discrimination task. The frequency biases introduced in our paradigm however concerned specifically the distractor and had no relationship whatsoever with the target, given that the stimulus locations associated with targets and distractors were different and independent of each other. In the study by Wang et al. instead, targets and distractors shared their spatial locations. Therefore, the independent association between spatial locations with targets or distractors might have led to a lower degree of competition in our study, perhaps explain why, differently from Wang et al., our frequency manipulations did not affect the processes involved in attentional suppression. Incidentally, in the study by Wang et al. the manipulations associated with distractor frequency also affected the frequency with which targets could appear, so that locations associated with a higher distractor frequency were also less frequently occupied by a target. Indeed, they reported that amplitude of the Pd component was closely related to stimulus location rather than to the item appearing therein, so that, for example, it was triggered even by a target appearing at the high distractor probability location.

One possible interpretation of these findings is that the attentional system might use probability information differently in order to strategically adapt either attentional selection or distractor suppression on a task basis. So said, in the task employed by Wang et al., avoiding to attend a given location might not have been an efficient strategy, since all locations could contain the relevant information too; on the other hand, in our task in which targets and distractors never shared their spatial locations, the deprioritization of locations with a relevant suppression history might have promoted the engagement of proactive mechanisms to avoid the selection of the locations with higher distractor frequency, thus avoiding the need for cognitively expensive post-selection active suppression processing.

The oculomotor data partially supported this hypothesis. Indeed, in addition to the oculomotor results described above, we also have found longer fixation times for distractors at LF location, which, at first glance, could be interpreted as more time needed for post-selection suppression. Nevertheless, further analyses have revealed that this finding was closely dependent on the higher tendency of these saccades to land closer to the distractor, and it is possible that these longer fixations were simply due to the fact that because the distractor was at the fovea, longer times were needed to discriminate it as a non-target item. In conclusion, the present results are in line with the recent studies showing that frequent experience of irrelevant information at specific locations can lead to reduced search costs and bias saccades in a productive way. Furthermore, the ERPs evaluation provided additional knowledge concerning the mechanisms behind the acquisition of these behavioral benefits. Salient distractors capture less attention when they appear at a location with a consistent history of suppression, suggesting that this location has been deprioritized thus reducing the amount of attentional resources needed for the processing of distractors appearing at these devaluated locations. However, when distractors manage to grab attention anyway, their processing needs to be suppression, but the implementation of the inhibitory mechanisms responsible for such post-selection processing is no longer affected by the history associated with stimulus location.

Finally, with respect to the possibility that the N2pc component may be an index of a generalized selectivity, simply reflecting the allocation of attentional resources towards an entire hemifield, our data have shown that this deflection was observable only when the eyes went toward the attended item, thus discarding this possibility and showing that N2pc is critically dependent on what is attended.

The results described in this chapter are still preliminary and further analyses need to be done, however, these findings might provide an important first step towards reaching a better understanding of the mechanisms involved in experiencedriven distractor filtering. Overall our data suggest that the filtering benefit due to suppression history might be supported by changes at pre-processing levels of attentional deployment, which bias a priori attentional priority across the visual space.



## **GENERAL DISCUSSION**



Previous research has shown that the allocation of attentional resources may depend on prior experience with the same visual environment. While spatial attentional biases due to the prior experience of attentional selection – i.e. the selection history – has long been demonstrated, a topic which has recently started to receive interest concerns the biases due to prior experience of distractor inhibition. The statistical learning of likely distractor locations – i.e. the suppression history – seems now determinant in controlling attentional deployment. In particular, it was shown that when a distractor is extensively experienced at given locations of the visual space, the accumulation of evidence associated with the suppression of this location leads to improvement in task performance, as reflected by faster RTs visual search tasks (e.g. Ferrante et., al. 2018; Wang & Theeuwes, 2018). The interpretations underlying these findings rely on the hypothesis that learning alters the "landscape" of spatial priority maps.

Spatial priority maps are topographically organized representations of the visual environment, in which the priority associated with a location is represented by rises or decreases of neural activations (e.g. Bisley & Goldberg, 2010). Consistently with this model, the location frequently associated with irrelevant information reduces its activation within these maps that, accordingly, drive the deployment of visual-spatial attention and of gaze (Bisley & Goldberg, 2010; Gottlieb, 2007; Itti & Koch, 2001; Zelinsky & Bisley, 2015).

However, previous studies describing the effects of statistical learning have considered manual reaction times as an index of attentional deployment, and such measure provides a limited possibility to define and dissociate the processing stages at which such effects could act. The definition of whether and how past experience may affect spatial priority maps is therefore yet to be clarified.

Here we have proposed three eye-movements studies in order to provide direct evidence of the bias induced by suppression history in a more ecologic way, by exploring its impact on the immediate attentional behavior, namely the execution of saccades. Crucially, our tasks were designed in such a way that participants were never expressly required to make saccades, as is instead commonly done in saccadetasks, but instead, they were asked to give manual responses while spontaneous eye-movements were recorded. Indeed, it was previously shown that when observers perform a saccade-task they exert more control over their saccades which may lead to un-natural oculomotor behavior and shadow systematically the subtle effects of crucial experimental manipulations (Becker, Ansorge, & Horstmann, 2009). Consequently, in our tasks, the stimuli of interest were designed in size and eccentricity so that they had to be fixated in order to be correctly discriminated. This design allowed us to measure spontaneous saccades that were informative of what was actually attended and first processed in the visual array, while avoiding the overriding control of saccade programming that is involved in saccadic tasks.

In the first study reported in this thesis (Chapter 2), we investigated how the accumulation of suppression history at two specific locations of the visual space can modulate both attentional and oculomotor control. In a visual search task for a color singleton target, we employed as distractor an onset, which is a new item in the array that was present on 64% of the trials. The onset is known to be a particularly efficient distractor in oculomotor paradigms, due to its intrinsic power to grab eye gaze (Irwin, et al., 2000; Jonides & Yantis, 1988). In order to investigate the issue of interest, when the distractor was present it appeared with different probabilities across locations in the array, so that two of these contained it with Higher Frequency (HF locations). The results have shown that task performance was significantly affected by the frequency unbalance, indeed manual RTs were faster when the distractor appeared at the HF locations, in line with previous findings (Ferrante et al., 2018; Wang & Theeuwes, 2018a). Most importantly, this finding was robustly supported by eye-movements data. The analyses performed on the percentage of first saccades made upon display onset revealed that much fewer saccades were misallocated toward the distractor when it appeared at HF locations. Notably, this strong reduction in oculomotor capture was already found immediately following the introduction of distractor frequency unbalances, so indicating that observers quickly (implicitly) learned to associate given locations with a higher probability of hosting irrelevant/distracting events. This fast adjustment due to learning is more clearly observable in eye-movements rather than in manual RTs, suggesting that the benefits immediately appreciated in the overt allocation of attentional resources took a little longer in order to affect significantly task performance. Therefore, the analysis of spontaneous saccades provided a more

sensitive measure of the plastic changes in attentional priority due to suppression history. These findings are in line with the conjecture that this phenomenon is supported by stable changes in spatial priority maps. The inhibition of gaze shifts toward distractors involves the same circuits representing visual saliency maps (LIP) (Ipata, et al. 2006; Gottlieb et al., 1998). Therefore, the reduction of oculomotor capture determined by distractors at HF locations should indicate the decrease of activation within the associated coordinates over the topographic map of visual space, thus leading to more efficient saccadic programming.

Interestingly, compared to the other findings in this field, the effects that we have obtained were relative to locations in the visual field that could either host a distractor of remain completely empty. These locations, therefore, were not discretely marked on the screen by visual placeholders, and thus no particular effort might have needed to either select or avoid them. Additionally, the impossibility for targets and distractors to share a spatial location allowed to obtain a clean picture of the effects of their reduced representation in terms of attentional priority, rather than those of a possible co-action of independent activation and deactivation mechanisms. Moreover, our design associated the higher distractor frequency with two lateralized locations, one for each hemifield. This display allowed to remove from the scenario any effects due to possible preferential lateral bias (Duecker, Schuhmann, Bien, Jacobs, & Sack, 2017) and to observe that, specifically for suppression history, the improvement in distractor filtering was not lateralized, differently from findings on other forms of learning that seem to determine asymmetrical effects (e.g. Carlei & Kerzel, 2018).

In sum, the first part of our research revealed the direct impact of prior experience of distractor filtering on the overt deployment of attention, providing clear-cut evidence of how spontaneous saccadic programming implicitly learn to productively avoid misallocation toward locations that have accumulated inhibitory traces. These traces might contribute to reduce the activation associated with these locations within the spatial priority maps, however, it is still unknown whether this deactivation can be maintained over time, as found in other forms of associative attentional learning (e.g. for reward-based learning; Chelazzi et al., 2014; Della Libera & Chelazzi, 2009). In this regard, the second study here reported dealt with the maintenance of these traces and the permanence of residual benefits in distractor filtering in the short and in the long term.

In line with past findings on selection history, that have provided compelling evidence of lingering effect over many days, we expected to find residual effects also with respect to learning based on suppression history. Any lasting effects would suggest that this kind of learning may be successful at shaping attentional plasticity in the long-term, therefore advantaging future efficient behaviors. With this scenario in mind, we replicated our first study and, furthermore, designed an additional Test phase that probed the residual effects surviving after the Biased phase (here referred to as Training). Crucially, in this Test phase, the distractor probability across locations was equally balanced, such as that any differences in performance would be attributed to the prior suppression history. In order to investigate the residual effects in time, we performed two different experiments, in which the Test phase was carried out 24-hours after the Training (Experiment 1) or immediately after it (Experiment 2). While on one hand the results obtained have provided further compelling evidence of the robust attentional bias due to the frequency unbalances, on the other hand, the interruption of statistical contingencies led to different consequences at different times. The observations in the long-term have revealed that no residuals effects of suppression history were maintained in any of the measures considered: both manual RTs and saccades data have shown a generalized improvement in filtering the onset distractor independently of its location. Therefore, the changes within the spatial priority maps didn't seem to reflect long-lasting alterations in the saliency attributed to specific spatial locations. This result suggests that this specific form of learning does not rely on suppression history-related memories associated with specific spatial locations, but rather on real-time adjustments encoding moment-to-moment the locations where irrelevant information is more likely to appear. In line with this hypothesis, the experiment exploring effects in the short-term has provided evidence that slight residual effects were still detectable immediately after the statistical unbalances were no longer active. However, these residual effects were observable only on saccadic data, again suggesting a higher sensitivity of eyemovements performance in detecting even slight differences in attentional deployment.

In light of these additional findings, we argue that, within spatial priority maps, which support programming and implementation of saccades, a significant history of suppression leaves "inhibition traces" in turn affecting the online encoding of the saliency associated with given locations, hence conferring less power to the distractor appearing therein. Such experience-dependent plasticity, however, seems functional and transient, sustaining adaptively the ongoing attentional and oculomotor control, but remaining anchored in memory for a very short time. The absence of long-term effects, however, can be even advantageous, ensuring that attentional priority tunes to the changing requirements of the environment, and accordingly adjusts behavior.

Whether the degree of learning based on suppression history depends crucially on changes at the level of priority maps, should also be reflected in the patterns of neural activation associated with attentional and oculomotor control.

Specifically, coherently with the attentional processing associated with specific ERPs components, changes in the priority of visual stimuli should be coupled with modifications of the N2pc amplitude, a negative-going wave triggered at the posterior-occipital sites which is commonly referred as an index of attentional selection (Luck, et al., 1997).

However, different hypotheses have been proposed on the possible mechanisms involved in suppression history, which are in contrast with respect to the processing stage in which the learned biases are thought to act. While changes in spatial priority maps might occur following modifications at pre-processing stages, some researchers have argued a role of suppression history in boosting the efficacy of suppressive mechanisms engaged after attentional misallocation, at post-selection stages. At the neural level this possibility may be addressed by another ERP component termed Pd, a positive-going deflection which is attributed to the deployment of active suppression (Gaspelin & Luck, 2018a; Gaspar & McDonald, 2014; Sawaki & Luck, 2013; Hickey, Di Lollo, & McDonald, 2009; Wang et al, 2019) The last study that we carried out aimed to investigate this point, assuming a significant reduction in the distractor-N2pc elicited by distractors appearing at locations with a stronger suppression history. For this purpose, we used a modified version of a visual search task previously employed to investigate the ERPs components of attentional selection and suppression (Liesefeld et al., 2017). Thus, differently from our previous experiments, here we used an array of vertical lines arranged in three concentric circles. The target was a right-tilted line, and participants had to discriminate by manual response the position of the hole inside it. On 78% of trials we also showed a salient distractor that, in this case, was a more tilted line, always orientated in the opposite direction of the target. Again, target and distractor never occupied the same locations across trials, and distractor probability locations was biased so that it appeared with HF at two specific locations. Most importantly, we co-recorded ERPs and eye-movements, in order to detect not only the EEG correlates of task performance but also the related saccadic implementation.

Our results have shown that distractors appearing at HF locations triggered a smaller N2pc, so indicating lower attentional capture. This result was supported by consistent adjustments in both manual and saccadic behavior. Indeed, distractors at HF locations led to lower costs on performance (i.e. faster RTs), and weaker oculomotor capture, increasing efficient eye-movements, namely a higher number first target-directed saccades. On the basis of our findings, we argue that the bias induced by suppression history is accomplished through changes in neural activity at relatively early stages of cortical visual processing, in place before the implementation of saccades. As further proof of this possibility, the saccades directed toward the target when the distractor appeared at HF locations were not only more numerous but also more accurate (i.e. higher saccadic gain), reflecting adjustments of saccade implementation on the basis of prior experience. Noteworthy, in our findings the Pd component was elicited by distractors independently of the suppression history of their location, suggesting that while post-selection suppression mechanisms are engaged in order to deal with salient distractors, the amount of resources they require is the same independently of suppression history.

In light of all of the findings obtained in our studies, we suggest that suppression history might lead to adjustments of priority levels within neural priority maps of the visual space such that, based on the previous filtering experience, distractor locations are coded with lower weights on these maps. Given these a priori unbalances in priority maps, the programming and implementation of saccades is biased accordingly, and distractors appearing at deprioritized locations become less able to elicit oculomotor capture and to hinder target-directed saccades.

In summary, our studies provide compelling evidence that suppression history dynamically affects attentional spatial priority through forms of implicit learning. Specifically, it triggers significant changes in neural activity at early stages of cortical visual processing, which lead to substantial biases in both task performance and oculomotor behavior.

These plastic adjustments seem functional and transient, the "inhibition traces" associated with specific locations in the visual field are not consolidated in long-term memory, and thus enable broader adaptability to change in the environment.

## REFERENCES

- Anderson, B. A. (2016). The attention habit: How reward learning shapes selection. Annals of the New York Academy of Sciences, 1369, 24–39.
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011a). Value-driven attentional capture. Proceedings of the National Academy of Sciences of the United States of America, 108, 10367–10371.
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2011b). Learned value magnifies saliencebased attentional capture. PLoS One, 6, e27926.
- Anderson, B. A., Laurent, P. A., & Yantis, S. (2014). Value-driven attentional priority signals in human basal ganglia and visual cortex. Brain Research, 1587, 88–96.
- Arcizet, F., Mirpour, K., & Bisley, J. W. (2011). A pure salience response in posterior parietal cortex. Cerebral Cortex, 21, 2498–2506.
- Arita, J. T., Carlisle, N. B., & Woodman, G. F. (2012). Templates for rejection: configuring attention to ignore task-irrelevant features. *Journal of experimental psychology: human perception and performance*, 38(3), 580.
- Awh, E., Armstrong, K. M., & Moore, T. (2006). Visual and oculomotor selection: Links, causes and implications for spatial attention. Trends in Cognitive Sciences, 10, 124–130.
- Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in cognitive sciences*, 16(8), 437-443.
- Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & psychophysics*, 55(5), 485-496.

- Becker, S. I. (2018). Reply to Theeuwes: Fast feature-based top-down effects, but saliency may be slow. Journal of Cognition, 1(28), 1–3.
- Becker, S. I., Ansorge, U., & Horstmann, G. (2009). Can intertrial priming account for the similarity effect in visual search?. Vision Research, 49(14), 1738-1756.
- Becker, W. (1989). The neurobiology of saccadic eye movements. Metrics. *Reviews of oculomotor research*, *3*, 13.
- Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. Annual Review of Neuroscience, 33, 1–21.
- Bonetti, F., & Turatto, M. (2019). Habituation of oculomotor capture by sudden onsets: Stimulus specificity, spontaneous recovery and dishabituation. Journal of Experimental Psychology: Human Perception and Performance, 45(2), 264.
- Carlei, C., & Kerzel, D. (2018). Stronger interference from distractors in the right hemifield during visual search. Laterality, 23, 152–165.
- Carlisle, N. B., & Woodman, G. F. (2011). When memory is not enough: Electrophysiological evidence for goal-dependent use of working memory representations in guiding visual attention. *Journal of Cognitive Neuroscience*, 23(10), 2650-2664.

Carrasco, M. (2011). Visual attention: The past 25 years. Vision Research, 51, 1484–1525.

Chelazzi, L., & Santandrea, E. (2018). The time constant of attentional control: Short, medium and long (infinite)? Journal of Cognition, 1(27), 1–3.

- Chelazzi, L., Della Libera, C., Sani, I., & Santandrea, E. (2011). Neural basis of visual selective attention. Wiley Interdisciplinary Reviews: Cognitive Science, 2, 392– 407.
- Chelazzi, L., Eštočinová, J., Calletti, R., Lo Gerfo, E., Sani, I., Della Libera, C., & Santandrea, E. (2014). Altering spatial priority maps via reward-based learning. Journal of Neuroscience, 34, 8594–8604.
- Chelazzi, L., Marini, F., Pascucci, D., & Turatto, M. (2019). Getting rid of visual distractors: The why, when, how and where. Current Opinion in Psychology, 29, 135–147.
- Chelazzi, L., Perlato, A., Santandrea, E., & Della Libera, C. (2013). Rewards teach visual selective attention. Vision Research, 85, 58–72.
- Chica, A. B., Bartolomeo, P., & Lupiáñez, J. (2013). Two cognitive and neural systems for endogenous and exogenous spatial attention. Behavioural Brain Research, 237, 107–123.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. Nature Reviews Neuroscience, 3, 201–215.
- Cousineau, D. (2005). Confidence intervals in within-subject designs: A simpler solution to Loftus and Masson's method. Tutorials in Quantitative Methods for Psychology, 1 (1), 42–45.
- Della Libera, C., & Chelazzi, L. (2006). Visual selective attention and the effects of monetary rewards. Psychological Science, 17, 222–227.
- Della Libera, C., & Chelazzi, L. (2009). Learning to attend and to ignore is a matter of gains and losses. Psychological Science, 20, 778–784.

- Della Libera, C., Perlato, A., & Chelazzi, L. (2011). Dissociable effects of reward on attentional learning: From passive associations to active monitoring. PLoS
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. Annual review of neuroscience, 18(1), 193-222.
- Di Caro, V., Theeuwes, J., & Della Libera, C. (2019). Suppression History of distractor location biases attentional and oculomotor control. *Visual Cognition*, 27(2).
- Duecker, F., Schuhmann, T., Bien, N., Jacobs, C., & Sack, A. T. (2017). Moving beyond attentional biases: Shifting the interhemispheric balance between left and right posterior parietal cortex modulates attentional control processes. *Journal of Cognitive Neuroscience*, 29(7), 1267-1278
- Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological review*, *96*(3), 433.
- Egeth, H. (2018). Comment on Theeuwes's characterization of visual selection. Journal of Cognition, 1(26), 1–3.
- Failing, M., & Theeuwes, J. (2018). Selection history: How reward modulates selectivity of visual attention. Psychonomic Bulletin & Review, 25, 514–538.
- Feldmann-Wüstefeld, T., Brandhofer, R., and Schubö, A. (2016). Rewarded visual items capture attention only in heterogeneous contexts. Psychophysiology 53, 1063–1073.
- Ferrante, O., Patacca, A., Di Caro, V., Della Libera, C., Santandrea, E., & Chelazzi, L. (2018). Altering spatial priority maps via statistical learning of target selection and distractor filtering. *Cortex*, 102, 67-95.
- Folk, C. L., & Remington, R. W. (2015). Unexpected abrupt onsets can override a topdown set for color. *Journal of Experimental Psychology: Human Perception and Performance*, 41(4), 1153.

- Folk, C. L., Remington, R. W., & Johnston, J. C. (1992). Involuntary covert orienting is contingent on attentional control settings. *Journal of Experimental Psychology: Human perception and performance*, 18(4), 1030.
- Folk, C. L., Remington, R. W., & Wright, J. H. (1994). The structure of attentional control: contingent attentional capture by apparent motion, abrupt onset, and color. *Journal* of Experimental Psychology: Human perception and performance, 20(2), 317.
- Gaspar, J. M., & McDonald, J. J. (2014). Suppression of salient objects prevents distraction in visual search. *Journal of neuroscience*, 34(16), 5658-5666.
- Gaspar, J. M., Christie, G. J., Prime, D. J., Jolicœur, P., & McDonald, J. J. (2016). Inability to suppress salient distractors predicts low visual working memory capacity. *Proceedings of the National Academy of Sciences*, 113(13), 3693-3698.
- Gaspelin, N., Leonard, C. J., & Luck, S. J. (2015). Direct evidence for active suppression of salient-but-irrelevant sensory inputs. Psychological Science, 26, 1740–1750.
- Gaspelin, N., & Luck, S. J. (2018a). Combined electrophysiological and behavioral evidence for the suppression of salient distractors. Journal of Cognitive Neuroscience, 15, 1–16.
- Gaspelin, N., & Luck, S. J. (2018b). The role of inhibition in avoiding distraction by salient stimuli. Trends in Cognitive Sciences, 22, 79–92.
- Gaspelin, N., & Luck, S. J. (2018c). "Top-down" does not mean "voluntary". Journal of Cognition, 1(25), 1–4.
- Geng, J. J. (2014). Attentional mechanisms of distractor suppression. Current Directions in Psychological Science, 23(2), 147-153.
- Geng, J. J., & Behrmann, M. (2005). Spatial probability as an attentional cue in visual search. *Perception & psychophysics*, 67(7), 1252-1268.

- Geng, J. J., & DiQuattro, N. E. (2010). Attentional capture by a perceptually salient nontarget facilitates target processing through inhibition and rapid rejection. *Journal* of Vision, 10(6), 5-5.
- Geyer, T., Müller, H. J., & Krummenacher, J. (2008). Expectancies modulate attentional capture by salient color singletons. *Vision research*, 48(11), 1315-1326.
- Gilbert, C. G., & Li, W. (2013). Top-down influences on visual processing. Nature Reviews Neuroscience, 14, 350–363.
- Goschy, H., Bakos, S., Müller, H. J., & Zehetleitner, M. (2014). Probability cueing of distractor locations: both intertrial facilitation and statistical learning mediate interference reduction. *Frontiers in psychology*, 5, 1195.
- Gottlieb, J. (2007). From thought to action: The parietal cortex as a bridge between perception, action, and cognition. Neuron, 53, 9–16.
- Graybiel, A. M. (2008). Habits, rituals, and the evaluative brain. Annual Review of Neuroscience, 31, 359–387.
- Hickey, C., Chelazzi, L., & Theeuwes, J. (2010). Reward changes salience in human vision via the anterior cingulate. Journal of Neuroscience, 30, 11096–11103.
- Hickey, C., Di Lollo, V., & McDonald, J. J. (2009). Electrophysiological indices of target and distractor processing in visual search. *Journal of cognitive neuroscience*, 21(4), 760-775.
- Hickey, C., McDonald, J. J., & Theeuwes, J. (2006). Electrophysiological evidence of the capture of visual attention. *Journal of cognitive neuroscience*, 18(4), 604-613.
- Ipata, A. E., Gee, A. L., Gottlieb, J., Bisley, J. W., & Goldberg, M. E. (2006). LIP responses to a pop-out stimulus are reduced if it is overtly ignored. Nature Neuroscience, 9, 1071–1076.

- Irwin, D. E., Colcombe, A. M., Kramer, A. F., & Hahn, S. (2000). Attentional and oculomotor capture by onset, luminance and color singletons. *Vision research*, 40(10-12), 1443-1458.
- Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. Vision Research, 40, 1489\_1506.
- Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature reviews neuroscience*, 2(3), 194.
- Itti, L., Koch, C., & Niebur, E. (1998). A model of saliency-based visual attention for rapid scene analysis. *IEEE Transactions on Pattern Analysis & Machine Intelligence*, (11), 1254-1259.
- Jiang, Y. V. (2018). Habitual versus goal-driven attention. Cortex, 102, 107-120.
- Jiang, Y. V., Li, Z. S., & Remington, R. W. (2015). Modulation of spatial attention by goals, statistical learning, and monetary reward. *Attention, Perception, & Psychophysics*, 77(7), 2189-2206.
- Jiang, Y. V., Swallow, K. M., & Rosenbaum, G. M. (2013a). Guidance of spatial attention by incidental learning and endogenous cuing. *Journal of Experimental Psychology: Human Perception and Performance*, 39(1), 285.
- Jiang, Y. V., Swallow, K. M., Rosenbaum, G. M., & Herzig, C. (2013b). Rapid acquisition but slow extinction of an attentional bias in space. *Journal of Experimental Psychology: Human Perception and Performance*, 39(1), 87.
- Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & psychophysics*, *43*(4), 346-354.
- Kincade, J. M., Abrams, R. A., Astafiev, S. V., Shulman, G. L., & Corbetta, M. (2005). An event-related functional magnetic resonance imaging study of voluntary and stimulus-driven orienting of attention. Journal of Neuroscience, 25, 4593–4604.

- Kiss, M., Driver, J., & Eimer, M. (2009). Reward priority of visual target singletons modulates event-related potential signatures of attentional selection. *Psychological science*, 20(2), 245-251.
- Kowler, E. (2011). Eye movements: The past 25 years. Vision Research, 51, 1457–1483.
- Kristjánsson, A., & Campana, G. (2010). Where perception meets memory: A review of repetition priming in visual search tasks. Attention, Perception, & Psychophysics, 72, 5–18.
- Kryklywy, J. H., & Todd, R. M. (2018). Experiential history as a tuning parameter for attention. Journal of Cognition, 1(24), 1–3.
- Lakens, D., & Albers, C. J. (2017, September 10). When power analyses based on pilot data are biased: Inaccurate effect size estimators and follow-up bias. Retrieved from https:// doi.org/10.31234/osf.io/b7z4q
- Leber, A. B., & Egeth, H. E. (2006). It's under control: Top-down search strategies can override attentional capture. *Psychonomic bulletin & review*, *13*(1), 132-138.
- Leber, A. B., Gwinn, R. E., Hong, Y., & O'Toole, R. J. (2016). Implicitly learned suppression of irrelevant spatial locations. *Psychonomic bulletin & review*, 23(6), 1873-1881.
- Lega, C., Ferrante, O., Marini, F., Santandrea, E., Cattaneo, L., & Chelazzi, L. (2019). Probing the neural mechanisms for distractor filtering and their history-contingent modulation by means of TMS. *Journal of Neuroscience*, *39*(38), 7591-7603.
- Liesefeld, H. R., & Müller, H. J. (2019). Distractor handling via dimension weighting. *Current opinion in psychology*.
- Liesefeld, H. R., Liesefeld, A. M., Töllner, T., & Müller, H. J. (2017). Attentional capture in visual search: Capture and post-capture dynamics revealed by EEG. *NeuroImage*, *156*, 166-173.

- Luck, S. J. (2005). An introduction to the event-related potential technique: Cognitive neuroscience.
- Luck, S. J. (2012). Event-related potentials. APA handbook of research methods in psychology, 1, 523-546.
- Luck, S. J., Girelli, M., McDermott, M. T., & Ford, M. A. (1997). Bridging the gap between monkey neurophysiology and human perception: An ambiguity resolution theory of visual selective attention. *Cognitive psychology*, 33(1), 64-87.
- Luck, S. J., & Hillyard, S. A. (1990). Electrophysiological evidence for parallel and serial processing during visual search. *Perception & psychophysics*, 48(6), 603-617.
- Luck, S. J., & Hillyard, S. A. (1994a). Electrophysiological correlates of feature analysis during visual search. *Psychophysiology*, 31(3), 291-308.
- Luck, S. J., & Hillyard, S. A. (1994b). Spatial filtering during visual search: evidence from human electrophysiology. *Journal of Experimental Psychology: Human Perception and Performance*, 20(5), 1000.
- Ludwig, C. J., & Gilchrist, I. D. (2002). Stimulus-driven and goal-driven control over visual selection. *Journal of Experimental Psychology: human perception and performance*, 28(4), 902.
- Marini, F., Chelazzi, L., & Maravita, A. (2013). The costly filtering of potential distraction: Evidence for a supramodal mechanism. *Journal of Experimental Psychology: General*, 142(3), 906.
- Marini, F., Demeter, E., Roberts, K. C., Chelazzi, L., & Woldorff, M. G. (2016). Orchestrating proactive and reactive mechanisms for filtering distracting information: Brain-behavior relationships revealed by a mixed-design fMRI study. *Journal of Neuroscience*, 36(3), 988-1000.

- Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: an open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, 44, 314-324.
- Morey, R. D. (2008). Confidence intervals from normalized data: A correction to Cousineau (2005). Tutorials in Quantitative Methods for Psychology, 4(2), 61–64.
- Mulckhuyse, M., van Zoest, W., & Theeuwes, J. (2008). Capture of the eyes by relevant and irrelevant onsets. Experimental Brain Research, 186, 225–235.
- Müller, H. J., Geyer, T., Zehetleitner, M., & Krummenacher, J. (2009). Attentional capture by salient color singleton distractors is modulated by top-down dimensional set. *Journal of Experimental Psychology: Human Perception and Performance*, 35(1), 1.
- Neo, G., & Chua, F. K. (2006). Capturing focused attention. *Perception & Psychophysics*, 68(8), 1286-1296.
- Noonan, M. P., Crittenden, B. M., Jensen, O., & Stokes, M. G. (2018). Selective inhibition of distracting input. Behavioural Brain Research, 355, 36–47.
- Nothdurft, H. C. (2002). Attention shifts to salient targets. *Vision research*, 42(10), 1287-1306.
- Parkhurst, D., Law, K., & Niebur, E. (2002). Modeling the role of salience in the allocation of overt visual attention. *Vision research*, *42*(1), 107-123.
- Perugini, M., Gallucci, M., & Costantini, G. (2014). Safeguard power as a protection against imprecise power estimates. Perspectives on Psychological Science, 9(3), 319–332.
- Plöchl, M., Ossandón, J. P., & König, P. (2012). Combining EEG and eye tracking: Identification, characterization, and correction of eye movement artifacts in electroencephalographic data. *Frontiers in Human Neuroscience*, 6, 278.

- Posner, M. I. (1980). Orienting of attention. *Quarterly journal of experimental psychology*, 32(1), 3-25.
- Qi, S., Zeng, Q., Ding, C., & Li, H. (2013). Neural correlates of reward-driven attentional capture in visual search. Brain Research, 1532, 32–43.
- Ratcliff, R. (1979). Group reaction time distributions and an analysis of distribution statistics. Psychological Bulletin, 86, 446–461.
- R Core Team. (2017). R: A Language and environment for statistical Computing. R Foundation for Statistical Computing.
- Reynolds, J. H., & Chelazzi, L. (2004). Attentional modulation of visual processing. Annual Review of Neuroscience, 27, 611–647.
- Sauter, M., Liesefeld, H. R., & Müller, H. J. (2019). Learning to suppress salient distractors in the target dimension: Region-based inhibition is persistent and transfers to distractors in a nontarget dimension. *Journal of experimental psychology*. *Learning, memory, and cognition*.
- Sauter, M., Liesefeld, H. R., Zehetleitner, M., & Müller, H. J. (2018). Region-based shielding of visual search from salient distractors: Target detection is impaired with same-but not different-dimension distractors. *Attention, Perception, & Psychophysics*, 80(3), 622-642.
- Sawaki, R., & Luck, S. J. (2013). Active suppression after involuntary capture of attention. *Psychonomic bulletin & review*, 20(2), 296-301.
- Sawaki, R., Luck, S. J., and Raymond, J. E. (2015). How attention changes in response to incentives. J. Cogn. Neurosci. 27, 2229–2239.
- Sawaki, R., Geng, J. J., & Luck, S. J. (2012). A common neural mechanism for preventing and terminating the allocation of attention. *Journal of Neuroscience*, *32*(31), 10725-10736.

- Sayim, B., Grubert, A., Herzog, M. H., & Krummenacher, J. (2010). Display probability modulates attentional capture by onset distractors. *Journal of Vision*, *10*(3), 10-10.
- Seger, C. A., & Spiering, B. J. (2011). A critical review of habit learning and the basal ganglia. Frontiers in Systems Neuroscience, 5, 66.
- Serences, J. T., & Yantis, S. (2007). Spatially selective representations of voluntary and stimulus-driven attentional priority in human occipital, parietal, and frontal cortex. Cerebral Cortex, 17, 284–293.
- Serences, J. T., Yantis, S., Culberson, A., & Awh, E. (2004). Preparatory activity in visual cortex indexes distractor suppression during covert spatial orienting. *Journal of Neurophysiology*, 92(6), 3538-3545.
- Sha, L. Z., Remington, R. W., & Jiang, Y. V. (2017). Short-term and long-term attentional biases to frequently encountered target features. *Attention, Perception, & Psychophysics*, 79(5), 1311-1322.
- Sisk, C. A., Remington, R. W., & Jiang, Y. V. (2018). The risks of down- playing topdown control. Journal of Cognition, 1(23), 1–3.
- Suzuki, M., & Gottlieb, J. (2013). Distinct neural mechanisms of distractor suppression in the frontal and parietal lobe. Nature Neuroscience, 16, 98–104.
- Theeuwes, J. (1991). Cross-dimensional perceptual selectivity. *Perception & psychophysics*, 50(2), 184-193.
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & psychophysics*, *51*(6), 599-606.
- Theeuwes, J. (1994). Stimulus-driven capture and attentional set: Selective search for color and visual abrupt onsets. *Journal of Experimental Psychology: Human Perception and Performance*, 20, 799-806.

- Theeuwes, J. (2010). Top–down and bottom–up control of visual selection. *Acta psychologica*, 135(2), 77-99.
- Theeuwes, J. (2018). Visual selection: usually fast and automatic; seldom slow and volitional. *Journal of Cognition*, 1(1).
- Theeuwes, J. (2019). Goal-Driven, Stimulus-Driven and History-Driven selection. *Current Opinion in Psychology*.
- Theeuwes, J., & Burger, R. (1998). Attentional control during visual search: The effect of irrelevant singletons. Journal of Experimental Psychology: Human Perception and Performance, 24, 1342–1353.
- Theeuwes, J., De Vries, G. J., & Godijn, R. (2003). Attentional and oculomotor capture with static singletons. *Perception & psychophysics*, *65*(5), 735-746.
- Theeuwes, J., Kramer, A. F., Hahn, S., Irwin, D. E., & Zelinsky, G. J. (1999). Influence of attentional capture on oculomotor control. Journal of Experimental Psychology: Human Perception and Performance, 25, 1595–1608.
- Thompson, R. F. (2009). Habituation: A history. Neurobiology of Learning and Memory, 92, 127–134.
- Todd, R. M., & Manaligod, M. G. M. (2018). Implicit guidance of attention: The priority state space framework. Cortex, 102, 121–138.
- Todd, S., & Kramer, A. F. (1994). Attentional misguidance in visual search. *Perception & Psychophysics*, 56(2), 198-210.
- Turatto, M., & Pascucci, D. (2016). Short-term and long-term plasticity in the visualattention system: Evidence from habituation of attentional capture. Neurobiology of Learning and Memory, 130, 159-169.

- Turatto, M., Bonetti, F., & Pascucci, D. (2018). Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. Psychonomic Bulletin and Review, 25, 1028–1034.
- Turatto, M., Bonetti, F., Pascucci, D., & Chelazzi, L. (2018). Desensitizing the attention system to distraction while idling: A new latent learning phenomenon in the visual attention domain. Journal of Experimental Psychology: General, 147, 1827–1850.
- Van der Stigchel, S., Belopolsky, A. V., Peters, J. C., Wijnen, J. G., Meeter, M., & Theeuwes, J. (2009). The limits of top-down control of visual attention. Acta Psychologica, 132, 201–212.
- Vatterott, D. B., & Vecera, S. P. (2012). Experience-dependent attentional tuning of distractor rejection. *Psychonomic bulletin & review*, 19(5), 871-878.
- Wang, B., & Theeuwes, J. (2018a). Statistical regularities modulate attentional capture. Journal of Experimental Psychology: Human Perception and Performance, 44, 13– 17.
- Wang, B., & Theeuwes, J. (2018b). How to inhibit a distractor location? Statistical learning versus active, top-down suppression. Attention, Perception, & Psychophysics, 80, 860–870.
- Wang, B., & Theeuwes, J. (2018c). Statistical regularities modulate attentional capture independent of search strategy. Attention, Perception, & Psychophysics, 80, 1763– 1774.
- Wang, B., Samara, I., & Theeuwes, J. (2019). Statistical regularities bias overt attention. Attention, Perception, & Psychophysics, 1-9.
- Wang, B., van Driel, J., Ort, E., & Theeuwes, J. (2019). Anticipatory distractor suppression elicited by statistical regularities in visual search. *Journal of cognitive neuroscience*, 1-14.

- Weaver, M. D., van Zoest, W., & Hickey, C. (2017). A temporal dependency account of attentional inhibition in oculomotor control. *NeuroImage*, 147, 880-894.
- Wolfe, J. M. (2018). Everything is foreseen, yet free will is given (Mishna Avot 3:15). Journal of Cognition, 1(22), 1–3.
- Woodman, G. F., & Luck, S. J. (1999). Electrophysiological measurement of rapid shifts of attention during visual search. *Nature*, 400(6747), 867.
- Woodman, G. F., & Luck, S. J. (2003). Dissociations among attention, perception, and awareness during object-substitution masking. *Psychological Science*, 14(6), 605-611.
- Wyatt, N., & Machado, L. (2013). Distractor inhibition: Principles of operation during selective attention. Journal of Experimental Psychology: Human Perception and Performance, 39, 245–256.
- Yantis, S., & Egeth, H. E. (1999). On the distinction between visual salience and stimulusdriven attentional capture. *Journal of Experimental Psychology: Human Perception and Performance*, 25(3), 661.
- Zelinsky, G. J., & Bisley, J. W. (2015). The what, where, and why of priority maps and their interactions with visual working memory. *Annals of the New York Academy of Sciences*, *1339*(1), 154-164.