Distractor filtering in the visual attention domain: evidence for habituation of attentional and oculomotor capture

PhD Candidate

Francesca Bonetti

Supervisor

Prof. Massimo Turatto

Ph.D. Thesis

2019

Doctoral School in Cognitive and Brain Sciences $32^{nd} \ \text{Cycle} \label{eq:cycle}$





In everyday life, we are constantly surrounded by a huge amount of information. Since our attentional resources are limited, we need to select just the stimuli that we want to process. Despite our voluntary attempt to select a precise information, it often occurs that a salient stimulus or event automatically captures our attention, regardless its irrelevance. The fact that we are immediately and unintentionally attracted by sudden visual onsets provides a clear advantage for our survival. However, in spite of that, the possibility to counteract visual distraction is fundamental for an efficient interaction with the environment, particularly when a salient but irrelevant stimulation repeatedly affects our visual system. And then, how can we resist from being continuously distracted by irrelevant repetitive onsets?

The current work is aimed to explore the mechanisms that we use to filter irrelevant information, with a focus on habituation, an ancestral form of learning that has recently been associated to the decrement of attentional capture observed in several studies. This experience-dependent learning process is defined as a behavioral response decrement that results from repeated stimulation and that does not involve sensory or motor fatigue. I will first provide the reader with a general introduction (Chapter 1) concerning the visual attention field, with a particular emphasis on attentional capture and the filtering of irrelevant information. I will then (Chapter 2) try to disentangle the two main accounts concerning the nature of the distractor filtering, the first claiming that filtering is accomplished to shield target processing from interference (top-down

inhibitory control hypothesis), and the second stating that the passive exposure to a repeating visual onset is sufficient to trigger learning-dependent mechanisms to filter the unwanted stimulation (habituation hypothesis). After providing strong evidence in favor of the latter account, I will then examine (Chapter 3) to what extent the filtering of irrelevant information that we achieve through the mechanisms underlying habituation is affected by contextual cues, showing that this kind of filtering is context-dependent. Finally (Chapter 4), motivated by the existence of a strong functional and anatomical link between attention and the oculomotor system, I will explore whether habituation affects also the oculomotor capture triggered by an onset distractor, showing that the execution of reflexive saccades is subject to habituation, while the programming component is not.

Taken together, the results of the present work give a strong contribution to the attentional capture field in showing that both attentional and oculomotor capture are subject to habituation, that this form of learning is context-specific and that it occurs also when we are passively exposed to a visual irrelevant stimulus.

Table of Contents

Abstract	3
Table of Contents	5
List of Figures	9
List of Tables	12
Publications	13
1. General introduction	14
1.1 The control of attention	14
1.2 When the attentional control fails: the phenomenon of attentional capture	15
1.3 How to resist attentional capture	16
1.4 The phenomenon of habituation	18
1.4.1 Characteristics of habituation	19
1.4.2 Theories on habituation	20
1.4.3 Neural correlates of habituation	22
1.5 Habituation and attention: an intimate but overlooked relation	22
1.6 Experimental questions	27
2. Filtering irrelevant information during passive viewing	28
2.1 Introduction	28
2.2 Experiment 1	30
2.2.1 Methods	30
2.2.1.1 Participants	30
2.2.1.2 Apparatus	31
2.2.1.3 Stimuli and procedures	31
2.2.1.4 Data analysis	33
2.2.2 Results and discussion	34
2.3 Experiment 2	35
2.3.1 Methods	36
2.3.1.1 Participants	36
2.3.1.2 Apparatus	36
2.3.1.3 Stimuli and procedures	36

2.3.1.4 Data	analysis	37
2.3.2 Results a	nd discussion	37
2.4 Experiment 3	3	39
2.4.1 Methods		39
2.4.1.1 Parti	cipants	39
2.4.1.2 Appa	ıratus	40
2.4.1.3 Stim	uli and procedures	40
2.4.1.4 Data	analysis	40
2.4.2 Results a	nd discussion	40
2.5 General discu	ussion	42
3. The role of conte	xtual cues in filtering irrelevant information	49
3.1 Introduction		49
3.2 Experiment	4	50
3.2.1 Methods		51
3.2.1.1 Parti	cipants	51
3.2.1.2 Appa	ratus	52
3.2.1.3 Stim	uli and procedures	52
3.2.1.4 Data	analysis	54
3.2.2 Results a	nd discussion	55
3.3 Experiment !	5	57
3.3.1 Methods		58
3.3.1.1 Parti	cipants	58
3.3.1.2 Appa	ıratus	59
3.3.1.3 Stim	uli and procedures	59
3.3.1.4 Data	analysis	61
3.3.2 Results a	nd discussion	62
3.4 Experiment	5	65
3.4.1 Methods		66
3.4.1.1 Parti	cipants	66
3.4.1.2 Appa	ıratus	66
3.4.1.3 Stim	uli and procedures	66
3.4.1.4 Data	analysis	67

3.4.2 Results and discussion	67
3.5 General discussion	70
4. Habituation in the oculomotor system	78
4.1 Introduction	78
4.2 Experiment 7	84
4.2.1 Methods	84
4.2.1.1 Participants	84
4.2.1.2 Apparatus	85
4.2.1.3 Stimuli and procedures	85
4.2.1.4 Data analysis	88
4.2.2 Results and discussion	90
4.3 Experiment 8	97
4.3.1 Methods	98
4.3.1.1 Participants	98
4.3.1.2 Apparatus	98
4.3.1.3 Stimuli and procedures	98
4.3.1.4 Data analysis	99
4.3.2 Results and discussion	99
4.4 Experiment 9	105
4.4.1 Methods	107
4.4.1.1 Participants	107
4.4.1.2 Apparatus	107
4.4.1.3 Stimuli and procedures	107
4.4.1.4 Data analysis	108
4.4.2 Results and discussion	108
4.5 Experiment 10	113
4.5.1 Methods	114
4.5.1.1 Participants	114
4.5.1.2 Apparatus	114
4.5.1.3 Stimuli and procedures	114
4.5.1.4 Data analysis	114
4.5.2 Results and discussion	114

4.6 Experiment 11	120
4.6.1 Methods	120
4.6.1.1 Participants	120
4.6.1.2 Apparatus	120
4.6.1.3 Stimuli and procedures	121
4.6.1.4 Data analysis	123
4.6.2 Results and discussion	124
4.7 General discussion	129
5. General summary and conclusions	141
5.1 Final summary and discussion	141
5.2 Practical and clinical implications	145
References	147

List of Figures

Figure 1. Schematic representation of the main events of Experiments 1, 2, an	d 3. Page 33
Figure 2. Attentional capture as a function of active blocks in Experiment 1.	Page 35
Figure 3. Attentional capture as a function of active blocks in Experiments 1 a	nd 2. Page 38
Figure 4. Attentional capture as a function of active blocks in Experiments 1 a	nd 3. Page 42
Figure 5. Experimental design of Experiment 4.	Page 51
Figure 6. Schematic representation of the main events of Experiment 4.	Page 54
Figure 7. Attentional capture as a function of blocks in Experiment 4.	Page 56
Figure 8. Experimental design of Experiments 5 and 6.	Page 58
Figure 9. Schematic representation of the main events of Experiments 5 and 6	5. Page 61
Figure 10. Attentional capture as a function of blocks in Experiment 5.	Page 64
Figure 11. Attentional capture as a function of blocks in Experiment 6.	Page 69
Figure 12. Schematic representation of the main events of Experiments 7-10.	Page 88

Figure 13. Percentage of oculomotor capture, as a function of trial number, in Experiment 7.

Page 92

Figure 14. Latency of saccades directed to the target as a function of trial number, in Experiment 7.

Page 95

Figure 15. Percentage of oculomotor capture, as a function of trial number, in Experiment 8.

Page 101

Figure 16. Latency of saccades directed to the target as a function of trial number, in Experiment 8.

Page 104

Figure 17. Percentage of oculomotor capture, as a function of trial number, in Experiment 9.

Page 110

Figure 18. Percentage of oculomotor capture at asymptotic level in Experiments 8 and 9.

Page 111

Figure 19. Latency of saccades directed to the target as a function of trial number, in Experiment 9.

Page 112

Figure 20. Percentage of oculomotor capture, as a function of trial number, in Experiment 10.

Page 115

Figure 21. Latency of saccades directed to the target as a function of trial number, in Experiment 10.

Page 116

Figure 22. Schematic representation of the main events of Experiment 11.

Page 122

Figure 23. Percentage of oculomotor capture, as a function of trial number, in Experiment 11.

Page 124

Figure 24. Mean latency of saccades directed toward the target, as a function of the distractor presence/absence, in Experiment 11.

Page 126

Figure 25. Correlation between microsaccades peak velocity and amplitude for all blocks of trials in Experiment 11.

Page 127

Figure 26. Time course of absolute microsaccadic frequency in response to the occurrence of the peripheral onset in Experiment 11.

Page 128

List of Tables

Table 1. Mean RTs and SD for correct trials in Experiment 5.	Page 65
Table 2. Mean RTs and SD for correct trials in Experiment 6.	Page 70
Table 3. Summary of the experimental conditions in Experiments 7-10.	Page 87

All the material in this thesis has been (or will be) published in the following papers:

- 1. Turatto, M., **Bonetti, F.**, & Pascucci, D. (2018). Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. *Psychonomic Bulletin & Review*, *25*(3), 1028-1034. http://dx.doi.org/10.3758/s13423-017-1320-x
- Turatto, M., Bonetti, F., Chiandetti, C., & Pascucci, D. (2019). Context-specific distractors rejection: contextual cues control long-term habituation of attentional capture by abrupt onsets. *Visual Cognition*.
 https://doi.org/10.1080/13506285.2019.1580233
- 3. 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(12), 1827. http://dx.doi.org/10.1037/xge0000503
- 4. **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), 264-284. http://dx.doi.org/10.1037/xhp0000605
- 5. **Bonetti, F.**, & Turatto, M. (2019). Microsaccades reveal that habituation affects the execution but not the programming of saccadic eye movements. *In preparation*.

Chapter 1

General introduction

1.1 The control of attention

Visual attention can be considered as a set of cognitive operations that allows us to concentrate on a limited portion of the surrounding environment. Because our attentional resources are limited, we can attend only few stimuli at a time, and when we need to change focus, our attention has to be shifted from one stimulus to another, in an overt or in a covert manner. Overt orienting is the act of selectively attending to a stimulus or an event over others by moving the eyes toward its direction (Posner, 1980), and it can be directly observed in the form of eye movements. Covert orienting is the act to mentally shifting the focus of attention without moving the eyes (Eriksen & Hoffman, 1972; Eriksen & Colegate, 1971; Posner, 1980), and it is a change in attention that is not attributable to saccadic eye movements. At the end of the eighties, it had been proposed that events can be attended for two reasons (James, 1890). First, attention can be directed toward a stimulus because it is important for achieving a goal. In this case, the intentions of the observer can control the allocation of attention, thus processing only the selected information. In the so-called *endogenous* attention, the control is exerted in a top-down manner. A prominent theory by Folk and colleagues (Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Folk, Remington, & Wright, 1994), proposed that capture is contingent upon the observer that established an attentional set for some visual feature or event. For capture to occur, the distracting event must in some way be

consistent with that attentional set. Second, the properties of a stimulus can attract the attention of the observer independently of his/her intentions. In the so-called *exogenous* attention, the control is exerted in a bottom-up manner.

1.2 When the attentional control fails: the phenomenon of attentional capture

Even if we are attending to a specific location, it is well known that a sudden stimulus that abruptly appears in the visual field can automatically capture our attention (Breitmeyer & Ganz, 1976; Jonides & Yantis, 1988; Yantis & Jonides, 1984, 1996; Ruz & Lupiáñez, 2002; Boot, Kramer, & Peterson, 2005; Schreij, Owens, & Theeuwes, 2008; Vecera, Cosman, Vatterott, & Roper, 2014; Folk & Remington, 2015). Attentional capture is said to occur when an irrelevant item that is unique in some dimension affects the time to detect a target (Ruz & Lupiáñez, 2002). In the past years, it has been argued that attentional capture can be modulated by the focus of attention. Several studies (Yantis & Jonides, 1990; Theeuwes, 1991a) argued that when attention is widespread, as in a visual search task, a sudden distractor is able to capture it. Conversely, if attention is focused previously on the upcoming target location, the distractor fails to capture it. Later studies (Neo & Chua, 2006) have shown that even when attention is focused away from the location of the distractor's appearance, the distractor can capture attention, as long as its frequency is not excessively high. The frequency of the distractor's appearance plays a very important role in capturing focused attention; the more frequent the distractor, the less it can capture attention, and vice versa. On the basis of this result it is possible to speculate that in previous studies (Yantis and Jonides, 1990; Theeuwes, 1991a) focused attention was not captured because the frequency of the distractor was too high (Neo and Chua, 2006).

1.3 How to resist attentional capture

Several studies investigated the neural and cognitive mechanisms implemented to resist visual distraction caused by salient stimuli (Gaspelin & Luck, 2018). Different views have been developed highlighting key conditions under which efficient top-down filtering control can be applied to distractors during a goal-directed attention task. One prominent view assumes that in searching the visual environment for a given target, salient distractors can be effectively rejected if the observer adopts a top-down attentional set accurately tuned to the specific target defining features (Bacon & Egeth, 1994). Hence, in this case, distractor filtering would be the consequence of the adoption of a well-specified target template (Leber & Egeth, 2006b). In alternative, researchers have proposed that distractor filtering would be implemented by means of a direct topdown inhibitory control onto the distractor's representation. According to this view, distractors are not simply ignored because of the adopted target template; rather, a specific top-down suppression strategy is applied to them to facilitate the analysis of behaviorally relevant stimuli (Dixon, Ruppel, Pratt, & De Rosa, 2009; Marini, Chelazzi, & Maravita, 2013; Müller, von Mühlenen, & Geyer, 2007). It should be noted that this filtering mechanism can take one of two forms: on the one hand, it can be engaged in a reactive manner, in response to actual distraction (Geng, 2014; Marini et al., 2013; Marini, Demeter, Roberts, Chelazzi, & Woldorff, 2016; Vissers, van Driel, & Slagter, 2016); on the other hand, it can be recruited strategically in anticipation of expected distraction, for instance in response to a cue stimulus (cued distractor filtering) that informs the observer about the properties of a forthcoming distractor, such as its color or location (Cunningham & Egeth, 2016; Moher, Lakshmanan, Egeth, & Ewen, 2014; Munneke,

Heslenfeld, Usrey, Theeuwes, & Mangun, 2011). Common to both views, however, is the key notion that the filtering of unwanted information takes place to protect target processing from interference. Put differently, distractor filtering would be functional to-and dictated by - the need of preserving successful target processing, an assumption that has reached a rather general consensus in the research community (Gaspelin & Luck, 2018; Geng, 2014; Marini et al., 2013; Moher et al., 2014).

Recently, efforts have been made to characterize mechanisms of distractor filtering that crucially depend on learning processes. For example, a number of studies have demonstrated that when distraction occurs frequently in a given context, the cognitive system is adjusted to better cope with such frequent distraction, adopting proactive and sustained mechanism to reject the distracting input (Geyer, Müller, & Krummenacher, 2008; Marini et al., 2013, 2016; Müller, Geyer, Zehetleitner, & Krummenacher, 2009). Researchers have also shown that the distractor filtering mechanism activated as a result of a learning process sensitive to the overall frequency of distraction, is also sensitive to spatial contingencies in the distribution of distracting stimuli across the visual field, a phenomenon now known as statistical learning of distractor filtering (Cosman & Vecera, 2014; Ferrante et al., 2018; Goschy, Bakos, Müller, & Zehetleitner, 2014; Leber, Gwinn, Hong, & O'Toole, 2016; Reder, Weber, Shang, & Vanyukov, 2003; Wang & Theeuwes, 2018). Therefore, the kind of filtering mechanism that is addressed in these studies is not only sensitive to the overall frequency of occurrence of distraction in a given context, but also to more subtle probabilistic contingencies regarding distractor occurrence. Importantly, it remains that in all conceptual developments that we are aware of, distractor filtering mechanisms - whether

reactively or proactively engaged - are considered as directly functional to shielding target processing in the face of potential or actual distraction.

In recent years an alternative view on distractor filtering has been offered by the process of habituation, an ancestral form of learning consisting in a response decrement to repeated irrelevant stimulation (Pascucci & Turatto, 2015; Turatto & Pascucci, 2016). Before addressing this issue, that is a key node for the current work, it is appropriate to better explain the concept of habituation.

1.4 The phenomenon of habituation

Habituation is one of the most basic forms of learning, and it is defined as a decrease in responding to a stimulus caused by its repeated presentation, a decrement in responsiveness that is not accounted for by sensory adaptation or motor fatigue (Harris, 1943; Thompson, 2009; Thompson & Spencer, 1966). It is a process that takes place in the central nervous system and it can be distinguished from other peripheral processes like sensory adaptation or motor fatigue. Between the end of the nineteenth century and the beginning of the twentieth century the interest in the phenomenon of habituation has literally exploded, bringing several researchers (e.g., Harris, 1943; Sharpless & Jasper, 1956) to carry out experimental studies and observations on the phenomenon in question. Sharpless and Jasper (1956) gave an important contribution to the study of habituation by recording the cortical activation of sleeping cats using implanted electrodes. They discovered that the repeated presentation of brief sounds resulted in a progressive decrease of the arousal and in a successive disappearance. A subsequent strong stimulation that differed from the familiar stimulus caused a recovery of the previously habituated response. A very interesting aspect that emerged from this study is that habituation is specific for some features of the stimulus; if the response was habituated to a 500-CPS (cycles per second) tone presentation until it disappeared, the presentation of a tone at 1000-CPS produced a strong recovery of the response.

1.4.1 Characteristics of habituation

During the sixties, Thompson and Spencer (1966) identified some basic features of habituation, subsequently revised (Rankin et al., 2009) considering the results of several years of studies. The main characteristics of habituation, which allow to distinguish this phenomenon from other minor sensory processes like sensory adaptation or motor fatigue, will be briefly described below.

- **#1**. The repeated presentation of a stimulus results in a progressive decrease in some parameter of a response, until it reaches an asymptotic level (habituation). This change may include decreases in the frequency or in the magnitude of the response.
- **#2**. If the stimulus is omitted after the response decrement, the response recovers at least partially when the stimulus is reintroduced (spontaneous recovery).
- #3. Following several series of stimulus repetitions and spontaneous recoveries, the response decrement becomes successively more rapid and/or more pronounced (potentiation of habituation).
- **#4**. Other things being equal, the higher the frequency of stimulation, the more rapid and/or more pronounced is the response decrement, and the more rapid is the spontaneous recovery (frequency-dependent habituation).
- **#5**. Within a stimulus modality, the less intense the stimulus, the more rapid and/or more pronounced the behavioral response decrement. If the stimulus is too intense, it may produce no significant response decrement.

- **#6**. The effects of repeated stimulation may continue to accumulate even after the response has reached an asymptotic level (below-zero habituation). This effect of stimulation beyond asymptotic levels can modify subsequent behavior (e.g., by delaying the onset of spontaneous recovery).
- #7. Within the same stimulus modality, the response decrement shows some stimulus specificity. To test for stimulus specificity/stimulus generalization, a new, different stimulus is presented, and a comparison is made between the changes in the responses to the habituated stimulus and the new stimulus.
- **#8**. The presentation of a different stimulus results in an increase of the habituated response to the original stimulus (dishabituation).
- **#9**. After repeated presentations of the dishabituating stimulus, the amount of dishabituation produced decreases (habituation of dishabituation).
- **#10**. Some stimulus repetition protocols may result in a response decrement that lasts hours, days or weeks (long-term habituation).

1.4.2 Theories on habituation

One of the most prominent theories on habituation was originally proposed by Sokolov (1963) to explain the reduction of the *orienting reflex* (OR) toward a recurrent stimulus. The OR (Pavlov, 1927) consists of different motor and physiological responses triggered by the occurrence of a novel stimulus, and represents the orienting of attention toward the new stimulus. To explain the habituation of the OR, Sokolov (1963) proposed the *stimulus-model comparator theory*, which postulates that the ability of a stimulus to capture attention diminishes when its occurrence is predicted by a neural model of the environment established by prior experience with the sensory input (the stimulus).

When a stimulus is repeatedly presented, a neural representation (or a neural model) of it is formed in the brain. The model becomes increasingly precise, as a function of the repeated exposition to the same stimulus. When a match is found between the expected stimulus (the one predicted by the model) and the incoming stimulus, the OR normally evoked by the latter is suppressed. By contrast, if the new incoming stimulus does not match the model, an OR toward the stimulus takes place, so that the organism can rapidly evaluate its significance.

Groves and Thompson (1970, 1973) developed the *dual-process theory*, according to which a stimulus results in two independent but interacting processes in the central nervous system, one decremental (habituation) and one incremental (sensitization). It is further assumed that habituation develops in the stimulus–response (S–R) pathway and that sensitization develops in a separate state system which then acts on the S–R pathway to yield the final behavioral outcome.

In 1967, Konorski (1967) further elaborated Sokolov's idea of habituation, and along the same line Wagner (1976) proposed an important theory of priming in short term memory (STM), which provides an interesting explanation of habituation, with greater emphasis on the role of short-term memory and on the existence of an associative network. The key notion is that the efficacy with which a stimulus representation activates further cognitive processes, or an unconditioned response, highly depends on whether or not the stimulus is pre-represented (i.e. primed) in STM. More specifically, the model postulates that a novel and salient stimulus attracts focused attention, thus entering a primary attentional state (A1) that promotes the unconditioned response. This representation decays rapidly, but at the same time a STM representation of the stimulus,

called the secondary state (A2), is formed. A2 is also short-lived, but crucially, while active, it prevents another presentation of the same stimulus to fully capture attention again, thus forming the basis for short-term habituation. Furthermore, when a stimulus is repeatedly presented in a given context, a long-term association is formed between the two corresponding representations. Long-term context-specific habituation takes place because, when encountered, the context acts like a cue, triggering the retrieval of the stimulus representation in STM, and thus decreasing the attentional capture response elicited by the stimulus. The theory proposed by Wagner refreshed the concept of habituation, assuming its associative nature. The model proposed by the theory nicely explains both short- and long-term habituation, and predicts that the latter should be context-specific.

1.4.3 Neural correlates of habituation

The first studies concerning the neural correlates of habituation were conducted on simple animal species like the sea snail *Aplysia* (Castellucci, Pinsker, Kupfermann & Kandel, 1970; Castellucci & Kandel, 1974), which has a series of defensive responses like the gill-withdrawal and the siphon-withdrawal reflexes, which can be considered similar to the most elementary reflexes of human beings. Following the stimulation of the siphon with a water jet, a strong retraction of both the gill and the siphon was observed (due to the L7 motoneuron), which in subsequent tests became less evident, almost to disappear. Change the stimulus (replacing the water jet with an electric shock), resulted in a return of the response to its original level (spontaneous recovery). During the electrical and the mechanical stimulation of the syphon, a postsynaptic excitatory potential took place, which decreased following the repeated stimulation of the syphon. This decrease (at least

as regards to short-term habituation) was not due to changes in the sensitivity or in the number of the postsynaptic receptors, but to the fact that, in the terminals of the sensory neurons, the channels responsible to control the calcium (Ca2+), if repeatedly open, became progressively less sensitive. This reduction in the sensitivity resulted in a lower Ca2+ input in the presynaptic area, with a consequent decrease of the neurotransmitter released into the synaptic space.

The neural correlates underlying habituation have also been investigated in more complex animal species. Kimble, Bagshaw and Pribram (1965), using the Galvanic Skin Response (GSR), demonstrated that monkeys with bilateral lesions of the latero-frontal cortex exhibited a marked reduction of the response to the familiar stimulus (habituated stimulus) and to the new stimulus, as compared to the control subjects (without injuries) and to the subjects with fronto-medial lesions. This implies that the latero-frontal cortex plays a fundamental role both in the OR and in the attentional habituation.

More recently, the development of sophisticated neuroimaging techniques has allowed the study of the neural basis of habituation also in humans. Using the Positron Emission Tomography (PET), Fischer and colleagues (2000) demonstrated that a repeated complex visual stimulation produced a neural habituation, resulting in a decreased regional cerebral blood flow (rCBF) in the secondary visual cortex, in the right temporo-medial cortex, in the amygdala and in the hippocampus. The cerebral blood flow in the thalamus and in the left premotor cortex, on the contrary, increased proportionally to the repeated presentations of the stimuli. This result gave an important contribution to the attempt to locate the brain network where the development of the neural representation, hypothesizes by the various theories of habituation, takes place. In light

of these findings, one could speculate that the development of the neural representation can be localized in the thalamus and not in the hippocampus, as suggested by Sokolov (1990), and that this could be the point at which non-relevant sensory information is suppressed (Fischer et al., 2000).

The neural basis of habituation was examined also with respect to the emotional valence of a stimulus (Schupp et al., 2006; Codispoti, De Cesarei, Biondi, & Ferrari, 2016; Codispoti, Ferrari, & Bradley, 2006; Codispoti, Ferrari, & Bradley, 2007). In a work by Codispoti and colleagues (Codispoti et al., 2007) a passive viewing picture repetition paradigm was used to evaluate the cognitive processes underlying affective modulation of early and late ERPs and to determine how the stimulus repetition affects short- and long-term habituation of each component. They discovered that these two ERP components may reflect different steps of image processing. Although both components were similarly modulated by emotional arousal, the repetition of the images had different effects on them; the early occipitotemporal component (150-300 ms) showed an amplitude decrease (across sub-blocks but not across blocks) that did not differ as a function of picture content (pleasant, unpleasant and neutral images). On the contrary, the late centroparietal component (300-600 ms) showed a decrease (both across subblocks and across blocks) with emotional pictures eliciting larger late positive potentials (LPPs) than neutral pictures. The authors interpreted the magnitude decrement of the LPP as an evidence that fewer resources were allocated to these pictures as their novelty and salience declined. Emotional pictures continued to elicit larger LPPs than neutral pictures, suggesting that affective pictures continue to draw attentional resources, despite previous presentation. The results suggest that the early ERP reflects a mandatory perceptual processing that occurs regardless of the relevance of the stimulus, whereas the late ERP reflects increased resource allocation due to the motivational relevance of the stimuli (Codispoti et al., 2007).

Because of the different experimental techniques used and the different populations taken into account, the results obtained so far are at least in part contradictory, and further studies are needed to understand with a higher precision what are the neural correlates involved in the phenomenon of habituation.

1.5 Habituation and attention: an intimate but overlooked relation

Since the pioneering work of Sokolov (1960, 1963), other studies have suggested that habituation of the orienting of attention would represent the operation of a gating mechanism for incoming sensory irrelevant information, and that there is a strong functional link between habituation and attention (e.g., Bell, Röer, Dentale, & Buchner, 2012; Röer, Bell, & Buchner, 2014; Cowan, 1988; Elliott & Cowan, 2001; Kraut & Smothergill, 1978; Mackworth, 1969; Waters, McDonald, & Koresko, 1977). Despite this, the possibility that distractors rejection can also occur because attentional capture can be subject to habituation, has not been taken into account for many years. Curiously, even if the research community working on visual attention seems to disregard the link between habituation and distractors rejection (but see, Cowan, 1988; Forster & Lavie, 2008; Gati & Ben-Shakhar, 1990; Codispoti et al., 2016; Neo & Chua, 2006; Pascucci & Turatto, 2015; Turatto & Pascucci, 2016), in the research field investigating this form of behavioral plasticity, habituation has always been considered to reflect a form of filtering mechanism for the unwanted stimulation, which allows the organism to focus selectively on the relevant stimuli (Rankin et al., 2009; Stephenson & Siddle, 1983). Since the

seminal work of Sokolov, several studies have documented how the different physiological responses associated to the OR habituate following the repeated presentation of a stimulus (e.g., Barry, 2009). The hypothesis that also the attentional capture elicited by a peripheral onset distractor can be subject to habituation was tested in a few studies (e.g., Forster & Lavie, 2008; Neo & Chua, 2006), but only recently a more systematic investigation has been carried out (Pascucci & Turatto, 2015; Turatto & Pascucci, 2016). The study of Turatto and Pascucci (2016), was the first to systematically investigate whether habituation could specifically modulate the capture of spatial attention. Participants were engaged in a speeded visual discrimination task in which attention was focused on the location of the visual target appearance. Crucially, in half of trials, 200 ms before the occurrence of the target, a sudden onset distractor (which consisted of a bright annulus) was added to the display. The authors documented that at the beginning of the experimental session the presence of the distractor increased the response times (RTs) of participants (attentional capture). However, a strong decrease in the amount of attentional capture was observed across blocks. Additionally, the authors documented spontaneous recovery of attentional capture, as the capture was restored when the distractor was reintroduced after a period (200 trials) of suspension. Finally, a long-term form of habituation was documented, which was subsequently confirmed by a more recent study using a very similar paradigm (Turatto, Bonetti, & Pascucci, 2018). The results of these studies clearly show that habituation of attentional capture can provide a convincing explanation for distractors rejection during a covert attention task.

1.6 Experimental questions

Since the habituation mechanisms seem to plausibly account for the decrement of the attentional capture, the current work wants to answer the following questions, which will be addressed in three different chapters.

- Chapter 2: Does habituation of attentional capture occur also during the passive exposure to an irrelevant stimulus?
- o Chapter 3: Is habituation of attentional capture context-specific?
- o Chapter 4: Does habituation affect also the oculomotor system?

Each chapter will be preceded by a brief introduction to provide the reader all the tools to understand the illustrated experiments.

Filtering irrelevant information during passive viewing

All the material in this chapter has been published in the following paper:

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(12), 1827.

2.1 Introduction

As previously discussed in the first chapter of the thesis, different mechanisms have been proposed to explain how we face distraction, and the majority of the models share the idea that distractor filtering is actively implemented in order to protect a target stimulus from the interference of an irrelevant distractor (Geng, 2014). An alternative view on distractor filtering is offered by the notion of habituation, which reflects the functioning of a filtering mechanism to discard unwanted information, preventing the continuous deployment of processing resources toward irrelevant, albeit salient, repetitive stimuli (Cowan, 1988). Some studies specifically concerned with habituation of visuospatial attentional capture have documented that the distracting property of sudden peripheral visual onsets diminishes as the exposure to the irrelevant distractors progresses (Neo & Chua, 2006; Pascucci & Turatto, 2015; Turatto, Bonetti, & Pascucci, 2018; Turatto & Pascucci, 2016). It should be noted that a Sokolovian-like mechanism for

attention habituation is not implemented strategically, but instead is assumed to operate automatically on the basis of the history of stimulation, irrespective of any task set implementation. It does not mean, however, that habituation does not require attentional or working memory (WM) resources, because there is convincing evidence showing that WM capacity affects the rate of habituation to irrelevant auditory distractors during visual-discrimination and memory tasks (Sörqvist, 2010; Sörqvist Nöstl & Halin., 2012; Sörqvist & Rönnberg, 2014). Rather, the idea is that the habituation-dependent filtering mechanisms are not implemented strategically, in a goal-driven manner, to reject the distracting information. By contrast, as discussed previously, the shared view emerging from the visual attention literature is that mechanisms for distractor rejection are strategically implemented, with the specific aim to shield target processing from interference (Geng, 2014).

Hence, the aim of the present chapter is to investigate whether distractor rejection is mandatorily achieved via top-down inhibitory signals applied to distractors for the successful completion of goal-directed behavior, such as target discrimination, or alternatively whether a bottom-up habituation mechanism not necessarily related to a concurrent discriminative task can account for the reduced distraction observed after repeated exposure to irrelevant peripheral onset stimuli. To address this issue, the first experiment measured how the distracting influence of peripheral onset stimuli diminishes as a function of practice while participants were engaged, for four "active" blocks of trials, in a fully focused attention task wherein they had to discriminate the orientation of a target line presented inside a cued circle (Turatto & Pascucci, 2016). Then, in the following experiments, participants were merely exposed to the same

distractor for two consecutive "passive" blocks of trials (i.e., in passive-viewing), before performing the discriminative task in two subsequent active blocks. The logic of these experiments combined was as follows: if the process of distractor filtering is dictated by the need to shield target processing from interference, then the passive exposure phase should have no beneficial effects on the subsequent target discrimination phase, and any learning to enhance distractor filtering should start anew in the first active block of trials. By contrast, the habituation view would predict that participants should be able to take advantage from past experience acquired during passive viewing to promptly attenuate distraction once they become engaged in target processing. In other words, even during passive viewing, the system should learn that a stimulus is behaviorally irrelevant, diminishing its impact on attention, even in the absence of a discriminative task.

2.2 Experiment 1

The first step was to characterize the pattern of decay of the distracting effect caused by peripheral onset stimuli as a function of practice when participants were engaged, for four active blocks of trials, in a fully focused attention task wherein they had to discriminate the orientation of a target line presented inside a cued circle (Turatto et al., 2018; Turatto & Pascucci, 2016).

2.2.1 Methods

2.2.1.1 Participants

Participants were 24 undergraduate students (17 female; mean age = 21.7 years) at the University of Trento and were recruited from the Department of Psychology and Cognitive Sciences for course credits or monetary compensation (8€). Participants had

normal or corrected to-normal vision and were all naïve as to the purpose of the experiment, and all provided informed consent to participate in the present study. All the experiments were carried out in accordance with the Declaration of Helsinki, and with the approval of the local institutional ethics committee (Comitato Etico per la Sperimentazione con l'Essere Umano, Universita` degli Studi di Trento, Italy).

2.2.1.2 Apparatus

Stimuli were presented on a 23.6-in. VIEWPixx/EEG color monitor (1920 x 1080, 100 Hz) and generated with a custom-made program written in MATLAB and the Psychophysics Toolbox (Pelli, 1997) running on a Dell Precision T1600 machine (Windows 7 Enterprise). Eye fixation (or any eye movement) was monitored with an Eyelink 1000 Desktop Mount system (sampling rate: 1000 Hz; SR Research, Ontario, Canada). Each block was preceded by a nine-point calibration procedure, which was repeated during the block if participants' gaze drifts exceeded 1.5°.

2.2.1.3 Stimuli and procedures

Each trial began with the presentation of a fixation point surrounded by four circles positioned at the corners of an imaginary square (diagonal of 22.62°) centered on the fixation point (see Figure 1). The circles were light gray (7 cd/m²) and were shown on a dark-gray background (0.07 cd/m²). Three circles had the same thickness (inner diameter of 4°; outer diameter of 4.15°), whereas the thickest one (inner diameter of 4°; outer diameter of 4.25°) served as a spatial cue to indicate the position of the upcoming target (100% validity). The position of the cue was randomly assigned on each trial. After 1,100 ms were elapsed, the target (31 cd/m²), consisting of an oblique line tilted 45°

either to the left or to the right, was presented within the cued circle for 100 ms. On 50% of the trials, 100 ms before target occurrence, a high luminance white annulus frame (inner diameter of 3.75°, outer diameter of 4.35°, 52.5 cd/m²) was superimposed for 100 ms onto one of the three thinner circles, thus creating a sudden visual onset, which served as an attentional distractor. The position of the distractor relative to the target position was counterbalanced across trials. The display with the four placeholders remained onscreen until the participant's response or until 1,500 ms were elapsed from the target onset. The next trial began after a variable interval, ranging from 1,000 to 1,200 ms from display offset, during which the screen was blank. Participants were instructed to maintain fixation on the central point while focusing their attention exclusively on the cued target location (100% validity). The task was to report as quickly and as accurately as possible the orientation (left vs. right) of the target line by pressing the corresponding arrow on the computer keyboard. RTs were recorded from the target appearance, and the maximum time allowed for responding was 1,500 ms. Error feedback was provided by a message presented on the screen for 500 ms at the end of the trial. When an eye movement or blink was detected in the first 500 ms of the trial, the trial was aborted and restarted. If an eye movement was detected during the presentation of either the distractor or the target, an error message appeared on the screen, and trial was discarded from the analysis.

The experiment consisted of four active blocks of 100 trials each. The term "active" indicates that a target discrimination task was performed on each trial of the block, whereas in the following experiments (see below) two passive blocks of 100 trials each, in which no task had to be performed, preceded the two active blocks. Before

starting the first active block participants performed a short block of 10 practice trials without the distractor. Task instructions and procedure, with information about the possible presence of the distractor in the active trials, were provided on screen before the beginning of the practice block.

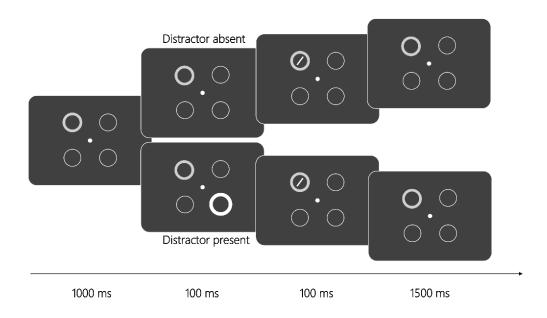


Figure 1. Schematic representation of the main events of Experiments 1, 2, and 3. The distractor (the bright annulus, here in the down-right corner) appeared on 50% of the trials, and the target was a tilted line that always appeared inside the thickest stable circle (here in the up-left corner), which served as a spatial cue. In the passive-viewing condition the distractor was presented whereas the target was omitted (see Methods for details).

2.2.1.4 Data analysis

All the analyses reported in this and the following experiments of the present chapter regard the active blocks only, as these were the only blocks in which participants were engaged in target discrimination and performance could therefore be measured.

For each participant, data on correct response trials were trimmed for RTs shorter than 150 ms (anticipations) or longer than 1,000 ms. In all experiments, errors were < 2% in each block and were not analyzed further, whereas the outlier-latency criterion removed less than 2% of the data. Attentional capture elicited by the distractor was defined as the RT difference between distractor-present and distractor-absent trials. A statistically reliable positive difference thus indicates that the distractor interfered with target processing by capturing visual attention.

2.2.2 Results and discussion

RT differences (distractor-present minus distractor-absent) for correct responses were entered into an analysis of variance (ANOVA) for repeated measures with Block (four levels) as the only factor, which resulted in a significant effect, F(3, 69) = 6.971, p < .001, $\eta^2_p = .233$, indicating that the amount of attentional capture changed across blocks, as depicted in Figure 2. Although capture was significantly larger than zero in all blocks (p = .01), pairwise comparisons (t test, two tails) confirmed that capture was significantly attenuated by practice: the degree of interference caused by the distractor in the first active block (M = 44 ms) was larger than in the second active block (M = 28 ms; p = .030), third active block (M = 22 ms; p = .005), and fourth active block (M = 21 ms; p < .001), respectively.

The weakening of the distractor effect across blocks confirmed our previous findings, and could be accounted for by a mechanism of attentional capture habituation (Pascucci & Turatto, 2015; Turatto & Pascucci, 2016). Alternatively, the reduction of capture as a function of training is also consistent with the possibility that participants learned to filter out the distracting stimulus to shield target processing from interference

(e.g., Awh, Matsukura & Serences, 2010). However, if the latter is the mechanism at play, then a straightforward prediction follows: no learning of distractor filtering should take place when there is no target to be analyzed and no task to be performed. Such prediction was tested in the following experiments.

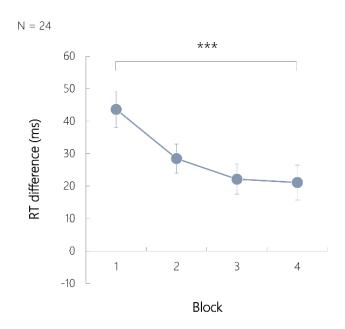


Figure 2. Attentional capture defined as the RT difference between distractor-present and distractor-absent trials (present minus absent) as a function of active block. Each active block consists of 100 trials, in which the distractor was presented with a frequency of 50%. Bars represent $\pm 1 \text{ SEM}$.

2.3 Experiment 2

In Experiment 2, to directly test the above prediction, for two initial blocks of trials participants were simply exposed to the distractor while maintaining central fixation (passive viewing). Then, two active blocks followed the passive ones. Under these conditions, according to the strategic filtering account, no significant learning should take

place during the initial passive blocks since no discriminative task is performed, and especially because participants had no expectation about the occurrence of the two subsequent active blocks. Consequently, attentional capture should be at full strength in the first active block requiring target processing. In other words, when the discriminative task was commenced at the start of the first active block, the amount of capture should be comparable to that found in the first active block of Experiment 1, while capture should then diminish in the next active block of trials. On the contrary, according to the habituation account, a learning process should have occurred during the passive viewing, and therefore the amount of attentional capture in the first active block should be significantly different from the capture observed in the first active block of Experiment 1.

2.3.1 Methods

2.3.1.1 Participants

Participants were 24 undergraduate students (18 female; mean age = 21.3 years) at the University of Trento and were recruited from the Department of Psychology and Cognitive Sciences for course credits or monetary compensation (8 \in). They had normal or corrected-to-normal vision, and were all naïve as to the purpose of the experiment.

2.3.1.2 Apparatus

The apparatus used was the same as in Experiment 1.

2.3.1.3 Stimuli and procedures

The experiment consisted of two active blocks (100 trials each), with the same procedure of Experiment 1, which followed two initial passive blocks. In the passive

blocks (100 trials each), the cue was presented but the target was not, and participants were asked to maintain fixation on the central spot, while passively viewing the display, which, on 50% of trials, included the peripheral onset. Before beginning the passive-viewing phase, participants were provided a description of the corresponding display. After the passive-viewing phase, participants received the new task instructions as in Experiment 1, and then performed a short block of 10 practice trials (without the distractor) before starting the two active blocks.

2.3.1.4 Data analysis

The analyses that I conducted were the same as Experiment 1.

2.3.2 Results and discussion

The ANOVA on the RT differences for correct responses revealed that the factor Block (two levels) was not significant, F(1,23) = 1.174, p = .290, $\eta^2_p = .049$ (see Figure 3); capture was significantly larger than zero in both the first (p = .001) and the second (p = .005) active block of trials. Crucially, however, in the first active block the amount of capture in this experiment (M = 26 ms) was significantly smaller than in Experiment 1 (M = 44 ms), p = .018 (independent-samples t test). By contrast, no significant difference emerged between the two experiments concerning the second active block (p = .234). To be thorough, I also compared the first active block of Experiment 2 (which is actually the third block of exposure) with the third block of Experiment 1, and the second active block of Experiment 2 (which is actually the fourth block of exposure) with the fourth block of Experiment 1, but the comparison revealed no significant differences (p = .509 and p = .917 respectively).

Hence, as shown in Figure 3, the distractor cost during the first active block was strongly reduced in Experiment 2 relative to the first experiment, indicating that in the second experiment a learning process taking place during the initial two blocks of passive viewing had greatly reduced the ability of the distractor to later interfere with task performance. In turn, this indicates that the learning process occurs even within a context wherein the distractor is actually unable to exert any negative impact on performance for the simple reason that there is no task to be performed during passive viewing.

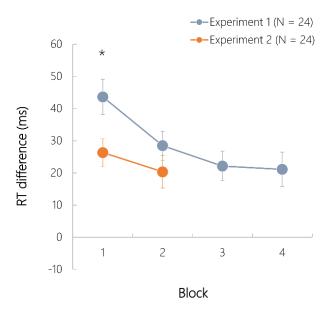


Figure 3. Attentional capture as a function of active block in Experiments 1 (in grey) and 2 (in orange). Only the active blocks are depicted. Each active block consists of 100 trials, in which the distractor was presented with a frequency of 50%. Bars represent \pm 1 SEM.

2.4 Experiment 3

The results from the previous two experiments clearly indicate that the distractor filtering process was already implemented during the passive-viewing phase, even in the absence of any discriminative task. However, because during passive viewing participants were instructed to maintain central fixation, which was monitored in both the previous experiments, one may argue that participants were actively engaged in trying to counteract any oculomotor capture triggered by the peripheral distractor (Theeuwes, Kramer, Hahn, & Irwin, 1998). In other words, the suppression mechanisms used to filter out the distractor could have been under goal-directed control, at least to some extent, to maintain attention and the eyes on the fixation cross. Because so far it was argued that distractor filtering was likely achieved via habituation, implying that it was implemented in a more automatic fashion and regardless of the current task, to exclude a major contribution of top-down goal-directed components necessary to maintain central fixation, in the present experiment participants were left free to move their eyes during the passive-viewing phase. If the previous findings of reduced capture after the passive viewing phase were replicated even under conditions of unconstrained eye movements, the strategic-filtering hypothesis would be very unlikely to account for our results.

2.4.1 Methods

2.4.1.1 Participants

Participants were 24 undergraduate students (16 female; mean age = 22.6 years) at the University of Trento and were recruited from the Department of Psychology and

Cognitive Sciences for course credits or monetary compensation (8€). They had normal or corrected-to-normal vision, and were all naïve as to the purpose of the experiment.

2.4.1.2 Apparatus

The apparatus used was the same as in Experiments 1 and 2.

2.4.1.3 Stimuli and procedures

These were the same as in Experiment 2, with the following exception: participants were required to maintain central fixation only during the first 200 ms after trial onset. Then, they were free to move their eyes during the remainder of the trial.

2.4.1.4 Data analysis

The analyses that I conducted were the same as Experiments 1 and 2.

2.4.2 Results and discussion

The results on RTs, depicted in Figure 4, replicated those of Experiment 2. When the RT differences for correct responses were analyzed as a function of block, the ANOVA showed that the factor Block (two levels) was not significant, F(1, 23) = 1.584, p = .223, η^2_p .223; however, the difference was larger than zero in both the first (M = 28 ms; p = .001) and the second (M = 20; p = .002) active block of trials. Importantly, in the present experiment, when participants were free to move their eyes, the rate of saccades directed toward the distractor in the passive viewing phase was much higher (34%) than that in the same phase of Experiment 2 (1%), when participants were instructed to maintain central fixation. To be thorough, I also compared the first active block of Experiment 3 (which is actually the third block of exposure) with the third block of exposure)

with the fourth block of Experiment 1, but the comparison revealed no significant differences (p = .396 and p = .882 respectively).

This pattern of results confirms that, when fixation was not required, participants made a consistent number of saccades toward the distractor, which in turn implies that they were not trying to resist (oculomotor) capture by the peripheral onset stimulus. However, in spite of this, the results were highly similar to those of the previous experiment in which eye movements were not allowed, thus confirming a strong reduction of capture as a result of the passive-viewing phase. Because in the present experiment participants were free to move their eyes during the passive viewing phase, this undermines the possibility that the attenuation of attentional capture, as found in this and the previous experiment, was achieved via a top-down goal-directed mechanism, that purposefully suppressed the distractor to avoid reflexive saccades toward the irrelevant visual onset. Rather, the results are consistent with a key role of habituation mechanisms, which attenuate the exogenous attentional capture independently of any strategic voluntary control.

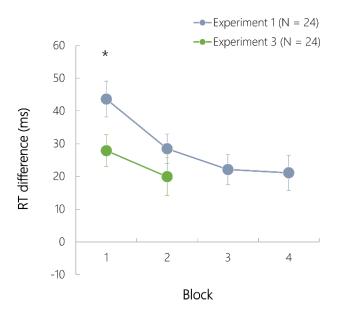


Figure 4. Attentional capture as a function of active block in Experiments 1 (in grey) and 3 (in green). Only the active blocks are depicted. Each active block consists of 100 trials, in which the distractor was presented with a frequency of 50%. Bars represent \pm 1 *SEM*.

2.5 General discussion

The attentional system is inherently responsive to salient stimuli, which makes distraction virtually inevitable. From the point of view of the organism's survival, distraction is, in the end, a cost that is worth paying to be always ready to inspect, and eventually react to, potentially relevant (e.g., aversive or appetitive) events, like those often signaled by sudden visual onsets. However, once a distracting stimulus has turned out to be innocuous and irrelevant, the cognitive system must be capable of ignoring further occurrences of the same stimulus to prevent repetitive, unwanted distraction, and consequently the continuous wasting of valuable limited-processing resources.

Therefore, the characterization of the specific cognitive and neural mechanisms for distractor filtering has recently become a central topic in the study of attention. Different strategic top-down mechanisms for distractor filtering have been proposed (Gaspelin & Luck, 2018; Geng, 2014), hinging on the idea that top-down inhibitory signals are applied to the distractors for the successful completion of goal-directed behavior. This strategicsuppression view explicitly assumes that distractor filtering is under top-down control, meaning that suppression of distractors would be actively implemented to restrict attentional processing to the target item. Suppression would either result from a direct inhibitory signal deliberately applied to the distractors (Awh et al., 2010; Geyer et al., 2008), or the consequence of the adoption of a precise attentional set (feature-search mode) tuned to the specific target features (Bacon & Egeth, 1994). Other studies have prevalently emphasized the role of learning processes rather than of explicit knowledge or strategy, and have shown that filtering can also take place because of experiencedependent attentional tuning of distractor rejection (Ferrante et al., 2018; Leber & Egeth, 2006a; Leber et al., 2016; Vatterott & Vecera, 2012; Wang & Theeuwes, 2018).

However, regardless of whether distraction is counteracted proactively, reactively, or as a consequence of a (statistical) learning process, the widely shared idea is that distractor rejection is dictated by the need to shelter target processing from interference (Awh et al., 2010; Dixon et al., 2009; Geng, 2014; Geyer et al., 2008; Marini et al., 2013, 2016). Alternatively, the ability of the cognitive system to progressively ignore a recurrent distractor can also be interpreted in light of the more general phenomenon of habituation (Thompson, 2009; Thompson & Spencer, 1966). As already pointed out in the Introduction (Chapter 1), this basic form of behavioral plasticity is

ubiquitously present in the animal kingdom (Harris, 1943), and reflects the ability of the organism to adapt its behavior on the basis of past experience. However, it is important to note that habituation reflects a response reduction that is not accounted for by sensory (perceptual adaptation) or motor fatigue, namely, habituation is a central process that relies on the ability of the nervous system to predict the incoming information on the basis of the history of stimulation (Ramaswami, 2014; Sokolov, 1963). Specifically, with practice, the organism learns to reduce its responsiveness to irrelevant and innocuous stimuli when these are repeatedly encountered.

The current study provides insightful information as to the plausibility of the distractor filtering mechanisms postulated by the strategic-suppression view as opposed to those underlying the habituation view. To summarize the main findings, this study showed that during the course of an active task, attentional capture exerted by a peripheral sudden onset distractor diminished gradually over the course of the experiment (Experiment 1). Next, the results showed that, similar to what found during an active task, repeated passive exposure to a peripheral onset strongly reduced its ability to capture attention when later presented during a subsequent discriminative task (Experiment 2). In addition, the reduced distraction developed during the passive-viewing phase appears to be largely independent from an inhibitory top-down control exerted to maintain central fixation while exposed to the peripheral distractor (Experiment 3).

Hence, although there is no doubt that the ultimate goal of avoiding distraction is that of keeping attention focused on the relevant task at hand, the results showed that to exclude unwanted information, the cognitive system can rely on a mechanism that starts

to operate even when there is neither a target to be processed, nor an advance knowledge of the target that will be presented in the subsequent phase (and of the task to be performed next). Rather, the results indicate the existence of a learning-dependent mechanism that is activated by virtue of the mere exposure to a recurring salient onset, even in the absence of any attentional set for the target features.

So far, to highlight the beneficial effects of the passive-viewing phase in reducing the amount of capture I have mainly considered the fact that the distractor cost in the first two active blocks of Experiments 2 and 3 (with passive viewing) was significantly lower as compared with the cost in the corresponding blocks of Experiment 1 (without passive viewing). However, the beneficial effects of passive viewing appear to be even more remarkable if one considers that the degree of attentional capture after this phase is comparable to that observed after two blocks of active trials in those experiments where there was no passive-viewing phase. Indeed, RTs in the 1st and 2nd active blocks of Experiments 2 and 3 were statistically indistinguishable from those of the 3rd and 4th active blocks of Experiment 1 (all p > .3). Put differently, the evidence suggests that the amount of learning associated with distractor rejection that is achieved in two blocks of passive viewing, during which the distractor did not interfere with any target-related processing, is equivalent to that obtained after two blocks of active task, when one might assume that the distractor is actively filtered to shield target processing from interference.

The collected evidence is fully consistent with the habituation view, whereby the filtering mechanism would operate in an automatic fashion on the basis of the sensory input, which is then confronted with an internal model built through past experience

(Sokolov, 1963). As already pointed out, by claiming that habituation mechanisms operate automatically (also see, Steiner & Barry, 2014) I do not mean that their functioning does not demand cognitive resources. In fact, as previous studies have shown, habituation rate correlates with WM capacity (Sörqvist, 2010; Sörqvist et al., 2012; Sörqvist & Rönnberg, 2014), which indicates that central cognitive resources may be used for the implementation of the habituation process. What it should be noted, instead, is that the implementation of this type of filtering mechanism is not under strategic or voluntarily control, but rather that through habituation mechanisms the cognitive system automatically and constantly monitors the correspondence between the predictive model of the external world and the incoming signals. Similarly to what was originally proposed by Sokolov (1963), and by more recent theories on adaptive filtering and dynamic predictive coding (Huang & Rao, 2011; Ramaswami, 2014), mechanisms based on a neural model of the history of stimulation would emphasize novelty by reducing the (attentional) response evoked by recurrent irrelevant stimuli, thus explaining habituation of attentional capture. Overall, the present pattern of results is in accordance with evidence from a related line of research on the habituation of attentional capture triggered by irrelevant auditory distractors during a visual memory task. Research on this topic has revealed that the detrimental effect of an irrelevant sound on the visual memory performance diminishes as exposure to the distractor repeats, thus revealing a form of habituation of cross-modal attentional capture (Bell et al., 2012; Röer et al., 2014; Röer, Bell, & Buchner, 2015; Sörgvist, 2010). It is important to underline that, to the best of my knowledge, this is the first study reporting a habituation-like reduction of attentional capture attributable to the passive exposure to a distractor within the visual modality. In turn, this is not a trivial advancement of our understanding of attention in general, and of the mechanisms supporting distractor filtering in particular, especially in view of the rapidly increasing literature exploring these mechanisms in the visual modality (Gaspelin & Luck, 2018; Geng, 2014), a literature that so far appears to have almost completely neglected the possibility that distractor rejection can be supported, at least under certain circumstances, by the sort of habituation-like mechanisms that has been explored in the present study (but see notable exceptions, e.g., Codispoti et al., 2016; Gati & Ben-Shakhar, 1990; Neo & Chua, 2006; Pascucci & Turatto, 2015; Turatto et al., 2018; Turatto & Pascucci, 2016).

One may wonder whether the reduced sensitivity to the visual distractor that we documented in the present set of experiments can be explained by perceptual adaptation rather than by habituation mechanisms, given that they both imply a response reduction at some level of the neural cascade. There is a strong reason to believe that the current results are an instance of habituation of capture, rather than of perceptual adaptation. As stated by Carandini (2000), visual adaptation is mainly observed when the visual system is presented with the same stimulation for seconds or minutes. Under these conditions, when a test stimulus is presented after a prolonged exposure to an adapting stimulus, perceptual appearance of the former is affected by the latter. The perceptual change reflects calibration mechanisms that adapt the visual system, from the retina to the cortex, to the dominant attributes of the adapting stimulus (e.g., light intensity, contrast, orientation, motion direction, etc.; Carandini, 2000). The prolonged stimulation induces a neural "fatigue" in the neurons that most strongly respond to the main characteristics of the adapting stimulus, thus leading to sensory adaptation. As a consequence, the same

neurons respond less vigorously than before the adapting stimulation, and perception is moved away from the adapting stimulus (e.g., the tilt aftereffect, or the motion aftereffect; Thompson & Burr, 2009; Webster, 2012). Given that in the current paradigm the distractor appeared for only 100 ms, and on 50% of the trials (i.e., with an average inter trial interval of approximately 4000 ms), and that it also randomly changed its spatial position on a trial-by-trial basis, it seems very unlikely that stimulus adaptation may have contributed to the results. In addition, previous studies have shown that attentional capture habituation can persist unchanged for days after training (Turatto et al., 2018; Turatto & Pascucci, 2016), which reasonably rules out a possible implication of visual adaptation.

To summarize, the present chapter directly addressed whether the learning-dependent phenomenon leading to reduced distraction is achieved via top-down inhibitory signals strategically applied to the distractor to protect target processing from interference, as is broadly assumed, or whether more automatic, habituation-like mechanisms can support reduced capture after repeated passive exposure to a given distracting stimulus. By showing that the ability to disregard distractors can be learned even during passive viewing, the results provided compelling and novel evidence in favor of a key role of habituation-like mechanisms.

The role of contextual cues in filtering irrelevant information

All the material in this chapter has been published in the following papers:

Turatto, M., **Bonetti, F.**, & Pascucci, D. (2018). Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. *Psychonomic Bulletin & Review*, 25(3), 1028-1034.

Turatto, M., **Bonetti, F.**, Chiandetti, C., & Pascucci, D. (2019). Context-specific distractors rejection: contextual cues control long-term habituation of attentional capture by abrupt onsets. *Visual Cognition*.

3.1 Introduction

If distractors can be ignored because of habituation, an interesting question is whether habituation of capture is determined only by the properties of the distractor, or is instead affected by the surrounding context. As already pointed out in the first chapter of the thesis, despite habituation is generally considered a form of non-associative learning, Wagner (1976, 1978, 1979) proposed an associative theory of habituation, postulating that with training an association is formed between the repetitive stimulus and the surrounding context. Later exposure to the same context generates the retrieval of the habituated stimulus representation in short-term memory. This representation reduces the attentional response usually triggered by the stimulus when it is initially presented and unexpected, thus showing response habituation. However, repeated presentation of the context without the stimulus would weaken the associative strength

between the two representations (extinction), so that when the stimulus is reintroduced in the same context, a spontaneous recovery of the habituated response is observed. Crucially, to claim that habituation is context specific, spontaneous recovery should not be observed if, after training, both the stimulus and the context are omitted before the test phase. The results of different animal studies confirmed this prediction, showing that habituation of different behavioral responses can indeed be context specific (e.g., Chiandetti & Turatto, 2017; Jordan, Strasser, & McHale, 2000; Rankin, 2000; Tomsic, Pedreira, Romano, Hermitte, & Maldonado, 1998).

The present chapter was aimed at exploring the role of contextual information in filtering an irrelevant stimulus, through three different experiments. The first experiment was designed to find out evidence of context-specific habituation from the phenomenon of extinction of the habituated response. In the second and third experiments, instead, participants were exposed to a direct change of the context (background) in which the distractor appeared.

3.2 Experiment 4

To establish whether habituation of capture is context specific in humans, participants were first exposed, on Day 1, to a visual distractor while they performed a discriminative task with focused attention, which should lead to habituation of capture. Then, spontaneous recovery of capture was evaluated after the distractor was removed for approximately 48 hours, but in two different conditions (see Figure 5). In the extinction condition the distractor was removed on Days 2 and 3 but reintroduced in the last block of trials of Day 3, to test capture. By contrast, in the control condition, participants did not perform the task on Day 2, and were tested with the distractor in a

single block of trials on Day 3. Therefore, the extinction and control conditions were identical in terms of exposure to the distractor (Day 1, and one block on Day 3), interval of time between training and test (two days), but differed in terms of context exposure between the training and the test phase.

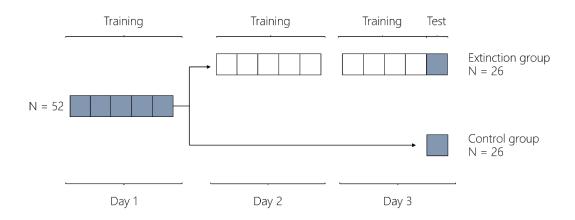


Figure 5. Each square represents a block of 100 trials. Grey squares are blocks in which the distractor was present on 50% of the trials. White squares are blocks in which the distractor was omitted. On Day 2 and on the first four blocks of Day 3, the extinction group performed the task without distractors, while the control group did not perform any kind of task.

3.2.1 Methods

3.2.1.1 Participants

Fifty-two undergraduate students (41 female; mean age = 22.1 years) of the University of Trento were recruited from the Department of Psychology for course credits. They had normal or corrected-to-normal vision and were all naïve as to the

purpose of the experiment. Informed consent was obtained from all participants. All the experiments were carried out in accordance with the Declaration of Helsinki, and with the approval of the local institutional ethics committee (Comitato Etico per la Sperimentazione con l'Essere Umano, Università degli Studi di Trento, Italy).

3.2.1.2 Apparatus

Stimuli were presented on a 23.6-inch VIEWPixx/EEG color monitor (1920 × 1080, 100 Hz) and generated with a custom-made program written in MATLAB and the Psychophysics Toolbox (Pelli, 1997) running on a Dell Precision T1600 machine (Windows 7 Enterprise). Eye fixation was monitored with an Eyelink 1000 Desktop Mount system (sampling rate: 1000 Hz; SR Research, Ontario, Canada). Each block was preceded by a nine-point calibration procedure, which was repeated during the block if participants' gaze drifts exceeded 1.5°.

3.2.1.3 Stimuli and procedures

Each trial started with the presentation for 1,200 ms of the fixation point surrounded by four circles (inner diameter of 4°; outer diameter of 4.15°) positioned at the corners of an imaginary square (diagonal of 22.62°) centered on the fixation point. Three circles were light gray (7 cd/m²) and one was red (17 cd/m²), and were shown on a dark-gray background (0.07 cd/m²). The red circle served as cue to indicate the position of the upcoming target. The position of the cue was randomly assigned on each trial. On distractor-present trials, 200 ms before the target occurrence a high-luminance white annulus frame (inner diameter of 3.75°, outer diameter of 4.25°, 52.5 cd/m²) was superimposed for 100 ms to one of the three light gray circles, thus creating a sudden

visual onset distractor (see Figure 6). The position of the distractor relative to the target position was balanced across trials. Participants were instructed to maintain fixation on the central point while focusing their attention exclusively on the cue. The task was to report as quick as possible the orientation (left vs. right) of the target line by pressing the corresponding arrow on the computer keyboard. RTs were recorded from the target appearance, and the maximum time allowed for responding was 1,500 ms. Trials in which participants did not respond within this time window were excluded from the analysis (<1% in total). Error feedbacks were provided by a message presented on the screen for 500 ms at the end of the trial. When an eye movement or blink was detected in the first 500 ms of the trial, the trial was aborted and restarted. If an eye movement was detected during the presentation of either the distractor or the target, an error message appeared on the screen, and trial was discarded from the analysis.

On Day 1, all participants (N = 52) performed the task with the distractor (50% frequency) in five blocks of 100 trials each. After Day 1, one group of participants (N = 26) was assigned to the extinction condition. On Day 2, and in the first four blocks of Day 3, they performed the same task as in Day 1 but without the distractor. They were then tested with the distractor on Block 5 of Day 3. The other group of participants (N = 26) was assigned to the control condition. These participants did not perform the task on Day 2 and were tested with the distractor in a single block of trials on Day 3. Each block of trials was preceded by the gaze calibration procedure. On Day 1, before the beginning of the experiment, participants performed 20 trials of practice to familiarize with the task, and in which the distractor was never presented.

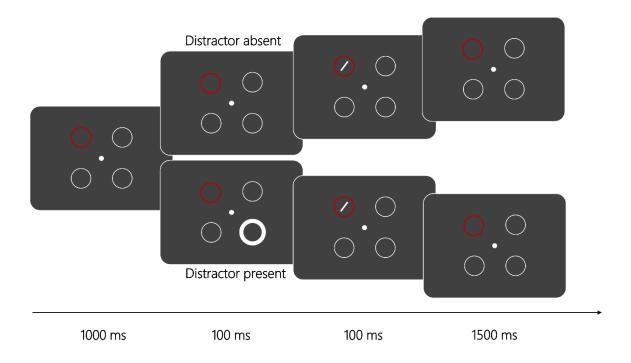


Figure 6. Schematic representation of the main events of Experiment 4. The distractor (the bright annulus, here in the down-right corner) appeared on 50% of the trials, and the target was a tilted line that always appeared inside the red circle, which served as a spatial cue. During Day 2 and for the first four blocks of Day 3, the *Extinction group* performed the task without the distractor (see Methods for details).

3.2.1.4 Data analysis

For each participant, data on correct response trials were trimmed for RTs shorter than 150 ms (anticipations) or longer than 1,000 ms. In all experiments, errors were < 2% in each block and were not analyzed further, whereas the outlier-latency criterion removed less than 2% of the data. Attentional capture elicited by the distractor was defined as the RT difference between distractor-present and distractor-absent trials. A statistically reliable positive difference thus indicates that the distractor interfered with target processing by capturing visual attention.

3.2.2 Results and discussion

To being with, RTs on correct trials of Day 1 (for all participants, N = 52) were entered into an ANOVA for repeated measures with onset (present vs. absent) and block as factors. The factor Onset F(1, 51) = 26.500, p < .001, $\eta^2_p = 0.342$, Block, F(4, 204) =24.712, p < .001, $\eta^2_p = 0.326$, and the Onset × Block interaction, F(4, 204) = 9.325, p < .001.001, $\eta^2_p = 0.155$, were significant. Figure 7 depicts the amount of capture defined as the RT differences between onset-present trials and onset-absent trials, as a function of block, and shows that, in agreement with the habituation hypothesis, the attentional capture response triggered by the onset decreased with practice. This was confirmed by pairwise comparisons (t test, two tails) showing that the amount of capture decreased significantly between Block 1 (M = 21 ms, SD = 3) and Block 5 (M = 4 ms, SD = 2; p < .001). Actually, habituation of the attentional response triggered by the onset was robust enough to make participants fully immune to distraction in the last two blocks of trials, as attested by the fact that the amount of capture did not differ from zero in Blocks 4 and 5 (all p > .1). The next crucial question was whether the attentional capture response recovered at test on Day 3, as a function of whether, before the test, participants were exposed to the context without the distractor (extinction condition) or not (control condition). To this aim, I first analyzed the amount of capture for the group of participants assigned to the control condition. The results at test (see Figure 7) clearly showed that there was no sign of spontaneous recovery of capture. RTs on Day 3 (M = -2ms, SD = 4) were significantly different from those in Block 1 of Day 1 (p = .001) and did not differ from those in Block 5 of Day 1 (p = .546). Conversely, for participants assigned to the extinction condition, the results at test showed a spontaneous recovery of capture

(see Figure 7). RTs on Day 3 (M = 18 ms, SD = 5) were significantly different from RTs in Block 5 of Day 1 (p < .001) but did not differ from RTs in Block 1 of Day 1 (p = .634).

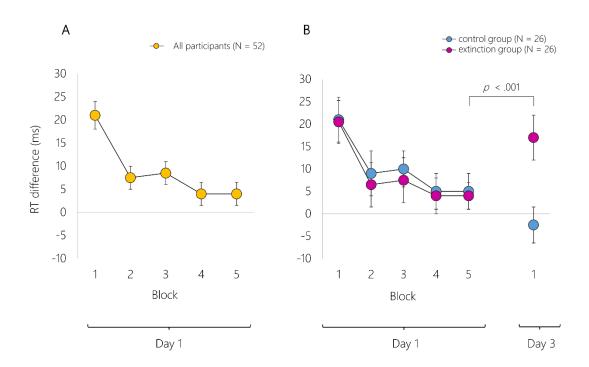


Figure 7. Results of Experiment 4. **Panel A.** Habituation of attentional capture (Day 1) across blocks of training for the group of 52 participants. **Panel B.** Habituation (Day 1) and spontaneous recovery of capture at test (Day 3) as a function of group. The control group (in blue, N = 26) did not perform the task on Day 2, and was directly tested on Day 3. The extinction group (in purple, N = 26) performed the task without the distractor on Day 2 and in the first four blocks of trials of Day 3, and was tested with the distractor in the last block of Day 3. Bars represent ± 1 *SEM*.

By showing recovery of capture only in the extinction condition, the results suggest that habituation of capture was context specific and that the neural model representing the distractor onset contained also contextual information (Wagner, 1979).

However, in in this experiment evidence of context-specific habituation was obtained from the phenomenon of extinction of the habituated response (for analogous results in different animal species see, Jordan et al., 2000; Rankin, 2000), not by a direct change of the context in which the distractor appeared in the training and test phases. For this reason, a second experiment was conducted, where the context in which the distractor appeared in the training (Day 1) and test (Day 2) sessions was directly changed.

3.3 Experiment 5

In the present experiment, participants had to discriminate a visual target with fully focused attention at a 100% valid cued location, while the distractor was occasionally presented (on 50% of trials) in one of three remaining possible locations. To evaluate the associative nature of habituation of capture, the context in which the target and the distractor appeared was defined by the background image. Despite in the present and in the following experiment the task was the same as Experiment 4, the paradigm was slightly different. In Experiment 4 the context was defined by the experimental display (namely by the placeholders), but here, to emphasize our manipulation, the context had to be defined only (or mainly) by the background image. For this reason, the display was composed by a single disk that served as a cue (and not by four placeholders, one of which was a cue, as in Experiment 4).

On Day 1, participants performed a focused attention task while being exposed for five blocks of trials to a peripheral sudden onset distractor (50% probability) in the same training context. Then, on Day 2 (the following day), participants performed a single block of trials in the test context: for half of them (same-context group) the context was the same of Day 1, whereas for the remaining (different context group) the context

changed (see Figure 8). Here, the context was defined by the background image associated with the target and the distractor (see Figure 9). Two naturalistic images were used, one depicting a countryside landscape, and one depicting an industrial landscape. The images defining the training and test contexts were counterbalanced across participants. On the basis of the results of Experiment 4 and in agreement with the Wagner's (1976) model, I expected capture to habituate in the first day of training and, crucially, on Day 2 to recover in the different-context group (when the background image was changed), but not in the same-context group.

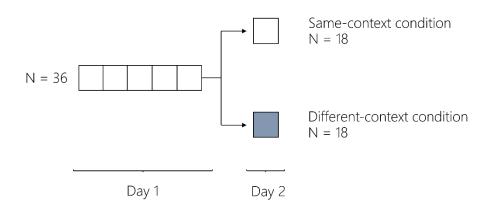


Figure 8. Each square represents a block of 100 trials. On Day 1 all participants performed the discrimination task with the same context (defined by the background image). On Day 2, participants were divided in two groups: the same-context group (white square of Day 2) maintained the same context, while for the different-context group (grey square of Day 2) the context was changed.

3.3.1 Methods

3.3.1.1 Participants

Thirty-six undergraduate students (28 female; mean age = 22.4 years) of the University of Trento were recruited from the Department of Psychology for course credits or monetary compensation ($6 \in$). They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiment. Informed consent was obtained from all participants. All the experiments were carried out in accordance with the Declaration of Helsinki, and with the approval of the local institutional ethics committee (Comitato Etico per la Sperimentazione con l'Essere Umano, Università degli Studi di Trento, Italy).

3.3.1.2 Apparatus

As in Experiment 4.

3.3.1.3 Stimuli and procedures

Each trial started with the presentation for 1,000 ms of a black central fixation point (0.07 cd/m²) together with a black disk (0.07 cd/m², diameter of 2°) positioned at one corner of an imaginary square (diagonal of 14.5°) centered on the fixation point. The black disk served as cue to indicate the position of the upcoming target. The position of the cue was randomly assigned on each trial. On distractor-present trials (50% of trials), 100 ms before the target occurrence a high-luminance white annulus frame (inner diameter of 2°, outer diameter of 2.5°, 74.4 cd/m²) appeared for 100 ms in one of the three remaining corners of the imaginary square, thus creating a sudden visual onset distractor (see Figure 9, panel A). The distractor position relative to the target position was balanced across trials. The key feature of the experimental design was the background image over which the target and the distractor were presented during the

training and the test phase, which consisted of a black-and-white full screen picture depicting either a countryside landscape or an industrial landscape. The two images of equal brightness (0.5 cd/m²) were counterbalanced across participants, who were instructed to maintain fixation on the central point while focusing their attention exclusively on the cue (the black disk). The task was to report as fast as possible the orientation (left vs. right) of a light-grey target line (42 cd/m²) by pressing the corresponding arrow on the computer keyboard. The target line was tilted 45° either to the left or to the right, and was presented within the black disk for 100 ms. RTs were recorded from the target appearance, and the maximum time allowed for responding was 1,500 ms. Trials in which participants did not respond within this time window were excluded from the analysis (<1% in total). Error feedbacks were provided by a message presented on the screen for 500 ms at the end of the trial. When an eye movement or a blink was detected in the first 500 ms of the trial, the trial was aborted and restarted. If an eye movement was detected during the presentation of either the distractor or the target, an error message appeared on the screen, and the trial was discarded from the analyses. For the same-context group (N = 18) the background image remained the same in the training and the test phase, whereas for the different-context group (N = 18) the background image changed between the two phases. On both Day 1 and Day 2, before the beginning of the experimental session participants performed 10 practice trials without the distractor to familiarize with the task in the assigned context. After the practice trials, on Day 1 participants were submitted to five blocks of 100 trials each, whereas on Day 2 they just performed a single block of 100 trials.

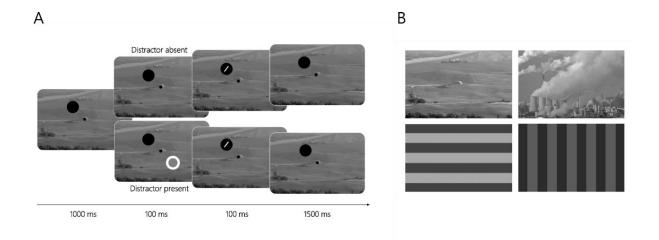


Figure 9. Panel A. Schematic representation of the trial events in Experiments 5 and 6. The cue (black disk) and the distractor (white annulus) appeared superimposed on a background image. In the training phase (Day 1) of Experiment 5 the background image consisted either of a countryside landscape (as in the example) or of an industrial landscape (see Panel B). In the test phase (Day 2), for the same-context group the background image remained the same, whereas for the different-context group the background image changed from the countryside to the industrial landscape (or vice-versa, see methods for details). In Experiment 6, the image of the background was either a series of vertically-alternated yellow and blue stripes, or a series of horizontally-alternated red and green stripes (see Panel B). Panel B. The top images were used as background in Experiment 5, whereas the bottom images were used as background in Experiment 5.

3.3.1.4 Data analysis

As in Experiment 4. Trials with eye movements (<2%) and incorrect responses (<3%) were discarded prior to the analyses on RTs, whereas RTs shorter than 200 ms or longer than 1,000 ms were treated as outliers and removed from the analyses (<1%).

3.3.2 Results and discussion

As a first step, I analyzed the time course of attentional capture during the training phase (Day 1). RTs for all participants (N = 36) on correct trials were entered into an ANOVA for repeated measures with Distractor (two levels, present vs. absent) and Block (five levels) as factors. The factor Distractor, F(1, 35) = 36.538, p < .001, $\eta^2_p = .511$, Block, F(4, 140) = 13.461, p < .001, $\eta^2_p = .278$, and the Distractor × Block interaction, F(4, 140)= 7.933, p < .001, $\eta^2_p = .185$, were significant. Figure 10 (panel A) depicts the amount of capture defined as the RT difference between distractor present trials and distractorabsent trials as a function of block, and shows that, in agreement with the habituation hypothesis, the attentional capture response decreases across blocks, thus confirming our previous findings (Turatto & Pascucci, 2016; Turatto et al., 2018). Pairwise comparisons (t test, two tails) showed that the amount of capture decreased significantly between Block 1 (M = 32 ms) and Block 5 (M = 13 ms; t(35) = 4.577, p < .001, d = 0.76). This pattern of results was confirmed also when the same analyses were conducted separately for the two groups of participants (see Figure 10, panel B). In the same-context group (N = 18), the ANOVA showed a significant effect of Distractor, F(1, 17) = 12.870, p= .002, η^2_p = .431, Block, F(4, 68) = 4.956, p = .001, η^2_p = .226, and a significant Distractor \times Block interaction, F(4, 68) = 2.876, p = .029, $\eta^2_p = .145$. Habituation of capture was significant between Block 1 (M = 31 ms) and Block 5 (M = 17 ms; t(17) = 2.166, p = .045, d = 0.48). In the different context group (N = 18), the ANOVA showed a significant effect of Distractor, F(1, 17) = 26.187, p < .001, $\eta^2_p = .606$, Block, F(4, 68) = 11.524, p < .001, η^2_p = .404, and a significant Distractor × Block interaction, F(4, 68) = 7.683, p < .001, $\eta^2_p =$

.311. Habituation of capture was significant between Block 1 (M = 34 ms) and Block 5 (M = 9 ms; t(17) = 4.519, p < .001, d = 1.07).

The next crucial question was whether in the test phase attentional capture recovered when participants were exposed to the same distractor but in a different context. Since habituation tends to be more rapid after each response recovery (Rankin et al., 2009; Thompson, 2009; Thompson & Spencer, 1966), to evaluate the dynamic of the recovery of attentional capture in the test phase (Day 2) RTs were analyzed by subdividing the single block of trials into 5 sub-blocks of 20 trials each (10 distractorpresent trials and 10 distractor-absent trials; see Figure 10, panel C). For each condition, RTs were entered into an ANOVA for repeated measures with Distractor (two levels) and Sub-Block (five levels) as factors. In the same-context group, the analysis resulted in a significant effect of Distractor, F(1, 17) = 10.605, p = .005, $\eta^2_p = .384$, but in a nonsignificant effect of Sub-Block, F(4, 68) = .361, p = .835, $\eta^2_p = .021$, and in a non-significant Distractor × Block interaction, F(4,68) = 1.988, p = .106, $\eta^2_p = .105$. This pattern of results showed that when the context remained the same, in the test phase the amount of capture did not change significantly across sub-blocks. Furthermore, the difference between the amount of capture in the last block of the training phase (M = 17 ms) and in the first subblock of the test phase (M = 21 ms; t(17) = -.330, p = .746, d = 0.09) was not significant, which indicates that habituation of capture persisted from Day 1 to Day 2, with no sign of recovery. In the different-context group, instead, the factor Distractor, F(1, 17) =44.720, p < .001, $\eta^2_p = .725$, and the Distractor × Block interaction, F(4, 68) = 4.513, p = .001.003, η^2_p = .210, were significant, whereas the factor Sub-Block only approached significance, F(4, 68) = 2.397, p = .059, $\eta^2_p = .124$. Crucially, in the first subblock of the

test phase participants were significantly slower (M = 43 ms) than in the last block of the training phase (M = 9 ms; t(17) = -5.20, p < .001, d = 1.21). In addition, RTs in the first sub-block of the test phase (M = 43 ms) were statistically indistinguishable from RTs in the first block of the training phase (M = 34 ms; t(17) = 1.541, p = .142, d = 0.37). This pattern of results indicates that the attentional capture response recovered completely when the distractor experienced during the training phase was presented in a new context, a result in agreement with the prediction of the Wagner model (1976, 1978, 1979), and that confirms the associative nature of habituation of capture with respect to the context in which it takes place (see Table 1).

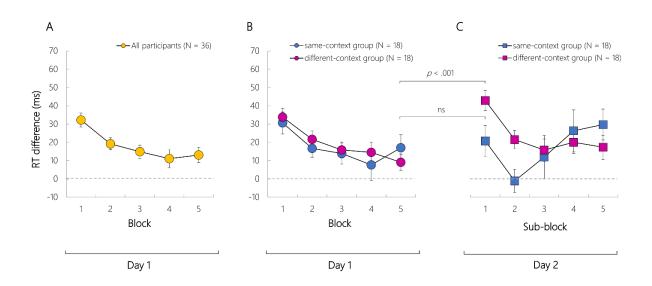


Figure 10. Results of Experiment 5. **Panel A.** Habituation of attentional capture as a function of block in the training phase (Day 1), for the group of 36 participants. **Panel B.** Habituation of attentional capture as a function of block in the training phase (Day 1), depicted separately for the same-context (in blue) and the different-context (in purple) groups. **Panel C.** Attentional capture as a function of sub-block in the test phase (Day 2), depicted separately for the same-context and the different-context groups. As compared to the last block of Day 1, the different-context group shows a significant recovery of capture,

which then rapidly habituates in the following sub blocks. No recovery of capture is evident in the same-context group. Bars represent \pm 1 SEM.

Same-context group

			Day 1					Day 2			
			Block			Sub-block					
•	1	2	3	4	5	1	2	3	4	5	
Distractor	409	396	387	384	373	357	362	354	349	353	
absent	(130)	(99)	(96)	(110)	(78)	(111)	(112)	(79)	(77)	(79)	
Distractor	440	413	401	392	391	378	361	366	375	383	
present	(138)	(94)	(98)	(88)	(76)	(109)	(91)	(99)	(96)	(79)	

Different-context group

			Day 1			Day 2 Sub-block					
			Block								
_	1	2	3	4	5	1	2	3	4	5	
Distractor absent	365 (86)	351 (74)	343 (62)	340 (66)	343 (68)	299 (46)	303 (47)	314 (53)	316 (52)	322 (54)	
Distractor present	399 (95)	373 (79)	359 (69)	355 (68)	352 (66)	342 (56)	325 (47)	330 (57)	336 (58)	339 (56)	

Table 1. Mean RTs and SD (in parenthesis) for correct trials in Experiment 5. On Day 1 each block consisted of 100 trials, whereas on Day 2 there was a single block of 100 trials, and each sub-block consisted of 20 trials.

3.4 Experiment 6

In Experiment 5, context-specific habituation of capture emerged when, in the test phase, the distractor was presented in a new context, thus suggesting that during the training phase associations were formed between the context and the distractor

representations (Wagner, 1976, 1978, 1979). One may wonder, however, to what extent such associations were favored by the realistic/ecological nature of the context images used in Experiment 5, or conversely, whether the associative learning process linking together context and distractor is so mandatory to operate also when the context is defined by images with minimal semantic/ecological contents. To address this issue, in the present experiment the background image was defined by simple geometrical shapes consisting either of a series of alternated red/green horizontal bars, or of a series of alternated yellow/blue vertical bars (see Figure 9, panel B).

3.4.1 Methods

3.4.1.1 Participants

Thirty-six undergraduate students (25 female; mean age = 20.0 years) of the University of Trento were recruited from the Department of Psychology for course credits or monetary compensation (6 \in). They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiment. Informed consent was obtained from all participants. All the experiments were carried out in accordance with the Declaration of Helsinki, and with the approval of the local institutional ethics committee (Comitato Etico per la Sperimentazione con l'Essere Umano, Università degli Studi di Trento, Italy).

3.4.1.2 Apparatus

As in Experiment 5.

3.4.1.3 Stimuli and procedures

The task and experimental design were the same as Experiment 5, with a single exception: here the context was defined by a background consisting either of vertically alternated yellow (1.35 cd/m²) and blue (0.82 cd/m²) bars, or of horizontally alternated red (0.62 cd/m²) and green (1.33 cd/m²) bars (see Figure 9, panel B). The type of background of the training and the test phase was counterbalanced across participants.

3.4.1.4 Data analysis

As in Experiment 5. Trials with eye movements (<2%) and incorrect responses (<3%) were discarded prior to the analyses on RTs, whereas RTs shorter than 200 ms or longer than 1,000 ms were treated as outliers and removed from the analyses (<1%).

3.4.2 Results and discussion

First, I analyzed the time course of attentional capture during the training session (Day 1). The RTs for all participants (N=36) on correct trials were entered into an ANOVA for repeated measures with Distractor (two levels, present vs. absent) and Block (five levels) as factors. The factor Distractor, F(1,35)=77.954, p<.001, $\eta^2_p=.690$, Block, F(4,140)=18.435, p<.001, $\eta^2_p=.345$, and the Distractor × Block interaction, F(4,140)=7.510, p<.001, $\eta^2_p=.177$, were all significant. As shown in Figure 11, panel A, capture habituated over the course of training, and pairwise comparisons (t test, two tails) confirmed that the amount of capture decreased significantly between Block 1 (M=40 ms) and Block 5 (M=20 ms; t(35)=4.465, p<.001, d=0.74). This conclusion was confirmed also when the same analyses were conducted separately for the two groups of participants (see Figure 11, panel B). In the same-context group (N=18), the ANOVA showed a significant effect of Distractor, F(1,17)=27.584, p<.001, $\eta^2_p=.619$, Block, F(4,17)

68) = 15.732, p < .001, $\eta^2_p = .481$, and a significant Distractor × Block interaction, F(4, 68)= 3.575, p = .011, η^2_p = .174. Habituation of capture was significant between Block 1 (M = 39 ms) and Block 5 (M = 20 ms; t(17) = 2.347, p = .031, d = 0.64). Analogously, in the different-context group (N = 18), the ANOVA showed a significant effect of Distractor, F(1, 17) = 59.88, p < .001, $\eta^2_p = .779$, Block, F(4, 68) = 5.918, p < .001, $\eta^2_p = .258$, and a significant Distractor × Block interaction, F(4, 68) = 4.866, p = .002, $\eta^2_p = .223$. Habituation of capture was reliable between Block 1 (M = 41 ms) and Block 5 (M = 20 ms; t(17) = 4.931, p < .001, d = 0.93). As in Experiment 5, I addressed whether in the test phase the attentional capture response recovered when participants were exposed to a different context. In the same-context group, the sub-blocks analysis on Day 2 revealed a significant effect of Distractor, F(1, 17) = 32.747, p < .001, $\eta^2_p = .658$, but a non-significant effect of Sub-Block, F(4, 68) = .418, p = .795, $\eta^2_p = .024$, and a non-significant Distractor × Block interaction, F(4, 68) = .141, p = .996, $\eta_p^2 = .008$. This pattern of results shows that when the training and test phase shared the same context, in the test phase the amount of capture did not change significantly across sub-blocks. Furthermore, no significant difference in the amount of capture was found between the last block of the training phase (M = 20 ms) and the first sub-block of the test phase (M = 20ms; t(17) = .024, p = .024.981, d = 0.007), thus showing no sign of recovery of capture in Day 2 (see Figure 11, panel C). In the different-context group, instead, the factor Distractor, F(1, 17) = 63.053, p < .001, $\eta^2_p = .788$, and the Distractor × Block interaction, F(4, 68) = 4.213, p = .004, η^2_p = .055, were significant, whereas the factor Sub-Block was not significant, F(4,68) = .986, p = .421, $\eta^2_p = .199$. Crucially, in the first sub-block of the test phase participants were significantly slower (M = 41 ms) than in the last block of the training phase (M = 20 ms;

t(17) = -3.966, p = .001, d = 0.94), thus revealing a reliable recovery of capture in the new context (see Figure 11, panel C), a result that replicated what I found in Experiment 5. Furthermore, the amount of recovery was complete, as attested by the fact that the RTs in the first sub-block of the test phase (M = 41 ms) were identical to the RTs in the first block of the training phase (M = 41 ms; t(17) = .009, p = .993, d = 0.02) (see Table 2).

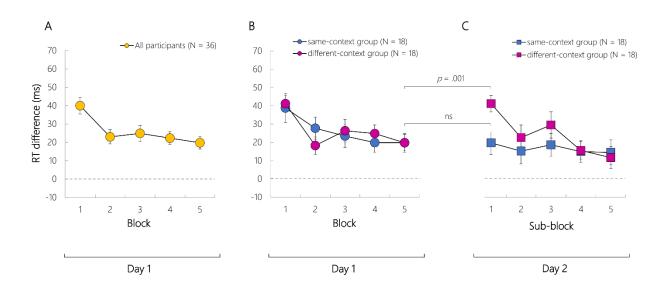


Figure 11. Results of Experiment 6. Panel A. Habituation of attentional capture as a function of block in the training phase (Day 1), for the group of 36 participants. Panel B. Habituation of attentional capture as a function of block in the training phase (Day 1), depicted separately for the same-context (in blue) and the different-context (in purple) groups. Panel C. Attentional capture as a function of sub-block in the test phase (Day 2), depicted separately for the same-context and the different-context groups. As compared to the last block of Day 1, the different-context group shows a significant recovery of capture, which then rapidly habituates in the following sub blocks. No recovery of capture is evident in the same-context group. Bars represent ± 1 SEM.

Same-context group

			Day 1			Day 2 Sub-block					
			Block								
_	1	2	3	4	5	1	2	3	4	5	
Distractor	503	493	484	473	466	426	434	433	432	437	
absent	(65)	(73)	(71)	(78)	(68)	(54)	(57)	(57)	(56)	(50)	
Distractor	541	521	507	493	486	446	449	452	447	451	
present	(66)	(72)	(66)	(69)	(71)	(46)	(51)	(58)	(42)	(57)	

Different-context group

			Day 1					Day 2			
			Block			Sub-block					
_	1	2	3	4	5	1	2	3	4	5	
Distractor	473	462	451	452	450	415	422	426	430	439	
absent	(82)	(77)	(74)	(70)	(72)	(60)	(48)	(66)	(62)	(70)	
Distractor	514	480	477	476	470	456	444	455	445	450	
present	(82)	(71)	(86)	(70)	(75)	(69)	(63)	(64)	(65)	(74)	

Table 2. Mean RTs and SD (in parenthesis) for correct trials in Experiment 6. On Day 1 each block consisted of 100 trials, whereas on Day 2 there was a single block of 100 trials, and each sub-block consisted of 20 trials.

3.5 General discussion

The results of the three experiments (Experiments 4, 5 and 6) were consistent and clear-cut, showing that, as exposure to the same onset distractor continues, attentional capture is subject to habituation and that the capture decrement is context-specific. The specificity of habituation for a given context was tested both indirectly, through the extinction procedure (Experiment 4), and directly, by actually changing the context (Experiments 5 and 6).

Although the results find a straightforward explanation in the Wagner's (1979) model, an alternative explanation must be carefully considered and ruled out, especially concerning Experiments 5 and 6. The prolonged exposure to the same background during the training phase, resulted in a salience loss of the corresponding image, which progressively favored the focusing of attention onto the cued location, and this would explain why the distractor interference diminished with practice. However, the introduction of a new background in the test phase led to an increment of the salience, due to its novelty; it then became more difficult for the participants to focus their attention on the cued location, so that they became more prone to attentional capture by the onset distractor. On the contrary, when the background did not change across the training and the test phase, this problem did not occur. Yet, if the background change caused the recovery of capture because its renewed saliency made it more difficult to remain focused on the cued location, then this disrupting effect on the focusing of attention should be evident also on distractor-absent trials, because also in this condition, by hypothesis, the renewed background saliency diminished the participants' ability to remain optimally focused on the cue. Hence, in the different-context group RTs for target discrimination should increase from the last block of Day 1 to the first subblock of Day 2 also in the absence of the distractor. To test this straightforward prediction, I compared RTs on distractor-absent trials before and after the background change, but I did not find evidence of a slowing down in the participants' response speed. On the contrary, if anything, in both experiments RTs in the first sub-block of Day 2 were shorter than in the last block of Day 1 (Experiment 5, before change M = 343 ms, after change M = 299 ms; t(17) = 5.149, p < .001, d = 0.69; Experiment 6, before change M = 0.69

450 ms, after change M = 415 ms; t(17) = 5.029, p < .001, d = 0.5) (see Tables 1 and 2). On the basis of this pattern of results the abovementioned alternative hypothesis can reasonably be dismissed, and the context specificity of habituation of capture can be considered as the most parsimonious and plausible explanation for the present findings.

The recovery of capture in the test phase emerges from the comparison of RTs in the last block of Day 1, consisting of 100 trials, with the first sub-block of Day 2, consisting of 20 trials. In the same vein, the extent of recovery is evaluated by comparing RTs in the first block of Day 1 (100 trials), with the first sub-block of Day 2 (20 trials). In order to rule out the possibility that statistical comparisons based on unequal numbers of trials might have affected the results, data were re-analyzed using the same number of trials (20) in each of the critical conditions. Hence, the first and last block of Day 1 have been split into five sub-blocks of 20 trials each. The results confirmed those emerged from the previous analyses, showing that when the context changed (different-context group) RTs in the first sub-block of Day 2 were longer than in the last sub-block of Day 1 (Experiment 5, t(17) = -3.578, p = .002, d = 0.98; Experiment 6, t(17) = -5.541, p < .001, d = 1.31), but did not differ from those of the first sub-block of Day 1 (Experiment 5, t(17) = .384, p =.706, d = 0.17; Experiment 6, t(17) = .486, p = .663, d = 0.14). Conversely, when the context did not change (same-context group), RTs in the first subblock of Day 2 were comparable to those in the last sub-block of Day 1 (Experiment 5, t(17) = -.422, p = .678, d = 0.14; Experiment 6, t(17) = -.027, p = .979, d = 0.03), but were longer than those in the first subblock of Day 1 (the difference only approached significance in Experiment 5, t(17) =1.847, p = .082, d = 0.5; Experiment 6, t(17) = 5.539, p < .001, d = 1.19). In Experiment 4 it was not necessary to split the test block (Day 3) into smaller sub-blocks, because the amount of spontaneous recovery in the extinction condition was strong enough to be detected considering the whole block of trials; the reason probably lies in the time elapsed between the end of the training session and the beginning of the test session (48 hours in Experiment 4, vs. 24 hours in Experiments 5 and 6), which might have favored a very strong spontaneous recovery.

Since habituation reflects a learning mechanism for rejecting the irrelevant stimuli, and because it can be context specific, it is questionable what is exactly learned during the exposure to the distractor. To shed light on this lawful question, it becomes necessary to recall two of the most important theories of habituation, originally proposed by Sokolov (1963) and Wagner (1976). Both theories predict that in the present paradigm the observers learned, directly or indirectly, to reduce the orienting response evoked by the distractor, although the two theories may slightly differ in the specific mechanism leading to habituation of attentional capture, and in the role of context. According to Sokolov (1963), following the repeated exposure to the distractor, a corresponding memory trace or neural model was progressively formed, and suppression of the attentional orienting became increasingly stronger the more the distractor matches the model. Despite this theory does not explicitly predict that habituation could be context specific, it is not difficult to imagine that the neural model used for comparing the incoming sensory input incorporated also contextual information. The theory proposed by Wagner (1976), instead, specifically claims that habituation is associative in nature, and invokes an explicit role of both short-term (STM) and long-term memory (LTM) in this form of behavioral plasticity. The key notion is that the efficacy with which a stimulus activates further cognitive processes, including an

unconditioned response, highly depends on whether or not the stimulus is prerepresented (i.e., primed) in STM. More specifically, the model postulates that a novel and salient stimulus attracts focused attention, thus entering a primary attentional state that promotes the unconditioned response (here the orienting response triggered by the distractor). This attentive stimulus representation decays rapidly, but at the same time a STM representation of the stimulus is formed. Crucially, if the stimulus is primed in STM it prevents another presentation of the same stimulus to enter the primary attentional state, thus forming the basis for short-term habituation. However, a stimulus can be active in STM also because its representation is retrieved from LTM on the basis of cues with which the stimulus has been associated during its past occurrences. For example, when a stimulus is repeatedly presented in a given context, long-term associations are formed between the two representations. Thus, long-term context-specific habituation takes place because the context acts like a cue triggering retrieval of the stimulus representation in STM, and thus decreasing the attentional capture response elicited by the stimulus. The Wagner's theory thus proposes an elegant model to explain both shortand long-term habituation, and predicts that the latter should be context specific.

Following Wagner's theory, one can therefore assume that with practice associations were formed in LTM between the context and the distractor information, and that such long-term relational memories affected habituation. Given this scenario, the results of the current study appear to be in general agreement with theories of control and automaticity, and with the idea that with training performance becomes to be controlled by LTM representations of the task and its context (Logan, 1988; Schneider & Shiffrin, 1977; Shiffrin & Schneider, 1977). More specifically, previous studies have

shown that, with practice, long-term relational information can control the deployment of attention toward the relevant part of the scene (Chun, 2000; Hannula & Ranganath, 2009). For example, the efficiency of attentional guidance during visual search largely improves when, across blocks, participants implicitly learn that the spatial context defined by the distractors configuration is predictive of the target location, as demonstrated by the contextual-cueing effect (Chun, 2000; Chun & Jiang, 1998). However, the effect of context documented in the current study is quite different, since the background image was completely irrelevant to find the target, because its location was cued with no uncertainty on each trial. However, since the four possible distractor locations were fixed, it is likely that associations were formed in LTM between the distractor features, including its possible spatial coordinates, and the context, which favored habituation of attention. These long-term associations were probably at least partially lost when the context changed, thus favoring the recovery of capture.

The context manipulation implemented in the current work is similar to the one adopted in the study of Cosman and Vecera (2013), in which the search array was presented superimposed on photographs of either forests or city streets. During training, participants searched for the target among distractors adopting either a singleton-detection mode or a feature-search mode (in separate blocks of trials); however, each search mode was paired with a given background image. Then, in the test phase the search array allowed participants to use either search modes to find the target, although the feature search mode was much more effective in protecting from distractor interference (Bacon & Egeth, 1994). Crucially, on each trial the search array was randomly embedded in either the street scene or the forest scene. The results showed

that the singleton distractor captured attention when presented in the context paired, during training, with the singleton-detection mode, but failed to capture attention when presented in the context previously paired with the feature search mode. This suggests that the search mode used in a given context during training was automatically activated by the same context when encountered in the test phase. The authors concluded that learned associations between a given attentional set and contextual information can determine how the attentional system operates in a specific context (Cosman & Vecera, 2013). Hence, contextual information can implicitly affect the possibility to overcome distraction by controlling the associated attentional set used to locate the target. By contrast, in the experiments presented in this chapter the context did not affect the attentional search set, as no visual search was required given that, because of the 100% valid cue, on each trial attention was fully focused on the target location. Rather, with practice associations were formed in LTM between the distractor and the surrounding context, leading to context-specific habituation of capture. The results thus suggest that with practice the context can also regulate the cognitive set (or neural model) for the task-irrelevant information, as postulated by the stimulus-model comparator theory (Sokolov, 1963; also see, Cowan, 1988; Gati & Ben-Shakhar, 1990; Ramaswami, 2014; Waters et al., 1977).

Although habituation of capture seems to be context specific, one may wonder to what extent, under the appropriate conditions, habituation could instead generalize across different contexts. Two reasons may suggest this possibility. The first, most obvious one, is that habituation is often regulated by a non-associative learning process, and therefore it could naturally generalize across different contexts (Marlin & Miller,

1981), though it was shown that for the attentional capture response this is not the case. The second more interesting possibility is suggested by the results of a recent study from Vatterott, Mozer, and Vecera (2018). The authors have found that observers can generalize learned distractor rejection to novel distractors if during the learning phase they are exposed, in different blocks, to different types of salient distractors (variable stimulus environment) than to a single type of distractor in all blocks (homogeneous stimulus environment; see Stilwell & Vecera, 2019 for a similar result).

To conclude, the results of the current chapter indicate that habituation of attentional capture is associative in nature, and more specifically that distractors rejection achieved via habituation mechanisms is context-specific, a result that is in agreement with the prediction of Wagner (1976, 1978, 1979), and with animal studies showing context-specific habituation of different overt behavioral responses (e.g., Chiandetti & Turatto, 2017; Jordan et al., 2000; Rankin, 2000; Tomsic et al., 1998).

Habituation in the oculomotor system

All the material in this chapter has been (or will be) published in the following papers:

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), 264-284.

Bonetti, F., & Turatto, M. (2019). Microsaccades reveal that habituation affects the execution but not the programming of saccadic eye movements. *In preparation*.

4.1 Introduction

Onset stimuli that abruptly appear in the visual field usually signal the occurrence of new objects. To rapidly detect such potentially relevant events, the human visual system is equipped with hard-wired mechanisms that make it sensitive to sudden luminance changes (Breitmeyer & Ganz, 1976), triggering an automatic orienting of attention toward sudden onsets (Boot, Kramer, & Peterson, 2005; Folk & Remington, 2015; Jonides & Yantis, 1988; Schreij, Owens, & Theeuwes, 2008; Yantis & Jonides, 1984, 1996).

However, because of the strong anatomical and functional links between attention and the oculomotor system (e.g., de Haan, Morgan, & Rorden, 2008; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Peterson, Kramer, & Irwin, 2004; Rizzolatti, Riggio,

Dascola, & Umiltá, 1987; Sheliga, Riggio, & Rizzolatti, 1994), and because spatial attention plays an important role in the generation of saccadic eye-movements (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Peterson et al., 2004), onset stimuli attract also our gaze, a phenomenon known as *oculomotor capture* (Irwin, Colcombe, Kramer, & Hahn, 2000; Ludwig, Ranson, & Gilchrist, 2008; Theeuwes et al., 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Therefore, attentional and oculomotor capture are two important reflexive responses that, by interrupting the current goal-directed behavior, allow the organism to give immediate priority of analysis to potentially relevant stimuli. However, when sudden onsets carrying no motivational significance for the organism are repeatedly encountered, it would be advantageous for the brain to have some mechanism to reduce, or even eliminate, the continuous attention and oculomotor distraction triggered by such irrelevant stimulation.

As already discussed in the first chapter of the thesis, different cognitive mechanisms for distractor filtering have been proposed. One prominent view suggests that distraction can be counteracted by means of a strategic top-down control (Awh, Matsukura, & Serences, 2003; Geng, 2014), which can be implemented either by adopting a top-down attentional set tuned on the target stimulus features (Bacon & Egeth, 1994; Leber & Egeth, 2006) or by directly applying a top-down inhibitory signal on distractors (Dixon et al., 2009; Marini et al., 2013; Müller et al., 2007). Alternatively, the reduction of attentional and oculomotor capture as a function of the repeated exposure to the same stimulus may also be seen as an instance of the more general phenomenon of habituation.

The role of habituation in attention-related phenomena has also been highlighted by Dukewich (2009), who argued that habituation may be involved in the inhibition of

return (IOR) effect, namely the fact that participants are typically slower at responding to a target when it is anticipated by another visual stimulus at the same location (Klein, 2000). Indeed, Dukewich and Boehnke (2008) found that IOR increased as a function of the number of cues presented at the same location of the target, and as a function of the cue repetition rate. Although different processes (attention-based, sensory-based and motor-based) contribute to the IOR effect (Lupiañez, Martín- Arévalo, & Chica, 2013), the results of Dukewich and Boehnke (2008) showed that the more the cue is presented at a given location, the less efficient is the processing of the target at that location, which suggests a role of habituation at the sensory or attentional level in the IOR.

In agreement with the view according to which attention and habituation are intimately related (Cowan, 1988), it was recently shown that the automatic capture of focused attention triggered by sudden peripheral visual onsets is subject to both short-term and long-term habituation (Pascucci & Turatto, 2015; Turatto & Pascucci, 2016; see also Neo & Chua, 2006) and that, as demonstrated in Chapter 3, this learning process can also be context specific (Turatto et al., 2018), thus revealing, in accordance with some previous studies on non-human animals (Chiandetti & Turatto, 2017; Rankin, 2000; Tomsic et al., 1998), that habituation can be associative in nature (Wagner, 1979). Furthermore, it seems plausible that a habituation-like mechanism can also account, at least to some extent, for the results of previous studies reporting a reduction of attentional capture as the exposure to the same distractor (onset or feature-singleton) continues across trials (e.g., Kelley & Yantis, 2009; Vatterott & Vecera, 2012; Vecera et al., 2014).

As for the possibility that also oculomotor capture by sudden visual onsets can be subject to habituation, the evidence is scant. In his original investigation of habituation of the OR, Sokolov measured how the different OR components (somatic, e.g., body, head, ears, and eye movements; autonomic, e.g., cardiovascular, galvanic, respiratory; encephalographic, e.g., α-rhythm desynchronization) changed as a function of exposure to the same stimulus. The Russian researcher reported that involuntary eye movements toward sudden tones and lights were the first response to habituate (Sokolov, 1960). Unfortunately, however, in these pioneering studies the saccadic response was detected only by means of the electromyographic activity of the extraocular muscles, so that important saccadic metrics currently used to investigate the oculomotor capture phenomenon (e.g., saccadic latency, endpoint location, and trajectory; Godijn & Theeuwes, 2002b; Theeuwes et al., 1998), were, to the best of my knowledge, not reported. In addition, as compared to the recent literature on oculomotor capture, Sokolov's research on habituation was mainly focused either on nonhuman animals, or on human participants who were only passively exposed to irrelevant visual/auditory stimulation, whereas nowadays it is more common to evaluate the distracting effect of an irrelevant stimulation when the observer is engaged in an active task.

However, more recently a study by Godijn and Kramer (2008) documented a progressively decrease in the rate of oculomotor capture triggered by a sudden peripheral onset when repeatedly presented during a saccadic task. According to the authors, since the distractor was not presented in the initial phase of the experiment (from Trial 1 to Trial 60), the participants' task set consisted only of the target and the nontarget elements, and no information about the distractor was included. When the

distractor was unexpectedly added to the display from Trial 61 onward, it initially captured the eyes because it was not part of the task set. An updating of the task set, which occurred after repeated presentation of the distractor, was needed to ignore the irrelevant stimulus, thus reducing the chances of making a saccade in its direction. Although the observed reduction of oculomotor capture triggered by the irrelevant onset distractor was not linked to a mechanism of habituation of the OR, in fact the interpretation offered by the authors seems to bear some clear similarities with the stimulus-model comparator theory proposed by Sokolov. In particular, the process of update of the task set to include the distractor information invoked by Godijn and Kramer (2008) appears to echoing the Sokolovian idea according to which the neural model of the world is continuously updated to include the new stimulation. The more the distractor is incorporated in the model, the more the OR triggered by the distractor is suppressed, and consequently the oculomotor capture vanishes with repeated exposure to the same irrelevant stimulus. It then becomes important to understand whether an oculomotor capture response decrement represents a case of habituation, or alternatively whether it can be ascribed to other peripheral or cognitive mechanisms.

As already pointed out in Chapter 1 (1.4.2), several studies have documented that habituation, irrespective of the type of response considered, usually presents some specific characteristics (Rankin et al., 2009; Thompson, 2009; Thompson & Spencer, 1966). Among the most prominent features are the phenomena of spontaneous recovery and dishabituation. *Spontaneous recovery* refers to the fact that if the repetitive stimulus is withheld the habituated response tends to recover; *dishabituation*, instead, is observed when a new stimulus is introduced after the response to the original stimulus has

habituated. Under these conditions, when the previous stimulus is reintroduced after the new one, the habituated response tends to return to the original level. Other important features of habituation are stimulus specificity (or, alternatively, generalization), and the fact that this form of learning is stimulation-frequency dependent, namely that it is affected by the rate of presentation of the stimuli, with more pronounced habituation the more rapid the frequency of stimulation. Finally, depending on the duration of the effects of training, habituation has both short-term and long-term components. Although the distinction between short- and long-term habituation on the basis of the duration of the effects of training can be quite arbitrary (Davis, 1970), the former usually refers to within-session effects, whereas the latter is observed when the response decrement persists for hours or days after the end of training (e.g., Castellucci, Carew, & Kandel, 1978; Ezzeddine & Glanzman, 2003; Rankin et al., 2009; Turatto et al., 2018; Turatto & Pascucci, 2016).

Therefore, the present chapter sought to systematically investigate whether the oculomotor capture triggered by sudden visual onsets is subject to habituation. To this aim, a modified version of the *oculomotor capture paradigm* (Godijn & Kramer, 2008) was adopted, in which participants, for 60 consecutive trials, had to make a saccade, as fast as possible, toward a target stimulus among non-target elements. Unexpectedly, from Trial 61 onward a salient onset distractor different in color was introduced with a certain frequency, depending on the experiment. To characterize the oculomotor behavior, both the saccadic endpoint location (i.e., whether it was directed toward the target or the distractor) and the saccadic latency were measured.

4.2 Experiment 7

The aim of Experiment 7 was to replicate previous findings showing that the oculomotor capture triggered by an onset distractor decreases as a function of repeated exposure to the irrelevant stimulus (Godijn & Kramer, 2008), and to investigate whether the decrement of oculomotor capture presents some specific features of the habituation phenomenon. Specifically, the paradigm was modified as to reveal short-term and longterm habituation, stimulus specificity, spontaneous recovery and dishabituation of the oculomotor capture. To this aim, participants performed a two-session experiment. The first session consisted of two identical blocks of 110 trials. In the first 60 trials of each block, the onset distractor was omitted, whereas it was unexpectedly introduced from Trial 61 onward. The repeated distractor appeared always in the same fixed position. To assess stimulus specificity and dishabituation, on Trial 91 the distractor changed, as it was presented in a different color (green vs. red or red vs. green, counterbalanced between participants) and in a different position (diametrically opposite to that of the original distractor). From Trial 92 onward, the original distractor was reintroduced. The second session consisted of a single block of 10 trials, in which the onset distractor was always presented, starting from Trial 1 (see Table 3 for a summary of the trial types).

4.2.1 Methods

4.2.1.1 Participants

Thirty undergraduate students (26 females; mean age = 21.5 years old) of the University of Trento were recruited from the Department of Psychology and Cognitive Sciences for course credits. They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiments. Informed consent was obtained from all

participants. All the experiments were carried out in accordance with the Declaration of Helsinki, and with the approval of the local institutional ethics committee (Comitato Etico per la Sperimentazione con l'Essere Umano, Universita` degli Studi di Trento, Italy).

4.2.1.2 Apparatus

Stimuli were presented on a 23.6-in. VIEWPixx/EEG color monitor (1920 x 1080, 100 Hz) and generated with a custom-made program written in MATLAB and the Psychophysics Toolbox (Pelli, 1997) running on a Dell Precision T1600 machine (Windows 7 Enterprise). Eye movements were monitored with an EyeLink 1000 Desktop Mount system (sampling rate: 1000 Hz; SR Research, Ontario, Canada). Each block was preceded by a nine-point calibration procedure, which was repeated during the block if participants' gaze drifts exceeded 1.5°.

4.2.1.3 Stimuli and procedures

Each trial started with the presentation of a gray fixation point (0.62 cd/m²) on a black background (0.07 cd/m²). After 500 ms, six equidistant gray circles (1.2° in diameter, 0.62 cd/m²) appeared on an imaginary circle with a radius of 4.6° centered around the fixation point. After 500 ms, the luminance of one of circles was increased (23.8 cd/m²), thus signaling the saccadic target, whose position was randomly assigned on each trial in four possible locations (at clock position 1, 5, 7 or 11). The task of the participants was to execute a saccade toward the target as fast and as accurate as possible. In the first 60 trials the distractor was omitted, whereas starting from Trial 61, an onset colored distractor was introduced on each of the remaining trials. The distractor was a colored circle (0.6° in radius) that appeared simultaneously with the target in a

fixed position for each subject (at clock position 2, 4, 8 or 10, counterbalanced between subjects). The color of the distractor could be either red or green (both 17 cd/m²), and the two colors were counterbalanced between participants, but for each participant both the distractor color and the distractor position remained fixed (see Figure 12). Participants were instructed to maintain their gaze on the central fixation point until the appearance of the target, and if a saccade was detected before the target occurrence, an error message appeared on the screen, and the trial was aborted and then represented. It was necessary to ensure that each saccade toward the target, or the distractor, started from the central fixation point. The experiment comprised two different daily sessions, carried out in two consecutive days. The first session (Day 1) consisted of two identical blocks of 110 trials each, for a total duration of 25 min. The second session (Day 2) consisted of one block of 10 trials, which lasted about 2 min. Each block of trials was preceded by a 9-point grid calibration procedure. Before the beginning of the experiment, in the first session, participants performed 10 trials of practice to familiarize with the task, and in which the distractor was never presented.

Experiment 7		
Distractor frequency – 100%. Distractor position – fixed.		
Blocks 1 and 2 (Session 1)	Trials 1-60	Distractor absent
	Trials 61-90	Distractor present (original distractor)
	Trial 91	Distractor present (new distractor)
	Trials 92-110	Distractor present (original distractor)
Block 1 (Session 2)	Trials 1-10	Distractor present (original distractor)
Experiment 8		
Distractor frequency – 100%. Distractor position – fixed.		
Block 1	Trials 1-60	Distractor absent
	Trials 61-90	Distractor present (original distractor)
	Trial 91	Distractor present (new distractor)
	Trials 92-110	Distractor present (original distractor)
ח ו ח	m: 1 4 60	District the state of the state
Block 2	Trials 1-60	Distractor absent
	Trials 61-70	Distractor present (original distractor)
	Trials 71-75	Distractor absent
	Trials 76-90	Distractor present (original distractor)
	Trials 91-95	Distractor present (new distractor)
	Trials 96-110	Distractor present (original distractor)
Experiment 9		
Distractor frequency – 30%. Distractor position – fixed.		
Block 1	Trials 1-60	Distractor absent
	Trials 61-236	Distractor present (original distractor) in 30%
		of trials
Block 2	Trials 1-60	
	Trials 61-119	Distractor absent
		Distractor present (original distractor) in 30%
		of trials
Experiment 10		
Distractor frequency – 100%. Distractor position – random.		
Blocks 1 and 2	Trials 1-60	Distractor absent
	Trials 61-110	Distractor present (original distractor)

Table 3. Summary of the experimental conditions (trial type) in Experiments 7, 8 9 and 10. For each experiment, the first column indicates the block number, the second column indicates the trial number, and the third column indicates the main characteristics of each trial in terms of distractor presence/absence and type.

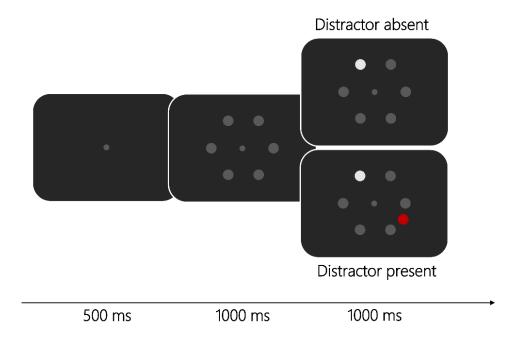


Figure 12. Example of the display sequence. After the presentation of a central fixation point, participants were presented with six equally spaced grey circles arranged on an imaginary circle around the central fixation point. After 500 ms, one of the circles turned to white, signaling the target item (the white disk) toward which a saccade had to be made. On distractor-present trials, simultaneously with the appearance of the target an additional colored distractor (here the red disk) was presented in an empty location. On some trials, as a function of the experiment, the distractor changed its color and position (see Methods for details).

4.2.1.4 Data analysis

In this and the following experiments two different types of analyses were performed: oculomotor capture and saccade latency. The first analysis addressed directly the effect of the distractor onset on the oculomotor behavior by calculating the amount of oculomotor capture defined as the percentage of participants who, in a given trial, erroneously made the first saccade toward the distractor (also see, Godijn &

Kramer, 2008). I considered only saccades with an amplitude larger than 1° of visual angle, and whose starting position was within 1.5° from the central fixation point. If the endpoint of the saccade had an angular deviation of less than 15° of arc from the center of either the target or the distractor (i.e., if the saccadic endpoint was within a 30° cone which extended from fixation to the stimulus, centered on the stimulus), the saccade was classified as landed on that particular stimulus. The second analysis was meant to detect any indirect effect of the distractor onset when the first saccade correctly landed on the target location. To this aim, I measured the latency of the saccade directed toward the target. Trials in which the saccade latency was either shorter than 80 ms or longer than 800 ms were excluded from the analysis (also see, Godijn & Kramer, 2008). Because of this outliers-detection criterion, less than 5% of the trials in each experiment were discarded from further analyses. The main effect of repeated exposure to the distractor on participant's oculomotor behavior was evaluated by grouping single trials into bins of five trials (also see, Godijn & Kramer, 2008). However, when we looked for specific characteristics of habituation (Thompson, 2009), like for instance, spontaneous recovery, specificity of habituation, and dishabituation, the analyses focused at the single-trial level. This approach is particularly suited for the paradigm used, in which some critical trials (i.e., the first trial in which the original distractor is presented; the first trial in which the new distractor is presented; the first trial in which the original distractor is reintroduced) required a single-trial analysis, because otherwise the underlying processes (e.g., spontaneous recovery, specificity of habituation), if any, could not be detected. As for the baseline against which to compare the performance in the critical trial, a bin of five trials preceding the critical one was considered, which allowed

to achieve a more reliable estimate of the oculomotor performance before the occurrence of the critical trial.

4.2.2 Results and discussion

Oculomotor capture

Short-term habituation. To test whether the oculomotor capture decreased with time I analyzed the data from Trial 61 to Trial 90 (i.e., before the distractor change, which occurred on Trial 91), and to increase the statistical power of the analysis the distractor-present trials were grouped into six bins of five consecutive trials each. A repeated measures ANOVA with Bin (from 1 to 6) as factor resulted significant both in the first block, F(5, 145) = 18.83, p < .001, $\eta^2_p = 1.00$, and in the second block, F(5, 145) = 4.76, p < .001, $\eta^2_p = 0.97$. The results depicted in Figure 13 (panels A and B) showed that the percentage of oculomotor capture diminished with exposition to the distractor (for a similar result see, Godijn & Kramer, 2008).

Specificity of habituation. The specificity (vs. generalization) of oculomotor capture habituation was measured by comparing (t-test, two tails) the percentage of capture in the trial in which the new distractor was presented (Trial 91, M = 53.33% in Block 1, M = 63.33% in Block 2) against the average amount of capture in the five trials before the distractor change, which were treated as baseline (Trials 86-90, M = 4.67% in Block 1, M = 4.00% in Block 2). The comparison showed a high degree of specificity both in the first block, t(29) = -5.28, p < .001, and in the second block, t(29) = -6.94, p < .001, as the introduction of the new distractor significantly elevated the percentage of oculomotor capture (Figure 13, panels A and B).

Dishabituation. To address the phenomenon of dishabituation I compared the average amount of capture in the baseline (Trials 86-90, M = 4.67% in Block 1, M = 4.00% in Block 2), with the percentage of capture in the first trial in which the original distractor was reintroduced (Trial 92, M = 13.33% in Block 1, M = 6.70% in Block 2). No significant difference in the percentage of capture emerged in both the first block, t(29) = -1.343, p = .190, and the second block, t(29) = -0.57, p = .573 (Figure 13, panels A and B).

Spontaneous recovery. The spontaneous recovery of oculomotor capture can be evaluated when the distractor is reintroduced after a period of suspension. Therefore, the percentage of capture in the first distractor-present trial of the second block (Trial 61, Block 2, M = 47.00%) was compared with the averaged amount of capture in the last five trials of the first block (Trials 106-110, Block 1, M = 6.00%), which served as baseline. The percentage of saccades to the distractor increased significantly when it was reintroduced after 60 trials of omission (i.e. the first 60 trials of the second block), t(29) = -4.21, p < .001, a result that is in line with the spontaneous recovery of habituation (Figure 13, panels A and B).

Long-term habituation. To explore whether the learning mechanism underlying the decrease of oculomotor capture has a long-term component, I compared the amount of capture in the first distractor-present trial of the first day (Trial 61, Block 1, M = 77.00%) with that of the second day (Trial 1, M = 17.00%). The analysis revealed a significant reduction of capture on the second day, t(29) = -5.83, p < .001. though long-term habituation across the two days of training was not complete because the level of capture at the beginning of the second day (Trial 1, M = 17.00%) was significantly higher

than in the baseline (Trials 106-110, Block 1, Day 1, M = 2.00%), t(29) = -2.12, p = .042 (see Figure 13, panel C).

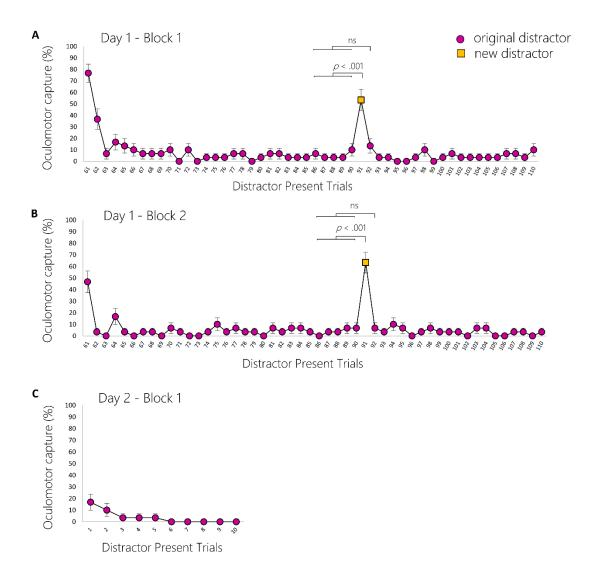


Figure 13. The figure shows the percentage of oculomotor capture in Experiment 7, triggered by the distractor onset, as a function of trial number, in Block 1 (A) and 2 (B) of the first session, and in Block 1 (C) of the second session. The purple markers represent trials with the original distractor, whereas the yellow markers represent trials in which the new distractor was presented. Bars represent ± 1 SEM.

Saccade latency

Indirect oculomotor capture. On average, the saccadic latencies to the target were shorter in the distractor-absent trials (M = 253 ms in Block 1, M = 249 ms in Block 2) than in the distractor-present trials (M = 278 ms in Block 1, M = 264 ms in Block 2), both in Block 1, t(29) = -5.95, p < .001, and in Block 2, t(29) = -4.59, p < .001. To verify whether the initial occurrence of the distractor slowed down the latency of the saccades directed to the target, I compared the last 5-trial bin of the distractor-absent phase (Trials 56-60, M = 245 ms in Block 1, M = 249 ms in Block 2) with the first 5-trial bin of the distractor-present phase (Trials 61-65, M = 316 ms in Block 1, M = 279 ms in Block 2). The results showed a significant difference both in the first block, t(28) = -7.80, p < .001, and in the second block, t(29) = -3.08, p = .004, thus indicating that even when the saccade was correctly deployed toward the target the distractor was still able to exert its effect on the participants' oculomotor behavior, both in Block 1 and in Block 2 (Figure 14, panels A and B).

Short-term habituation. Whether the lengthening of the saccades latency caused by the distractor decreased as a function of its repetition was evaluated by performing a repeated measures ANOVA with Bin (from 1 to 6) as factor, which revealed a significant effect of Bin in the first block, F(5, 140) = 7.10, p < .001, $\eta^2_p = 0.99$, but not in the second block, F(5, 145) = 1.51, p = .190, $\eta^2_p = 0.52$ (Figure 14, panels A and B).

Specificity of habituation. Stimulus specificity of habituation (i.e. a slowdown of the saccadic latency caused by the new distractor), was evaluated by comparing the average saccadic latency in the baseline (Trials 86-90, M = 268 ms in Block 1, M = 265 ms in Block 2) with the latency in the trial in which the new distractor was presented (Trial

91, M = 305 ms in Block 1, M = 360 ms in Block 2). Evidence of stimulus specificity emerged in the second block, t(10) = -2.40, p = .037, whereas in the first block the difference did not reach the statistical significance, t(9) = -1.77, p = .110, (Figure 14, panels A and B).

Dishabituation. The average saccadic latency in the baseline (Trials 86-90, M = 268 ms in Block 1, M = 265 ms in Block 2) was compared with the saccadic latency in the first trial in which the original distractor was reintroduced (Trial 92, M = 286 ms in Block 1, M = 269 ms in Block 2). There was no evidence of dishabituation on saccadic latencies to the target, both in the first block, t(24) = -1.92, p = .067, and in the second block, t(25) = -0.45, p = .657, (Figure 14, panels A and B).

Spontaneous recovery. To test whether the reintroduction of the distractor after 60 trials of suspension exerted an effect on the saccadic latency to the target, the average latency in the baseline (Trials 106-110, Block 1, M = 273 ms) was compared with the latency in the first distractor-present trial of the second block (Trial 61, Block 2, M = 289 ms). The result showed no significant differences in the saccadic latencies, t(14) = -0.53, p = .600, (Figure 14, panels A and B).

Long-term habituation. The comparison between the baseline (Trials 106-110, Block 2, Day 1, M = 259 ms) and the first distractor-present trial of the second session (Trial 1, Day 2, M = 367 ms), revealed a significant difference in the saccade latency to the target, t(21) = -5.01, p < .001 (Figure 14, panels A and B).

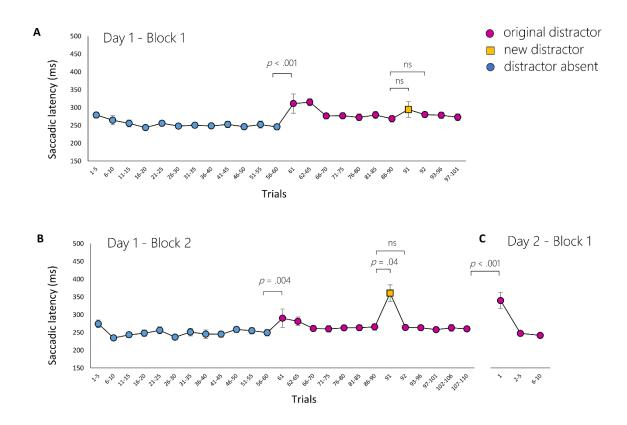


Figure 14. The figure shows the latency of saccades directed to the target, as a function of trial number in Block 1 (A) and 2 (B) of the first session, and in Block 1 (C) of the second session. The purple markers represent trials with the original distractor, the yellow marker represents trials in which the new distractor was presented, and the blue markers represent trials in which the distractor was omitted. Bars represent \pm 1 SEM.

Overall the results of Experiment 7 showed a decrement in the oculomotor capture that is consistent with some of the characteristics of habituation (Thompson, 2009). First of all, in an oculomotor capture paradigm modeled after that of Godijn and Kramer (2008) it was confirmed that after repeated presentations an onset distractor ceased to capture the eyes while participants were trying to make a saccade toward the

target. Second, the results showed that the learning process underlying such reduction of oculomotor capture was stimulus specific, since capture recovered when the features of the distractor (i.e., color and position) changed. Third, spontaneous recovery of capture was also found when the distractor was omitted for some trials within the same training session. However, it was also documented that the oculomotor capture reduction was maintained almost unaltered across two consecutive days of training, thus showing the involvement of a long-term memory component in this form of learning. All considered, this pattern of results is consistent with the phenomenon of habituation, which has been shown to affect also the covert orienting of attention (Turatto & Pascucci, 2016; Chapters 2 and 3 of the current thesis). Among the investigated characteristics of habituation, I failed to find evidence of dishabituation of oculomotor capture, namely a recovery of capture for the habituated distractor when it was presented after the introduction of a new distracting stimulus. According to the Sokolovian model, dishabituation would take place because the introduction of a new different stimulus produces a disruption of the neural model of the unwanted stimulation (Steiner & Barry, 2011, 2014). It follows that when the original stimulus is reintroduced, it matches the current neural model only partially, and the corresponding response tends to reappear. Hence, one would have expected to find at least a partial recovery of capture for the old distractor in the trial after the occurrence of the new distractor, but this is not what I found. Evidence of dishabituation has been indeed reported, for example, in previous studies investigating the habituation of the OR to an acoustic stimulus when the response considered was the skin conductance response (SCR; Steiner & Barry, 2011, 2014). In the aforementioned studies, a series of identical acoustic stimuli were delivered with a random SOA of 13–15 seconds, among which a single deviant stimulus (with a different frequency) was presented. During the task, the electrodermal activity of participants was recorded, in order to test habituation, spontaneous recovery and dishabituation of the SCR. Interestingly, the authors found evidence of dishabituation following a single deviant tone, a result that apparently is not in agreement with the current findings. We should note, however, that the present study differs from those of Steiner and Barry in some important respects. Hence, while Steiner and Barry (2011, 2014) investigated the dishabituation of the OR in the auditory modality, and measured the SCR as an index of orienting, the current work was instead concerned with the visual modality and eye movements were the variable of interest. One possibility, for example, is that the oculomotor system, as compared to the auditory system, requires more than a single deviant event (i.e., the distractor) to start changing the neural model responsible of the habituation of oculomotor capture. Experiment 8 was aimed at exploring this possibility.

4.3 Experiment 8

The present experiment addressed the possibility that a single occurrence of the new visual distractor may have been insufficient to cause a substantial disruption of the neural model based on the previous recursive occurrence of the same distractor, and therefore to generate dishabituation. The experiment was divided into two blocks (see Table 3). In the first block the distractor was changed in a single trial (Trial 91), a condition that served to replicate the lack of dishabituation found in Experiment 7. In the second block, instead, once introduced the new distractor appeared for five consecutive trials (Trials 91–95), thus increasing the possibility to observe dishabituation of capture, and then the old distractor was presented again for the remaining trials. However, even

if the amount of oculomotor capture triggered by the repeated old distractor were larger when presented after five repetitions of the new distractor (i.e., on Trial 96) than before (i.e., on Trial 90), this per se would not be evidence of dishabituation. Indeed, such increase of capture could be due to the phenomenon of spontaneous recovery induced by the fact that the old distractor was omitted for five consecutive trials. To rule out this alternative interpretation, before introducing the new distractor, the old distractor was omitted for an equivalent number of trials (Trials 71–75) to evaluate the amount of spontaneous recovery, if any, elicited by an equivalent number of distractor omission trials. Any increase in the amount of capture caused by the old distractor after five trials with the new one (i.e., on Trial 96) could be taken as evidence of dishabituation only if such increase is larger than that observed when the old distractor is introduced after that it has been omitted for five trials (i.e., on Trial 76).

4.3.1 Methods

4.3.1.1 Participants

Forty undergraduate students (30 females, mean age = 21.6 years old) of the University of Trento were recruited from the Department of Psychology and Cognitive Sciences for course credits. They had normal or corrected-to-normal vision, and were all naïve as to the purpose of the experiments.

4.3.1.2 Apparatus

The apparatus was the same as Experiment 7.

4.3.1.3 Stimuli and procedures

The paradigm and the task were identical to that of Experiment 7, except that participants performed only one session of two blocks (110 trials each). In the first 60 trials of each block, the distractor was never presented, and it surprisingly appeared from Trial 61 onward. However, in Block 1 the new distractor was presented only on Trial 91 (as in Experiment 7), whereas in Block 2 the new distractor appeared for five consecutive trials (Trials 91–95). In addition, in the second block five trials were introduced, in which the old distractor was not presented (Trials 71–75).

4.3.1.4 Data analysis

Data analyses were the same as Experiment 7.

4.3.2 Results and discussion

Oculomotor capture

Short-term habituation. To test whether the oculomotor capture decreased with time I analyzed the data from Trial 61 to Trial 90 (i.e., before the distractor change, which occurred on Trial 91) in the first block and from Trial 61 to Trial 70 (i.e., before the distractor omission, which occurred starting from Trial 71) in the second block. To increase the statistical power of the analysis the distractor-present trials were grouped into bins (six in the first block and two in the second block) of five consecutive trials each. A repeated measures ANOVA with Bin (from 1 to 6 in the first block, from 1 to 2 in the second block) as factor, showed a significant effect of Bin both in the first block, F(5, 195) = 24.51, p < .001, $\eta^2_p = 1.00$, and in the second block, F(1, 39) = 37.51, p < .001, $\eta^2_p = 1.00$, thus confirming that oculomotor capture decreased as a function of distractor repetition (Figure 15, panels A and B).

Specificity of habituation. The average amount of capture in the baseline (Trials 86-90, M = 1.00% in Block 1, M = 1.50% in Block 2) was compared with the percentage of capture in the first trial in which the new distractor was presented (Trial 91, M = 48.00% in Block 1, M = 38.00% in Block 2). When the distractor was changed for the first time, oculomotor capture increased both in the first block, t(39) = -5.79, p < .001, and in the second block, t(39) = -4.47, p < .001 (Figure 15, panels A and B).

Dishabituation. The average amount of capture in the baseline (Trials 86-90, M =1.00% in Block 1, M = 1.50% in Block 2) was compared with the percentage of capture in the first trial in which the original distractor was reintroduced (Trial 92 in the first block, M = 3.00%, and Trial 96 in the second block, M = 13.00%). When the old distractor was reintroduced after the presentation of the new distractor for a single trial (Block 1), the amount of capture was not larger than that observed in the baseline, t(39) = -0.57, p =.570. By contrast, when the old distractor was reintroduced after five trials with the new distractor, capture increased significantly as compared to the baseline, t(39) = -2.31, p =.026. Crucially, however, a comparable increase in the level of capture with respect to the baseline (Trials 66-70, Block 2, M = 3.00%) was also found when the old distractor was presented after that it was withheld for five consecutive trials (Trial 76, Block 2, M =15.00%), t(39) = -2.06, p = .046. This result suggests that the recovery of capture found after the presentation of five new distractors cannot be taken as evidence of dishabituation. Rather, the more parsimonious explanation for such increase of oculomotor capture seems to be a spontaneous recovery of capture due to the omission of the old distractor for some trials (Figure 15, panels A and B).

Spontaneous recovery. The average amount of capture in the baseline (Trial 106-110, Block 1, M = 3.00%) was compared with the percentage of capture in the first distractor-present trial of the second block (Trial 61, Block 2, M = 58.00%). The percentage of saccades to the distractor increased significantly when it was reintroduced after 60 trials of omission, t(39) = -6.97, p < .001, thus indicating a spontaneous recovery of oculomotor capture (Figure 15, panels A and B).

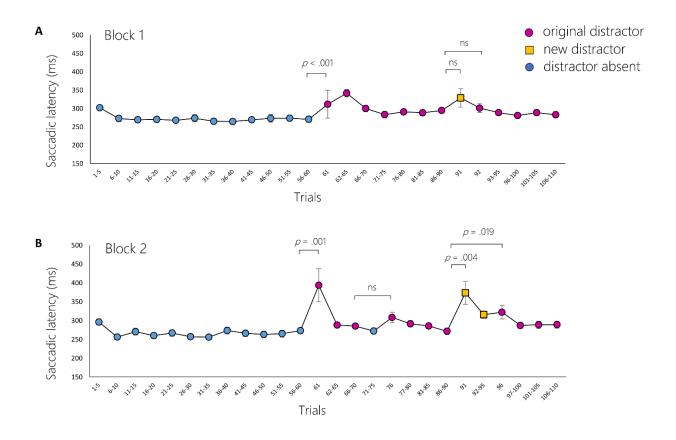


Figure 15. The figure shows the percentage of oculomotor capture in Experiment 8, triggered by the distractor onset, as a function of trial number, in Block 1 (A) and 2 (B). The purple markers represent trials with the original distractor, the yellow markers represent trials in which the new distractor was presented, and the blue markers represent trials in which the distractor was omitted. Bars represent ± 1 SEM.

Saccade latency

Indirect oculomotor capture. On average, the saccadic latencies to the target were shorter in the distractor-absent trials (M = 271 ms in Block 1, M = 266 ms in Block 2) than in the distractor-present trials (M = 293 ms in Block 1, M = 289 ms in Block 2), both in Block 1, t(39) = -5.00, p < .001, and in Block 2, t(39) = -5.80, p < .001. The impact of the distractor on the saccades directed to the target, was evaluated by comparing the last 5-trial bin of the distractor-absent phase (Trials 56-60, M = 270 ms in Block 1, M = 272 ms in Block 2) with the first 5-trial bin of the distractor-present phase (Trials 61-65, M = 333 ms in Block 1, M = 298 ms in Block 2). The results showed a significant difference both in the first block, t(39) = -7.01, p < .001, and in the second block, t(39) = -3.65, p = .001, thus confirming (see Experiment 7) that the distractor influenced the saccades toward the target (Figure 16, panels A and B).

Short-term habituation. A repeated measures ANOVA with Bin (from 1 to 6 in the first block, and from 1 to 2 in the second block) as factor revealed a significant effect of Bin both in the first block, F(5, 195) = 10.59, p < .001, $\eta^2_p = 1.00$, and in the second block, F(1, 39) = 8.50, p = .006, $\eta^2_p = 0.81$, (Figure 16, panels A and B).

Specificity of habituation. The average saccadic latency in the baseline (Trials 86-90, M = 293 ms in Block 1, M = 269 ms in Block 2) was compared with the latency of the first trial in which the new distractor was presented (Trial 91, M = 328 ms in Block 1, M = 373 ms in Block 2). Evidence of stimulus specificity emerged in the second block, t(23) = -3.23, p = .004, whereas in the first block the difference did not reach the statistical significance, t(17) = -1.76, p = .097, (Figure 16, panels A and B).

Dishabituation. The saccadic latency in the baseline (Trials 86-90, M = 293 ms in Block 1, M = 269 ms in Block 2) was compared with the saccadic latency in the trial in which the original distractor was reintroduced (Trial 92 in the first block, M = 301 ms, and Trial 96 in the second block, M = 321 ms). When the original distractor was reintroduced after that it was changed for one trial (Block 1), there was no evidence of dishabituation on saccade latencies to the target, t(36) = -0.40, p = .691. However, when the original distractor was reintroduced after it was changed for five trials (Block 2), the results showed a significant increase in the latency of the saccades directed toward the target, as compared to the average saccadic latency of the baseline prior to its change, t(31) = -2.48, p = .019. Crucially, in the second block, when the original distractor was reintroduced after that it was withheld for five trials (Trial 76, Block 2, M = 308 ms), the results showed no significant differences in the latency of the saccades toward the target, as compared to the average saccadic latency of the baseline prior to its omission (Trials 66-70, Block 2, M = 285 ms), t(32) = -1.50, p = .142, (Figure 16, panels A and B). The lack of an increase in the saccadic latency when the original distractor is introduced after its omission for five trials allows us to interpret the significant delay in the saccadic latency elicited by the same distractor after five presentations of the new distractor as evidence of dishabituation.

Spontaneous recovery. To evaluate whether the reintroduction of the distractor after 60 trials of suspension exerted an effect on the target saccadic latency, I compared the average latency in the baseline (Trials 106-110, Block 1, M = 281 ms) with the latency in the first distractor-present trial of the second block (Trial 61, Block 2, M = 393 ms).

The results showed a significant difference in the saccadic latency, t(12) = -2.67, p = .020, (Figure 16, panels A and B).

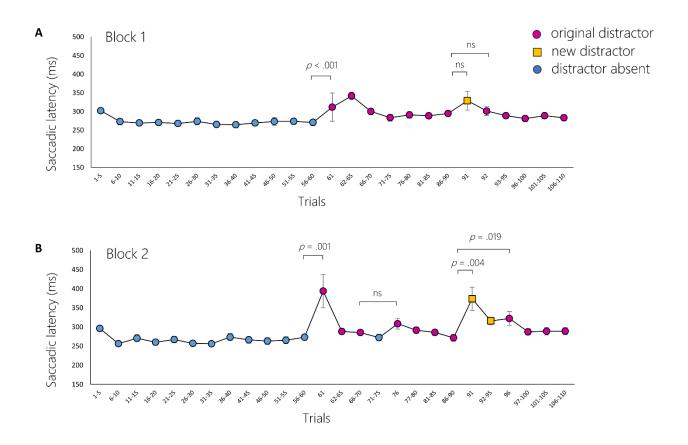


Figure 16. The figure shows the latency of saccades directed to the target, as a function of trial number in Block 1 (A) and 2 (B). The purple markers represent trials with the original distractor, the yellow markers represent trials in which the new distractor was presented, and the blue markers represent trials in which the distractor was omitted. Bars represent ± 1 SEM.

The present experiment confirmed the main findings of Experiment 7. However, when the saccadic RTs were considered, evidence of dishabituation of oculomotor capture emerged when the new distractor was presented for more than one trial, which

suggests that perhaps the neural model used to filter the irrelevant stimulation requires more than a single instance of the new distractor to be changed substantially. In sum, Experiments 7 and 8 showed that the decrement of oculomotor capture documented here and in the previous study of Godijn and Kramer (2008) agrees with some important characteristics of habituation. Indeed, the results revealed both short-term and long-term components of habituation, stimulus specificity, spontaneous recovery and, as far as saccadic latency is concerned, I found evidence of dishabituation of oculomotor capture.

4.4 Experiment 9

One of the key features of habituation is that it varies as a function of the frequency of stimulation (Rankin et al., 2009; Thompson & Spencer, 1966). Specifically, the higher the frequency of stimulation, the more rapid and/or pronounced is habituation. In the first two experiments of the present chapter, once introduced the distractor appeared on each trial, namely with a frequency of 100%. Hence, to give further support to the idea that the oculomotor capture reduction found here conforms to the characteristics of habituation, in the present experiment the distractor was presented with a frequency of approximately 30%. Under these conditions, habituation is expected to occur more slowly and to be less pronounced, namely to reach the asymptote at a higher level than in Experiments 7 and 8. To this goal, participants performed a 2-block experiment (see Table 3) in which, starting from Trial 61, the distractor was presented with a frequency of approximately 30%, and to have an equivalent number of distractor-present trials as in the previous experiments, in the first block the number of trials was increased from 110 to 236. The second experimental block had a different purpose, namely it served to

exclude the hypothesis that the decrement in the oculomotor capture was due to sensory fatigue caused by the distractor. As already noted by Rankin et al. (2009), habituation can be distinguished from sensory fatigue by showing frequency-dependent spontaneous recovery, that is more rapid spontaneous recovery following stimulation delivered at high frequency than to low frequency. Specifically, according to the habituation hypothesis, the higher the frequency of stimulation the more rapid and pronounced is spontaneous recovery after a period of lack of stimulation. Indeed, because the neural model of past stimulation (i.e., here the distractor) is used to predict the upcoming events (Ramaswami, 2014; Sokolov, 1960, 1963), when a 100%-frequency distractor is omitted for some trials the prediction of the model is immediately violated, and consequently the model is updated. Because the new expectation generated by the model is now the absence of the distractor, the reintroduction of the distractor after its omission for some trials creates a new violation of the model, and therefore capture is reinstated again. Clearly, the distractor omission for some trials leads to a strong violation of the model prediction when the distractor was previously presented with a frequency of 100%, but a marginal (if any) violation with a 30%-frequency distractor, where trials without the distractor are relatively frequent. The sensory fatigue or adaptation hypothesis, on the contrary, makes the opposite prediction, namely it should take longer to recover after a continuous (100% frequency) than a discontinuous (30% frequency) stimulation, because sensory fatigue is expected to be stronger the higher the frequency of stimulation. Because in Experiment 8 (Block 2) the amount of spontaneous recovery when the distractor was reintroduced after five omission trials was measured, in the second block of the present experiment the distractor was removed for an equivalent number of consecutive trials (Trials 95–99), which allowed us to measure the amount of spontaneous recovery for a distractor with a 30% frequency when it was reintroduced (Trial 100), and to compare it with that found with a 100%-frequency distractor (Experiment 8).

4.4.1 Methods

4.4.1.1 Participants

Thirty undergraduate students (22 females; mean age = 23.0 years old) of the University of Trento were recruited from the Department of Psychology and Cognitive Sciences for course credits. They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiments.

4.4.1.2 Apparatus

The apparatus was the same as Experiment 8.

4.4.1.3 Stimuli and procedures

The paradigm and the task were identical to that of Experiment 8, except that participants performed a single session of two blocks (236 trials in the first block, and 119 in the second block). In the first 60 trials of both blocks the distractor was never presented, whereas it surprisingly appeared from Trial 61 onward, with a frequency of 30%. A fixed sequence of trials was adopted, the same for all participants, in which the distractor appeared, in a fixed position, every 2, 3 or 4 trials. However, to evaluate the amount of spontaneous recovery with a 30%-frequency distractor, and to compare it with that elicited by a 100%-frequency distractor (Experiments 7 and 8), in the second block a series of five consecutive trials in which the distractor was omitted was

incorporated in the sequence. In the current experiment, in which the distractor appeared with a lower frequency as compared to Experiments 7 and 8, the habituation hypothesis would predict a limited (or no) recovery of capture after a suspension of the distractor for five consecutive trials.

4.4.1.4 Data analysis

Data analyses were the same as Experiments 7 and 8.

4.4.2 Results and discussion

Oculomotor capture

Short-term habituation. To test whether the oculomotor capture decreased with time I analyzed the data of the distractor-present phase (i.e. from Trial 61 onward), and to increase the statistical power of the analysis the distractor-present trials were grouped into bins (10 in the first block and 3 in the second block) of five consecutive trials each. A repeated measures ANOVA with Bin (from 1 to 10 in the first block, from 1 to 3 in the second block) as factor, showed a significant effect of Bin both in the first block, F(9, 261) = 6.44, p < .001, $\eta^2_p = 1.00$, and in the second block, F(2, 58) = 7.53, p = .001, $\eta^2_p = 0.93$. The results depicted in Figure 17 (panels A and B) showed that the percentage of oculomotor capture diminished with exposition to the distractor.

Frequency-dependent habituation. I compared the average percentage of oculomotor capture in the first block of Experiment 1 and Experiment 3, once it reached the asymptotic level, namely from the third 5-trial bin onward (see Figure 18). The results showed that in Experiment 9 habituation reached an asymptotic level for higher values of oculomotor capture, t(58) = -2.72, p = .009, thus indicating that the frequency

of stimulation exerted a crucial effect on the level of habituation (Figure 18). To control that the different asymptotic levels were not due to a difference in the initial level of oculomotor capture between the two experiments, I compared capture in the first distractor-present trial of Experiment 8 (Trial 61, M = 76.67%) and Experiment 9 (Trial 61, M = 73.33%). The comparison showed that when the distractor was introduced for the first time, the level of oculomotor capture was comparable in the two experiments, t(58) = 0.29, p = .770.

Frequency-dependent spontaneous recovery. To show that, as predicted by the habituation hypothesis, spontaneous recovery diminishes as the frequency of the stimulation (i.e. of the distractor) is reduced, I addressed whether, when the distractor rate was low (30%), spontaneous recovery emerged after a sequence of five omission trials. In the second block of Experiment 9, the average values of the five distractor-present trials before the distractor omission (Trials 80, 83, 87, 90, 94) were considered as baseline. The results (Figure 17, panel B) showed that the percentage of saccades directed toward the distractor in the first trial in which it was reintroduced (Trial 100, Block 2) was not significantly different from the amount of capture that we found in the baseline, t(29) = -0.91, p = .370, namely no sign of spontaneous recovery of capture after five trials in which the 30%-frequency distractor was omitted, as instead observed in Experiment 8 in which the distractor had a frequency of 100%.

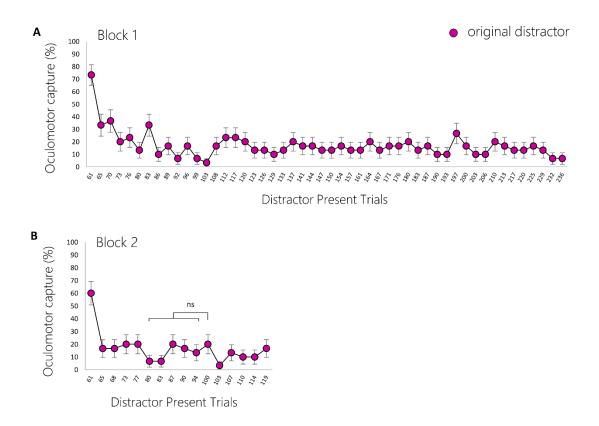
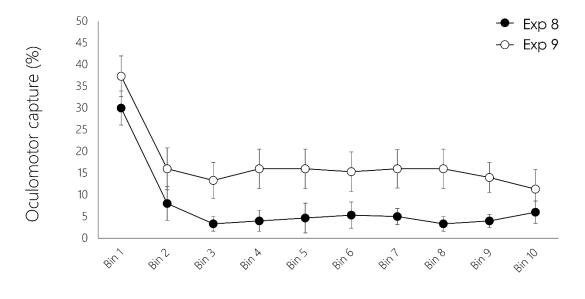


Figure 17. The figure shows the percentage of oculomotor capture in Experiment 9, triggered by the onset distractor, as a function of trial number, in Block 1 (A) and 2 (B). The purple markers represent distractor-present trials. In this experiment, trial numbers are not sequential because 2-4 distractor-absent trials (not depicted) were inserted between each distractor-present trial. There was a single sequence of five consecutive distractor-absent trials, between Trial 94 and Trial 100 of the second block. Bars represent \pm 1 SEM.



Distractor Present Trials

Figure 18. The figure shows the percentage of oculomotor capture in Experiment 8 (100% distractor frequency) and in Experiment 9 (30% distractor frequency). Each bin consists of five trials, with the exception of Bin 7 of Experiment 8, which contains four trials because of the exclusion of Trial 91. Bars represent \pm 1 SEM.

Saccade latency

Short-term habituation. A repeated measures ANOVA with Bin (from 1 to 10 in the first block, from 1 to 3 in the second block) as factor revealed a significant effect of Bin on the saccadic latencies both in the first block, F(9, 252) = 6.04, p < .001, $\eta^2_p = 1.00$, and in the second block, F(2, 58) = 7.53, p = .001, $\eta^2_p = 0.93$, (Figure 19, panels A and B), which confirmed the habituation of oculomotor capture.

Frequency-dependent spontaneous recovery. The average values of saccade latency in the baseline (Trials 80, 83, 87, 90, 94, Block 2) was compared with the first trial in

which the original distractor was reintroduced after the omission (Trial 100, Block 2). The results showed no significant difference in the latency of saccades to the target, t(22) = -0.61, p = .547, (Figure 19, panel B).

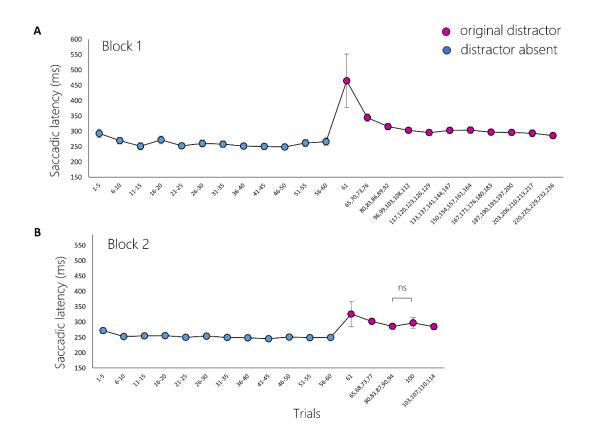


Figure 19. The figure shows the latency of saccades directed to the target, as a function of trial number in Block 1 (A) and 2 (B). The purple markers represent trials with the original distractor, and the blue markers represent trials in which the distractor was omitted. Bars represent \pm 1 SEM.

In sum, the results of Experiment 9 showed that the distractor frequency had an impact on the reduction of oculomotor capture: the amount of capture observed at the asymptotic level was higher the lower the distractor frequency. In addition, the results showed that with a 100% frequency, the omission of the distractor for five trials

generated a significant recovery in the percentage of oculomotor capture, whereas the same omission did not generate a recovery of capture with a 30%-frequency distractor, neither in the percentage of saccades toward the distractor, nor in the latency of the saccades directed toward the target. All considered this pattern of results gives further support to the habituation account.

4.5 Experiment 10

The results emerged so far find a straightforward explanation in the habituation phenomenon, and in particular in a Sokolovian mechanism of habituation according to which the distractor is compared against a neural model of past stimulation. One of the main functions of the model is that of providing a prediction about the upcoming events (Sokolov, 1960, 1963), and, consequently, the stronger the match between the current stimulation and the expectation generated by the model, the more the oculomotor response normally evoked by the distractor is suppressed. The results of Experiment 9, in which I compared the amount of spontaneous recovery observed with a 30%frequency distractor with that of a 100%-frequency distractor (Experiment 7), have also undermined an alternative explanation based on sensory fatigue. Habituation, indeed, can be distinguished from sensory fatigue by showing more rapid spontaneous recovery following stimulation delivered at high frequency than at low frequency (Rankin et al., 2009). However, because in previous experiments the position of the original distractor remained fixed, which may have still partially favored a sensory adaptation process, in the present experiment the position of the distractor was randomly changed on each trial (see Table 3). A reduction of oculomotor capture for a distractor presented at random

locations is less likely to be caused by sensory fatigue and would thus provide further support to the habituation account.

4.5.1 Methods

4.5.1.1 Participants

Thirty undergraduate students (16 females; mean age = 23.6 years old) of the University of Trento were recruited from the Department of Psychology and Cognitive Sciences for course credits. They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiments.

4.5.1.2 Apparatus

The apparatus was the same as Experiments 7-9.

4.5.1.3 Stimuli and procedures

The paradigm and the task were identical to that of Experiment 9, except that participants performed only one session of two blocks (110 trials each), and that the distractor could be randomly located in one of four possible positions (at clock positions 2, 4, 8, and 10).

4.5.1.4 Data analysis

Data analyses were the same as Experiment 7-9.

4.5.2 Results and discussion

Oculomotor capture

Short-term habituation. To test whether the oculomotor capture decreased with time I analyzed the data of the distractor-present phase (i.e. from Trial 61 onward) and to increase the statistical power of the analysis the distractor-present trials were

grouped into 10 bins of five consecutive trials each. A repeated measures ANOVA with Bin (from 1 to 10) as factor showed a significant effect of Bin both in the first block, F(9, 261) = 6.93, p < .001, $\eta^2_p = 1.00$, and in the second block, F(9, 261) = 6.14, p < .001, $\eta^2_p = 0.99$. The results depicted in Figure 20 (panels A and B) showed that the percentage of oculomotor capture diminished with exposition to the distractor.

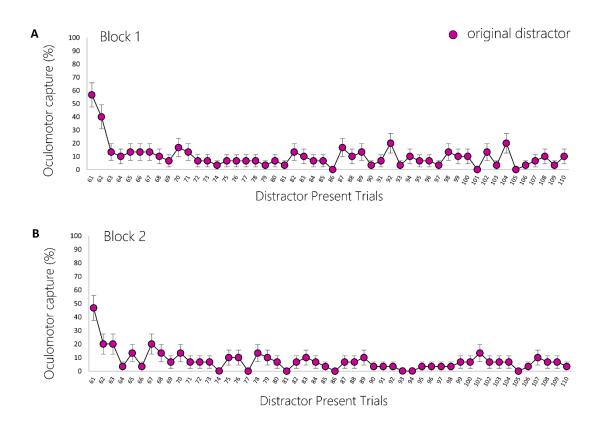


Figure 20. The figure shows the percentage of oculomotor capture in Experiment 10, triggered by the onset distractor, as a function of trial number, in Block 1 (A) and 2 (B). The purple markers represent distractor-present trials. Bars represent \pm 1 SEM.

Saccade latency

Short-term habituation. A repeated measures ANOVA with Bin (from 1 to 10) as factor revealed a significant effect of Bin in the first block, F(9, 252) = 5.80, p < .001, $\eta^2_p = 1.00$, but not in the second block, F(9, 261) = 1.64, p = .103, $\eta^2_p = 0.76$, (Figure 21, panels A and B).

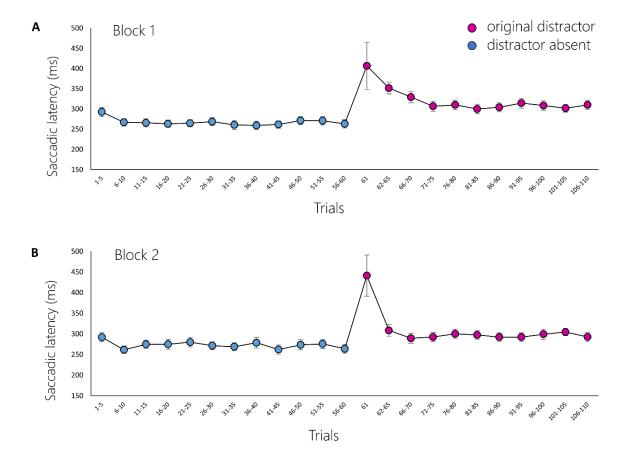


Figure 21. The figure shows the latency of saccades directed to the target, as a function of trial number in Block 1 (A) and 2 (B). The purple markers represent trials with the original distractor, while the blue markers represent trials in which the distractor was omitted. Bars represent \pm 1 SEM.

The reduction of oculomotor capture emerged in the present experiment, in which the position of the distractor changed randomly on each trial, was similar to that found in previous experiments in which the position was fixed. This result thus gives further support to the habituation account, whereas it further undermines the possibility that the oculomotor capture decrement observed could be ascribed to sensory fatigue.

The present set of experiments (Experiments 7-10) clearly showed that reflexive saccades triggered by an irrelevant distractor are subject to habituation; however, it remains unclear whether the learning process progressively reducing the oculomotor capture response affects the saccadic programming or the saccadic execution (or both). This question arises because eye movements programming and execution are two distinct processes that rely on different brain structures (e.g., Fuchs, Kaneko, & Scudder, 1985; Moschovakis, 1996; Robinson, 1968; Scudder, Kaneko, & Fuchs, 2002). The saccadic programming involves cortical regions like the Frontal Eye Fields (FEFs) and the Parietal Eye Fields (PEFs), and subcortical structures like the Superior Colliculus (SC). The saccadic execution, instead, involves neural structures located in the brainstem, and in particular the Saccadic Burst Generator (SBG), which receives the program from the abovementioned structures and sends the corresponding motor command to the extraocular muscles to move the eyes accordingly.

To understand whether habituation of oculomotor capture affects the saccadic programming stage, it is necessary to isolate this process from the subsequent saccadic execution stage. To this aim, I investigated how and to what extent a peripheral visual stimulus affects a specific type of fixational eye movements, known as microsaccades (Martinez-Conde, Otero-Millan, & Macknik, 2013). Indeed, the absolute frequency of

microsaccades is modulated by the programming of a large-scale saccade while fixation is maintained (Rolfs, Laubrock & Kliegl, 2006; Rolfs, Engbert & Kliegl, 2008), a condition that thus allows to elucidate the processing stage at which habituation affects the oculomotor behavior. Microsaccades share some important characteristics with normal saccades. For example, they are both binocular eye movements, with the same amplitude and direction in both eyes (Ditchburn & Ginsborg, 1953; Krauskopf, Cornsweet, & Riggs, 1960; Lord, 1951), and they both follow the main sequence (Zuber, Stark, & Cook, 1965), namely a linear relationship between peak velocity and amplitude. Furthermore, saccades (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995) and microsaccades (Engbert & Kliegl, 2003; Galfano, Betta, & Turatto, 2004; Hafed & Clark, 2002; Laubrock, Engbert, & Kliegl, 2005; Laubrock, Engbert, Rolfs, & Kliegl, 2007; Rolfs, Engbert, & Kliegl, 2004; Rolfs, Engbert, & Kliegl, 2005) are also similarly affected by spatial attention. Finally, microsaccades and saccades originates from neural activities in the same SC motor map (Rolfs, Kliegl, & Engbert, 2008), which explains why they are considered part of the same eye movement continuum (Martinez-Conde, Otero-Millan, & Macknik, 2013; McCamy et al., 2012; Otero-Millan, Troncoso, Macknik, Serrano-Pedraza, & Martinez-Conde, 2008).

Crucially, however, whereas the programming of saccades arises from activity in saccadic burst neurons located in the caudal portion of the SC, which code the extrafoveal portion of the visual field, the programming of microsaccades originates, though indirectly, from activity in fixation neurons, located in the rostral portion of the SC, and involved in maintaining gaze fixed. Indeed, a fundamental characteristic of the SC motor map is that the activation of a given region of the map spreads to neighboring locations,

whereas at the same time it reduces the neural activations in distant regions. In particular, this inhibitory mechanism applies to the activity of saccadic burst neurons on fixation neurons, so that the programming of a saccade toward a peripheral stimulus generates a reduction of the neural activity in the rostral zone of the map, favoring the disengagement of fixation. However, when fixation neurons are engaged to maintain the gaze fixed, the corresponding neural activation spreads to the neighboring saccadic burst neurons, which code for immediately adjacent positions of the visual field, thus leading to the generation of microsaccades. This mechanism would explain the typical microsaccadic response elicited by a peripheral stimulus when fixation is maintained, which consists in an early reduction of the absolute microsaccade frequency about 100 ms after the onset of a stimulus (inhibition phase), followed by an absolute frequency enhancement about 300 ms after the stimulus onset (enhancement phase). The rapid phase of microsaccadic frequency inhibition was first reported by Engbert and Kliegl (2003), and is thought to reflect a fast subcortical processing of the stimulus, presumably involving the direct retinotectal pathway from the retina to the SC (Engbert, 2006).

Therefore, if habituation of oculomotor capture elicited by a peripheral onset takes place at the level of saccade programming, I predict that the initial inhibition of microsaccades should decrease as exposure to the peripheral onset progresses. Ideally, if the activity related to the saccade programming reaches a level of complete habituation, then as the experiment unfolds no inhibition of microsaccades should be observed. By contrast, if habituation of oculomotor capture regards only the execution of saccades, then no change in the saccade programming activity will develop with repeated

exposure to the onset, and consequently the initial microsaccadic inhibition should remain unaffected across the experiment.

4.6 Experiment 11

The first block of the present experiment was designed replicate the evidence of habituation of oculomotor capture that emerged from Experiments 7-10. For this reason, participants were asked to make, as fast and as accurate as possible, a saccade toward a target stimulus, while in some trials an additional peripheral onset, serving as distractor, was shown on the screen. By contrast, from the second block onward (Blocks 2-4), participants were asked to maintain fixation on the central spot and to perform a simple counting task, while they were exposed to the same irrelevant distractor of Block 1. The maintaining of fixation in Blocks 2-4 was necessary to record microsaccadic eye movements.

4.6.1 Methods

4.6.1.1 Participants

Twenty-four participants (19 females, mean age = 21.2 years old) of the University of Trento were recruited from the Department of Psychology for course credits or monetary compensation (6 \in). They had normal or corrected-to-normal vision and were all naïve as to the purpose of the experiment. Informed consent was obtained from all participants.

4.6.1.2 Apparatus

As in Experiments 7-10, with a single exception: in order to analyze microsaccades, eye movements were recorded binocularly using an Eyelink 1000 Desktop Mount system (SR Research, Ontario, Canada), with a sampling rate of 500 Hz.

4.6.1.3 Stimuli and procedures

Block 1. Each trial (see Figure 22, Panel A) started with the presentation of a grey fixation point (diameter of 0.73°; 0.75 cd/m²) on a black background (0.07 cd/m²), surrounded by four equidistant grey disks (diameter of 1.2°, 0.62 cd/m²) that were placed on an imaginary circle (at clock positions 1, 5, 7 and 11) with a radius of 5° around the central fixation point. After 2,500 ms one of the disks turned green (17 cd/m²) while the others remained grey. The unique green disk was the saccadic target, and on each trial its position was randomly assigned in one of the four possible locations. Participants were asked to make a saccade toward the target disk as fast as possible. In the first thirty trials there was no distractor, whereas starting from Trial 31, an onset white disk (diameter of 2°; eccentricity of 5°; 45.3 cd/m²) could appear simultaneously with the target (30% frequency) in one of two possible locations (at clock position 3 or 9). If a saccade was detected before the target occurrence, an error message appeared on the screen, and the trial was aborted and then restarted. This allowed us to ensure that each saccade toward the target or the distractor started from the central fixation point. Each trial was followed by a blank inter-trial interval of 3,000 ms. The total length of the trial was about 8 seconds.

Blocks 2-4. The stimuli (see Figure 22, Panel B) were identical to those used in the first block, except that no target was presented, namely none of the grey disks turned to green. In addition, in a small proportion of trials the fixation point turned to red for 200

ms. Participants were instructed to maintain fixation on the central fixation point throughout the whole trial, and were informed that the peripheral onset would have appeared with a frequency of 100%, but in the same positions of Block 1. After the disappearance of the peripheral onset, the fixation point remained on the screen for other 2,500 ms, during which it could turn to red for 200 ms. Each trial was followed by a blank inter-trial interval of 3,000 ms. The total length of the trial was about 8 seconds. The participants' task was to silently count the number of times in which the fixation point turned to red, and to report this number at the end of each block by using the computer keyboard.

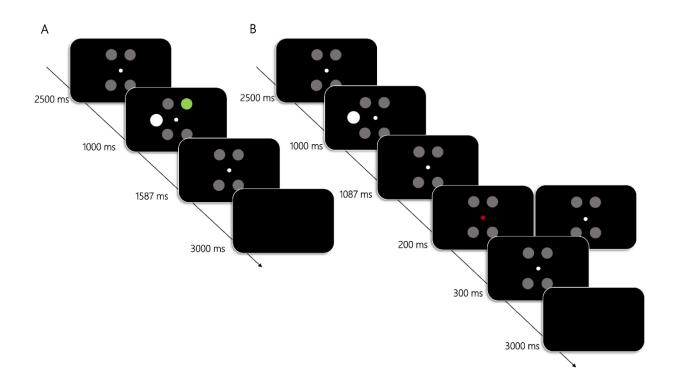


Figure 22. Example of stimuli used in Experiment 11. Panel A depicts the main events of Block 1. A grey central fixation point was presented for 2,500 ms, surrounded by four grey disks. After that, one of the grey disks turned to green for 1,000 ms (here the up-right disk) and served as saccadic target, while the others remained grey. At the same time, on 30% of trials an additional white disk was added to the display, in one of two possible locations (at clock positions 3 or 9), and served as distractor. The task was to make a saccade as fast and as accurate as possible toward the target stimulus. Panel B depicts the main events of Blocks 2-4, in which the trial sequence was similar, with some exceptions: the target stimulus never appeared (i.e. none of the grey disks turned to green); after the disappearance of the distractor the central fixation point could turn to red for 200 ms, or alternatively it could remain grey. On each block, the central fixation point turned to red in a variable number of trials (from five to eight). The task was to silently count the number of times in which the fixation point turned to red, and to report this number at the end of each block. In all blocks (Panels A and B), each trial was followed by a blank inter-trial interval of 3,000 ms. The total duration of each trial was about 8 seconds.

4.6.1.4 Data analysis

The analyses concerning oculomotor capture and saccade latency (Block 1) were the same as Experiments 7-10. Microsaccades (Blocks 2-4) were detected using a velocity-based algorithm developed by Engbert and Kliegl (2003), and were then analyzed using custom-made scripts in Matlab. The algorithm was applied to 1300-ms epochs of eye-position recording, ranging from 300 ms prior to the presentation of the lateral stimulus to 1000 ms after the stimulus onset. The algorithm defines microsaccades as part of the eye movement trajectory, where velocity (calculated over a moving window of nine samples) exceeds a relative velocity threshold multiple (λ) of the median SD. I used a relative velocity threshold set to five median-based SDs of the velocity values observed (λ = 5), a minimum temporal threshold of six samples (12 ms,

since the refresh rate was set to 500 Hz), and a maximum peak velocity of 300° s⁻¹. Epochs with eye blinks or saccades exceeding 1.5° in amplitude were discarded from analysis. Less than 5% of data was discarded from the analysis.

4.6.2 Results and discussion

Block 1 - Saccades

Oculomotor capture

In Block 1 the oculomotor capture was defined as the percentage of participants that, on each trial, erroneously made the first saccade toward the distractor. To test whether the oculomotor capture decreased with time the 15 distractor-present trials were divided into three bins of five trials each. The results depicted in Figure 23 showed that the percentage of oculomotor capture diminished with exposure to the distractor, a pattern corroborated by a repeated measure ANOVA with Bin (from 1 to 3) as factor, which resulted significant, F(2, 46) = 7.854, p = .001, $\eta^2_p = .255$.

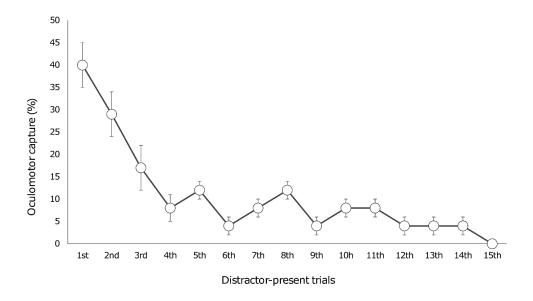


Figure 23. The figure shows the percentage of oculomotor capture triggered by the peripheral onset distractor, as a function of trial number, in the first block of Experiment 11. On the *x-axis*, only distractor present-trials are depicted, and each marker represents the amount of oculomotor capture in a single distractor-present trial (from the 1^{st} to the 15^{th}). Bars represent ± 1 SEM.

Saccade latency

The saccade latency analysis, conducted only on Block 1, was meant to detect any indirect effect of the distractor on the saccades correctly landing on the target location. To this aim, I measured the latency of the saccades directed toward the target. On average, in the first block the saccadic latencies to the target were shorter in the distractor-absent trials (M = 326 ms) than in the distractor-present trials (M = 381 ms), t(29) = -4.45, p < .001, d = -.909 (see Figure 24). In order to analyze the time course of the latency of the saccades directed toward the target, I divided the 15 distractor-present trials into three 5-trial bins, and I conducted a repeated measures ANOVA with Bin (from 1 to 3) as factor, which resulted significant, F(2, 46) = 18.097, p < .001, $\eta^2_p = .440$ (see Figure 24). This means that the latency of the saccades correctly landing on the target, when the distractor was presented, decreased significantly following the repeated exposure to the distractor.

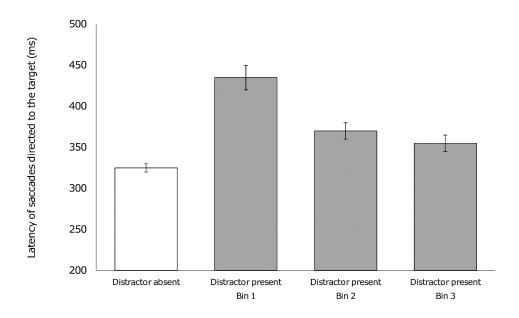


Figure 24. The figure shows the mean latency of saccades directed toward the target, as a function of the distractor presence/absence. The white histogram depicts the mean saccadic latency when no distractor was presented (i.e. in the first 30 trials of Block 1), whereas the grey histograms depict the mean saccadic latency in the distractor-present trials, divided into three consecutive 5-trial bins. Bars represent ± 1 SEM.

Block 2-4 - Microsaccades

Accuracy

The first step was to calculate participants' accuracy in the counting task. The accuracy of participants in Blocks 2-4 was quite high (99% in Block 2, 99% in Block 3 and 97% in Block 4), thus confirming that they were really focused on the counting task.

The main sequence

Before analyzing the data, I checked whether the detected microsaccadic eye movements satisfied the velocity-amplitude relationship criterion (Zuber et al., 1965). According to this criterion, a positive correlation, called the *main sequence*, must exist between saccadic amplitude ad saccadic peak velocity. Figure 25 shows that the linear relation between microsaccades amplitude and peak velocity was strongly positive, and this was confirmed by a very high correlation coefficient (r = 0.91).

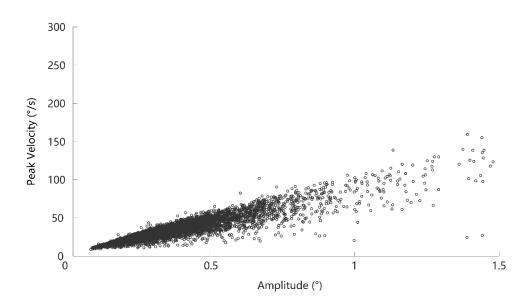


Figure 25. The panel depicts the correlation between microsaccades peak velocity and amplitude for all blocks of trials in Experiment 11. The plot contains microsaccades from the whole pool of participants (5279 microsaccades).

Absolute frequency of microsaccades

The absolute frequency of microsaccades was then computed, which was calculated separately for each participant and for each block, and then averaged across

participants. The rate of microsaccades was calculated over a 100-ms wide time window moving in 2-ms steps (the highest temporal resolution allowed by our sampling rate). Visual inspection of Figure 26 reveals a microsaccadic inhibition about 100 ms after the stimulus onset followed by a microsaccadic enhancement (\sim 300 ms after the stimulus onset). The crucial question is whether the inhibition phase (50-150 ms after the stimulus onset) changes across blocks, and in particular whether the change is evident between the first and the last block. To this aim, a single 100-ms time window of interest (WOI) centered on 100 ms post stimulus onset was considered. The WOI refers to the absolute frequency of microsaccades from 50 to 150 ms after the onset of the stimulus. A paired-sample t test was performed to compare the microsaccadic frequency in response to the target between Block 2 and Block 4. No evidence of habituation during the inhibitory phase emerged, t(23) = -.938, p = .358, d = -.191.

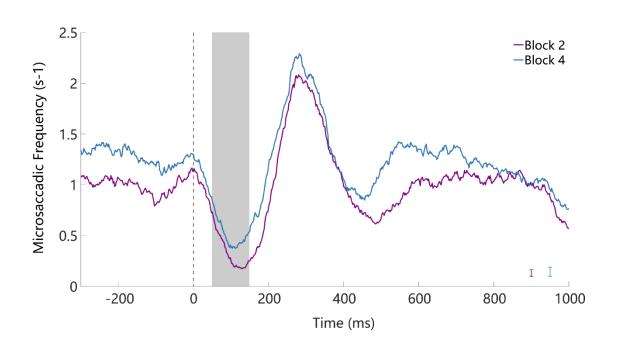


Figure 26. Time course of absolute microsaccadic frequency in response to the occurrence of the peripheral onset in Experiment 11 (Block 2 vs. 4). The plots were constructed by calculating the frequency of microsaccades in a window of 100-ms width moving in 2-ms steps. The *vertical dashed line* indicates the onset of the peripheral onset, whereas the *grey area* delimits the time window on which the comparisons (*t* tests) between the microsaccadic frequency in the two blocks has been conducted. *Error bars* (bottom-right) represent the average inter-subject standard error of the mean absolute microsaccadic frequency calculated on each time window of the corresponding plot.

4.7 General discussion

While previous studies, in addition to the current work, have already shown that the repetitive exposure to visual onsets leads to habituation of attentional capture (Pascucci & Turatto, 2015; Turatto et al., 2018; Turatto & Pascucci, 2016; also see Neo & Chua, 2006), the aim of this chapter was to investigate whether onset-driven oculomotor capture is also subject to habituation.

However, before discussing our results in the framework of habituation, it is necessary to consider whether the progressive reduction of oculomotor capture could be accounted for by the notion of *neuronal fatigue*, at either the motor or the sensory level. Two reasons can easily dismiss the motor fatigue explanation: first, in all the experiments (Experiments 7-11) no indication of motor fatigue (e.g., a lengthening of the saccadic RT) was found for the saccades correctly deployed to the target, and therefore motor fatigue does not explain the progressive reduction of oculomotor capture; second, the motor fatigue explanation is incompatible with the documented stimulus specificity effect: if the reduced exogenous oculomotor orienting were due to a general motor fatigue, the same response should not recover when a new stimulation is delivered, as instead we found

(i.e. a recovery of capture) when a new distractor, different in color and position, was presented.

We now turn to the sensory fatigue hypothesis. This view assumes that a sort of neuronal fatigue in the sensory representation of the repetitive onset distractor would be the cause of the oculomotor capture decrement; in other words, after recurring stimulation (i.e. presentation of the onset) the visual neurons representing the distractor would respond less efficiently (Carandini, 2000). A weaker sensory response in these neurons would translate into a reduced distractor saliency, which in turn would cause a progressive decrement in the distractor ability to capture attention and the eyes. However, if this were the case, after a period of distractor omission spontaneous recovery should be less likely to occur the higher the frequency of the previous stimulation, because at high frequency neuronal fatigue is more pronounced, and consequently it becomes harder to recover after stimulation at high than low frequency. On the contrary, a stronger spontaneous recovery was found for a 100%-frequency distractor (Experiment 8) than for a 30%-frequency distractor (Experiment 9). As already discussed, this pattern of results is instead in agreement with the idea that habituation is a central process relying on a neural model generating a prediction of the upcoming events on the basis of the past stimulation (Ramaswami, 2014; Sokolov, 1960, 1963). Therefore, five trials of distractor omission caused a more consistent violation of the model prediction when the distractor had appeared on each of the previous trials (100% frequency, Experiment 8) than on a third of the previous trials (30% frequency, Experiment 9). It follows that the distractor omission initiated an update of the neural model in the former but not in the latter case, which explains why the reintroduction of the same distractor after five trials restored capture in Experiment 8 but not in Experiment 9. Furthermore, another aspect that undermines the sensory-fatigue hypothesis is the long-term reduction of oculomotor capture, which was still present on the second day of stimulation, therefore lasting for at least 24 hours; this finding suggests the involvement of a learning mechanism operating on a timescale that is much longer than that usually exhibited by early sensory adaptation phenomena (Kohn, 2007). By contrast, it is well established that habituation can have both short-term (within session) and long-term (across sessions) components (Rankin et al., 2009), with the former due to a decrease in the release of presynaptic neurotransmitters (Bailey & Chen, 1983; Castellucci & Kandel, 1974), and the latter involving morphological and structural changes of the presynaptic terminals (Bailey & Chen, 1983).

Once the sensory and motor fatigue accounts have reasonably been ruled out, we can start considering the results as evidence that the oculomotor capture triggered by a repetitive sudden onset is subject to habituation. To begin with, the previous findings (Godijn & Kramer, 2008) showing that the oculomotor capture decreased as the exposure to the same irrelevant onset distractor progressed, were replicated. Crucially, such oculomotor capture reduction presented some specific features of the general phenomenon of habituation (Thompson, 2009). First, the re-occurrence of the distractor after its omission for some trials caused the *spontaneous recovery* of the oculomotor capture; second, *specificity* of habituation of capture emerged when a new distractor, different in color and location, was introduced; third, the occurrence of the new distractor led also to *dishabituation* of the oculomotor capture triggered by the previous distractor; fourth, the amount of oculomotor capture habituation varied as a function of

the distractor frequency, that is, habituation was *frequency dependent*; fifth, habituation of oculomotor capture exhibited both *short-term* and *long-term* components (Rankin et al., 2009).

In particular, the phenomenon of dishabituation of oculomotor capture deserves a deepen discussion, but to this aim it is useful to recall that in the current study the onset distractor could affect the oculomotor behavior in a direct and/or in an indirect manner. The direct manner is expressed by the oculomotor capture measure, namely by the percentage of participants making, on a given trial, the first saccade toward the distractor (Godijn & Kramer, 2008); by contrast, the indirect manner is indexed by the increase in the latency of the saccade directed toward the target, in the presence of the distractor. As for dishabituation (Thompson, 2009), this phenomenon is observed when the presentation of another stimulus (here the new distractor) results in the recovery of the habituated response to the original stimulus (here the old distractor), and it is explained by two main accounts. The *stimulus-model comparator theory* (Sokolov, 1963) maintains that dishabituation is a disturbance in the process of habituation. According to this view, in the present experiments the new distractor initiated the update of the neural model of the unwanted sensory input, so that when the previous old distractor was re-introduced, it tended to capture the eyes again because it only partially matched the current neural model. Dishabituation has been accounted for also by the *dual-process theory* (Groves & Thompson, 1970), which suggests that dishabituation reflects a process of *sensitization*, namely an increased response sensitivity superimposed on the pattern of habituation. Sensitization would be due to an augmented arousal level caused by the occurrence of the new stimulation. Two reasons make me prefer the explanation of dishabituation offered by the stimulus-model comparator theory: first, this model was specifically devised to explain habituation of the OR, of which the oculomotor capture is a key component (Sokolov, 1960, 1963); second, there is convincing evidence, from both animal and human studies, to consider dishabituation and sensitization two distinct processes (Rankin & Carew, 1988; Steiner & Barry, 2014). However, in the present study evidence of dishabituation emerged only when the detrimental effect of the distractor was measured in the indirect manner, namely when the latency of the saccades directed toward the target was considered. By contrast, the amount of oculomotor capture triggered by the old distractor after five presentations of the new one was not different from the spontaneous recovery of capture elicited by the omission of the old distractor for an equivalent number of trials (see discussion of Experiment 8). On the one hand, the lack of a consistent evidence of dishabituation when a direct oculomotor capture measure is considered seems at odds with recent findings showing, in a completely different paradigm, a clear dishabituation of the SCR component of the OR elicited by the interpolation of a single oddball acoustic stimulus in a stream of standard acoustic stimuli (e.g., Steiner & Barry, 2014). On the other hand, previous studies investigating habituation and dishabituation of different responses in humans, including the SCR in an OR-paradigm (Houck & Mefferd, 1969), have failed to reveal evidence of dishabituation (Havermans, 2012; Havermans, Hermanns, & Jansen, 2010; Kagan, Linn, Munt, Reznick, & Hiatt, 1979). However, a lack of dishabituation does not challenge the interpretation of the reduced responsiveness in terms of habituation when other specific characteristics of this phenomenon, like stimulus specificity, spontaneous recovery and frequency dependency, are present.

Experiment 10 attested a decrement of oculomotor capture also when the onset distractor randomly changed its location on each trial. This finding may reveal some characteristics of the mechanism underlying habituation of the reflexive saccades triggered by the onset distractor. The fact that habituation occurred also for a distractor appearing at different positions could indicate that habituation relies on a neural model of unwanted stimulation that operates on a spatially-invariant object-based representation of the onset stimulus (Biederman, 1987; Marr, 1982). While the attention system can certainly operate in a purely object-based manner (Vecera & Farah, 1994), this possibility could be more problematic for the saccadic system, which is intrinsically spatial in nature, since any saccade is programmed on the basis of precise spatial coordinates. In particular, exogenous saccades are mainly controlled by the SC, which contains a topographic map of the surrounding world in retinotopic coordinates. Hence, one possibility is to postulate a mechanism to map the higher-level object-based representation of the distractor to its representation in lower-level visual or visuo-motor areas, where the distractor spatial coordinates are coded. Alternatively, the neural model could effectively operate on a topographic representation of the distractor. This would imply, however, that when the distractor appears at different locations each saccade directed toward one of these locations is subject to an independent habituation process, which in turn entails that the neural model can store multiple objects and locations. Then, an interesting question for future investigations is the memory capacity of the neural model underlying habituation of attention and oculomotor capture (for a possible relation between WM and habituation to distraction see, for example, Bell, Röer, Dentale, & Buchner, 2012; Röer, Bell, & Buchner, 2014).

A consistent pattern of results emerged from the present set of experiments is that habituation of oculomotor capture was very fast, reaching the asymptotic level within a few trials, a result also in agreement with the studies of Sokolov (1960), who reported that involuntary eye movements toward a sudden visual or acoustic stimulus were the first component of the OR to habituate. In other words, the oculomotor system learned very quickly to almost completely ignore a salient onset distractor that initially grabbed the eyes of the majority of participants. This rapid habituation of oculomotor capture stands in sharp contrast with the fact that habituation of covert attention shifts, triggered by a peripheral onset similar to the one used here (both in terms of frequency, number of possible locations and physical salience, see Experiment 10), requires at least a hundred of trials to take place (Turatto & Pascucci, 2016; also see Chapters 2 and 3 of the current work). The marked discrepancy between the time course of habituation in the oculomotor and attentional system can be reconciled if one considers the possibility that the two systems, although often operating together, are actually independent, and rely on separate functional (e.g., Klein & Pontefract, 1994) and neurophysiological mechanisms (e.g., Ignashchenkova et al., 2004).

Given that exogenous saccades elicited by a peripheral onset distractor are subject to habituation, the last experiment was aimed to establish whether this phenomenon takes place at the saccadic execution stage, or involves the earlier stage of saccadic programming. To address this issue, I exploited the fact that during fixation the programming of reflexive saccades triggered by a peripheral onset generates an initial drop in the microsaccadic frequency (e.g., Rolfs et al., 2008). Because saccadic programming alters the microsaccadic frequency, it is safe to assume that if habituation

affects saccadic programming (in addition to saccadic execution), then this should impact also the rate of microsaccades, and specifically, habituation of saccadic programming should be accompanied by a progressive attenuation of the initial microsaccadic inhibition.

In the last experiment, I compared the absolute microsaccadic frequency during the inhibitory phase between the beginning and the end of the experimental session. The results confirmed that the saccade execution triggered by an irrelevant onset is subject to habituation, whereas the microsaccadic response elicited by the same stimulus is not. The latter finding suggests that despite the oculomotor capture habituation, the programming of the corresponding reflexive saccades does not habituate.

It is the first time, to the best of my knowledge, that habituation has been shown to affect reflexive saccade execution without altering the corresponding programming stage, a result that is relevant for the current models of saccades generation. Different brain regions, from the cortex to the brainstem, are involved in the generation of saccades (e.g., Fuchs et al., 1985; Moschovakis, 1996; Robinson, 1968; Scudder et al., 2002), as confirmed by many quantitative models that simulate saccade production (for a review see Girard & Berthoz, 2005). A key role in saccadic programming is played by cortical structures like the FEFs and the PEFs, and subcortical structures like the SC, in which information from FEFs and PEFs are integrated. More specifically, whereas the FEFs activity is more concerned with the programming of voluntary saccades, activity in the SC (and in the PEFs) is central for the programming of reflexive saccades (Müri & Nyffeler, 2008). In particular, when the saccadic neurons in the SC motor maps exceed an activation threshold, the corresponding program, specifying the direction and amplitude

of the saccade, is sent to the SBG (Godijn & Theeuwes, 2002b; Trappenberg, Dorris, Munoz, & Klein, 2001). The SBG, located in the reticular formation of the brainstem, consists of interconnected neural populations that transform the saccadic program in motor commands that activate the extraocular muscles controlling the eye movements (Fuchs et al., 1985; Scudder et al., 2002). Since the current results strongly indicate that saccadic programming is not subject to habituation, habituation of oculomotor capture must arise from the neural activity of the SBG, a possibility that finds support in important models of saccadic eye movements control, and according to which the final decision related to the generation of a saccade occurs in the SBG (e.g., Fuchs et al., 1985; Moschovakis, 1996; Robinson, 1968; Scudder et al., 2002).

The models postulate that when there is a competition between maintaining fixation and executing a saccade, two different activations emerge from the SC, a rostral one related to fixation, and a caudal one related to the movement of the eyes. The competition between the different activations, however, is not resolved at the programming stage within the SC, but rather at the execution stage in the SBG. More specifically, the competition arises between omnipause neurons (OPNs), which maintain fixation, and long-lead burst neurons (LLBNs), which are active during a saccade. Hence, as put forward by Otero-Millan and colleagues "...the mutually inhibitory circuit between OPNs and LLBNs, driven by the SC, is a likely candidate for the mechanism that normally triggers and suppresses saccades and microsaccades" (Otero-Millan, Macknik, Serra, Leigh, & Martinez-Conde, 2011) (p. 111). In a similar fashion, also the competition between the execution of reflexive and voluntary saccades would not be resolved within the SC, but rather it would involve a competitive interaction between different

populations of LLBNs within the SBG. Hence, oculomotor capture habituation is caused by a progressive decrease in the LLBNs neural activity controlling the reflexive saccade, whereas the LLBNs neural activity related to the target remains unaltered. It also follows that as habituation develops, the competition between the two populations of LLBNs should be resolved faster in favor of the saccade directed toward the target, as attested by the decrease in the latency of endogenous saccades that we have documented (Experiments 7-11).

The results fit nicely with models of saccade generation that place the competition at the SBG level (e.g., Fuchs et al., 1985; Moschovakis, 1996; Robinson, 1968; Scudder et al., 2002), whereas they seem to challenge one of the central tenets of *competitive integration model* (Godijn & Theeuwes, 2002b), which assumes that the competition between exogenous and endogenous saccades is resolved at the programming stage within the SC. According to this model, a single neural activation corresponding to the winning program (either the endogenous or the exogenous one) would emerge from the SC, and would be sent forward to the SBG. However, if habituation of oculomotor capture would reflect a progressive weakening of the reflexive saccade programming activity, then we should have also observed habituation in the microsaccadic inhibitory response, but this was clearly not the case.

A further implication of our findings concerns the long-lasting debate about the relation between attention shifts and eye movements. According to one view, the two forms of orienting are tightly coupled but independent (Hunt & Kingstone, 2003a, 2003b; Klein, 1980; Klein & Pontefract, 1994; Posner & Petersen, 1990), with separate neural networks involved in the control of covert and overt attention shifts (Smith & Schenk,

2012). An opposite view if proposed by the influential premotor theory of attention (Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Smith, Rorden, & Jackson, 2004), according to which spatial attention and eye movements are functionally equivalent, since a shift of attention results from the programming of an oculomotor command, with the two types of orienting sharing common neural substrates (e.g., de Haan, Morgan, & Rorden, 2008; Moore & Fallah, 2001). However, because previous studies have consistently shown that the exogenous orienting of attention elicited by a peripheral onset is subject to habituation (e.g., Turatto & Pascucci, 2016), the fact that the programming of a reflexive saccade toward the same repetitive onset is not subject to habituation, seems to challenge the main tenant of the premotor theory of attention, namely that the programming of a saccade is not equivalent to the orienting of attention. By contrast, when the results from experiments on habituation exogenous attention and microsaccades are considered altogether, they strongly suggest that eye movements and attention shifts are controlled by independent mechanisms (Smith & Schenk, 2012).

To conclude, the results of the last chapter confirmed that the execution of a reflexive saccade is subject to habituation, an ancestral form of learning that attenuated the organism's response toward irrelevant stimuli. On the contrary, this form of plasticity does not take place in the neural activity related to the programming of eye movements, such that the iterative presentation of the same peripheral onset always generates the corresponding saccadic program. This may have an adaptive value for the organism, because the oculomotor program associated with an irrelevant but salient stimulus remains available in case the same stimulus becomes motivationally significant. Indeed,

a saccade that has already been programmed is executed faster than a saccade whose program must be generated from scratch (Walker & McSorley, 2006).

General summary and conclusions

5.1 Final summary and discussion

The attentional system is innately responsive to salient stimuli, which makes distraction virtually inevitable. From the point of view of the organism's survival, distraction is, in the end, a cost that is worth paying to be always ready to inspect, and eventually react to, potentially relevant (e.g., aversive or appetitive) events, like those often signaled by sudden visual onsets. However, once a distracting stimulus has turned out to be innocuous and irrelevant, the cognitive system must be capable of ignoring further occurrences of the same stimulus to prevent repetitive, unwanted distraction, and consequently the continuous wasting of valuable limited-processing resources. Therefore, the characterization of the specific cognitive and neural mechanisms for distractor filtering has recently become a central topic in the study of attention.

The current work was aimed to study the habituation mechanisms responsible of the irrelevant information filtering. The first experimental part of the thesis (Chapter 2) was meant to disentangle between different points of view concerning the distractor filtering. On the one hand the strategic-suppression view explicitly assumes that distractor filtering is under top-down control, meaning that suppression of distractors would be purposefully implemented to restrict attentional processing to the target item (Awh, Matsukura, & Serences, 2003; Geng, 2014; Bacon & Egeth, 1994; Leber & Egeth, 2006; Dixon, Ruppel, Pratt, & de Rosa, 2009; Marini, Chelazzi, & Maravita, 2013; Müller,

von Mühlenen, & Geyer, 2007). On the other hand, the ability of the cognitive system to progressively ignore a recurrent distractor was recently interpreted in light of the more general phenomenon of habituation (Pascucci & Turatto, 2015; Turatto & Pascucci, 2016; see also Neo & Chua, 2006). The results are fully consistent with the habituation hypothesis, since the filtering of the irrelevant information took place also in the absence of a task, and consequently without a target stimulus to process. The demonstration that the distractor filtering takes place through the mechanisms of habituation, is helpful to shed light on the debate between bottom-up and top-down attentional control. Habituation reflects an automatic learning process (bottom-up), that occurs regardless the subject's intentions, and it is dictated only by the features of the stimulus. Our results argue against the theories claiming that the shift of attention is always volitional, and dictated by the specific goals of a person (Folk, Remington & Johnston, 1992); on the contrary, they are in agreement with theories according to which, at least in the very beginning phase, attentional control is always bottom-up (Theeuwes, 2010). The basic idea of the stimulus-driven selection (Theeuwes, 1991 b, 1992) is that when two or more stimuli are presented in the visual field, attention is divided between them, and a preattentive processing takes places, which is exclusively driven by the bottom-up properties of the stimulus. Only after an item has been selected, top-down control determines whether attention resides at a particular location (engagement) or is quickly disengaged from that location (Theeuwes, 2010). To accomplish preattentive selection we use a saliency map that encodes the salience of objects in their visual environment (Koch and Ullman, 1985; also see Theeuwes, 1994). Neurons in the map start a competition, giving rise to a single winning location that contains the most salient element. If this location is inhibited, spatial attention will be deployed to the next salient location. The fact that habituation mechanisms are responsible of the attentional capture reduction, suggests that the decrease in the relevance given to the irrelevant stimulus (from which it follows that the competition within the saliency map is won over time by the relevant stimulus) is mainly due to the modification of the perceived characteristics of the stimulus itself (automatic process), and not to the fact that we give an increasing importance to the target (voluntary process), as instead argued by the top-down inhibitory control theories.

Once established that habituation mechanisms are the most likely explanation that account for the decrement of attentional capture over time, the third chapter of the thesis was aimed at assessing whether habituation is context-dependent or if it generalizes across different contexts. The results strongly and clearly support the idea that the context plays a crucial role in the development and maintenance of habituation, since the neural representation of the stimulus that it is developed following its repeated presentation is linked to the context in which the stimulus is presented. When the context changes, the stimulus-context association decays and the habituation process breaks down, thus leading to a recovery of the previously habituated response. Knowing that a familiar stimulus regains value if moved in a new and different context, can be useful when the interest in a stimulus must be constantly kept alive, such in a training or learning situation, for example.

So far (Chapters 2 and 3), I investigated the way the attention system handles attentional capture; indeed, in all experiments participants were tested during a covert attention task, namely a type of task in which they were not allowed to move their eyes

in the visual scene. However, since attention and the oculomotor system often operate together, the fourth chapter of the thesis was dedicated to understand whether habituation affects also overt attention, using a task in which participants were asked to move the eyes. The results clearly showed that the oculomotor capture triggered by a peripheral onset distractor is subject to both short-term and long-term habituation. In addition, it was demonstrated that this learning process affects only the execution of an eye movement, and not its programming. This means that the oculomotor program associated with irrelevant but salient information remains always available, making us immediately ready to react, if necessary. This is the first study, to the best of my knowledge, that systematically investigated whether the exogenous saccadic programming, as well as the saccadic execution, is subject to a consistent reduction following the repeated presentation of the same irrelevant stimulus. The results of this last part can be helpful to understand the dynamics of the irrelevant information filtering. The fact that the habituation mechanisms affect only the last phase of the eye movements generation process (namely the saccadic execution) suggests that despite its repeated presentation, the distractor continues to indirectly capture attention, albeit at a minimum level. This idling attentional capture presumably has an adaptive value, since it can be necessary to keep the attentional system always ready for action in case of danger.

To summarize, the contribution of this work to the attentional capture issue is to have shown that (a) attentional capture is subject to habituation, a basic form of learning that takes place also when participants are passively exposed to an irrelevant stimulus; (b) this form of learning is context-dependent and (c) it affects also the oculomotor

system. However, (d) although the execution of a saccade is subject to habituation, the programming component is not.

Despite the results emerged from the current work, further studies will be needed in order to better understand what are the neural bases of attentional and oculomotor capture habituation and to characterize the brain regions involved in this type of information filtering mechanism.

5.2 Practical and clinical implications

The study of the mechanisms that we daily use to counteract distraction is essential to better understand how our cognitive system treats a sudden and unwanted event. Despite healthy people can rapidly learn to ignore an irrelevant stimulus that appears in the visual field, there are people that struggle to ignore irrelevant information (attention deficit hyperactivity disorder - ADHD) or who are distressed by intrusive thoughts that they cannot ignore (obsessive-compulsive disorder – OCD), with serious consequences for daily life. Having found that in healthy people the attentional and oculomotor capture is subject to habituation could have implications also on the clinical level, since it can offer a novel perspective to interpret the overmentioned mental disorders, which have dramatic consequences for the human beings, in both the childhood and the adulthood. As for ADHD, it is well known that affected people have constant problems in focusing only on relevant events/stimuli, and they are easily and constantly subject to distraction; it could be speculated that the difficulty one may have to remain focused on the primary task, without being continuous distracted by irrelevant stimuli, could depend on a non-optimal modulation of the exogenous attentional system by habituation. Similarly, OCD is a common disorder in which people have irrepressible

and recurrent thoughts (obsessions) and behaviors (compulsions) that they need to repeat over and over again; one could hypothesize that the continuously intrusive ideas experienced by these patients might reflect an insufficient modulation of habituation of the automatic orienting of attention toward the same irrelevant thoughts, which then become highly intrusive and disturbing. But it is merely a speculation, and further studies are needed in order to evaluate the correct functioning of the habituation process in people affected by mental deficits (also see, Ramaswami, 2014).

- Awh, E., Matsukura, M., & Serences, J. T. (2003). Top-down control over biased competition during covert spatial orienting. *Journal of Experimental Psychology:*Human Perception and Performance, 29(1), 52–63. https://doi.org/10.1037//0096-1523.29.1.52
- Awh, E., Matsukura, M., & Serences, J. T. (2010). Top-down modulation of biased competition during covert spatial orienting. *Journal of Vision, 2,* 15–15. http://dx.doi.org/10.1167/2.7.15
- Bacon, W. F., & Egeth, H. E. (1994). Overriding stimulus-driven attentional capture. *Perception & Psychophysics*, *55*(5), 485–496. https://doi.org/10.3758/BF03205306
- Bailey, C. H., & Chen, M. (1983). Morphological basis of long-term habituation and sensitization in Aplysia. *Science*, *220*(4592), 91–93. https://doi.org/10.1126/science.6828885
- Barry, R. J. (2009). Habituation of the orienting reflex and the development of Preliminary Process Theory. *Neurobiology of Learning and Memory, 92,* 235–242. http://dx.doi.org/10.1016/j.nlm.2008.07.007
- Bell, R., Röer, J. P., Dentale, S., & Buchner, A. (2012). Habituation of the irrelevant sound effect: Evidence for an attentional theory of short-term memory disruption. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *38*(6), 1542-1557. http://dx.doi.org/10.1037/a0028459
- Biederman, I. (1987). Recognition by components: A theory of human image understanding. *Psychological Review*, *94*(2), 115–117. https://doi.org/10.1037/0033-295X.94.2.115
- Boot, W. R., Kramer, A. F., & Peterson, M. S. (2005). Oculomotor consequences of abrupt object onsets and offsets: Onsets dominate oculomotor capture. *Perception & Psychophysics*, *67*(5), 910–928. https://doi.org/10.3758/BF03193543

- Breitmeyer, B. G., & Ganz, L. (1976). Implications of sustained and transient channels for theories of visual pattern masking, saccadic suppression, and information processing. *Psychological Review*, 83(1), 1-36. https://doi.org/10.1037/0033-295X.83.1.1
- Carandini, M. (2000). Visual cortex: Fatigue and adaptation. *Current Biology, 10*(16), 605–607. https://doi.org/10.1016/S0960-9822(00)00637-0
- Castellucci, V. F., & Kandel, E. R. (1974). A quantal analysis of the synaptic depression underlying habituation of the gill-withdrawal reflex in Aplysia. *Proceedings of the National Academy of Sciences of the United States of America*, 71(12), 5004–5008. https://doi.org/10.1073/pnas.71.12.5004
- Castellucci, V. F., Carew, T. J., & Kandel, E. R. (1978). Cellular analysis of long-term habituation of the gill-withdrawal reflex of Aplysia californica. *Science*, *202*(4374), 1306–1308. https://doi.org/ 10.1126/science.214854
- Castellucci, V., Pinsker, H., Kupfermann, I., & Kandel, E. R. (1970). Neuronal mechanisms of habituation and dishabituation of the gill-withdrawal reflex in Aplysia. *Science*, *167*(3926), 1745-1748.
- Chiandetti, C., & Turatto, M. (2017). Context-specific habituation of the freezing response in newborn chicks. *Behavioral Neuroscience*, *131*(5), 437–446. https://doi.org/10.1037/bne0000212
- Chun, M. M. (2000). Contextual cueing of visual attention. *Trends in Cognitive Sciences*, *4*(5), 170–178. doi:10.1016/S1364-6613(00)01476-5
- Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology*, *36*(1), 28–71. doi:10.1006/cogp.1998.0681
- Codispoti, M., De Cesarei, A., Biondi, S., & Ferrari, V. (2016). The fate of unattended stimuli and emotional habituation: Behavioral interference and cortical changes. *Cognitive, Affective and Behavioral Neuroscience*, *16*(6), 1063–1073. https://doi.org/10.3758/s13415-016-0453-0

- Codispoti, M., Ferrari, V., & Bradley, M. M. (2006). Repetitive picture processing: autonomic and cortical correlates. *Brain research*, *1068*(1), 213-220.
- Codispoti, M., Ferrari, V., & Bradley, M. M. (2007). Repetition and event-related potentials: distinguishing early and late processes in affective picture perception. *Journal of Cognitive Neuroscience*, *19*(4), 577-586.
- Cosman, J. D., & Vecera, S. P. (2013). Context-dependent control over attentional capture. *Journal of Experimental Psychology: Human Perception and Performance,* 39(3), 836–848. doi:10. 1037/a0030027
- Cosman, J. D., & Vecera, S. P. (2014). Establishment of an attentional set via statistical learning. *Journal of Experimental Psychology: Human Perception and Performance*, 40(1), 1–6. doi:10.1037/a0034489
- Cowan, N. (1988). Evolving conceptions of memory storage, selective attention, and their mutual constraints within the human information-processing system. *Psychological Bulletin, 104*(2), 163-191. https://doi.org/10.1037/0033-2909.104.2.163
- Cunningham, C. A., & Egeth, H. E. (2016). Taming the white bear: Initial costs and eventual benefits of distractor inhibition. *Psychological Science*, *27*, 476–485. http://dx.doi.org/10.1177/0956797615626564
- Davis, M. (1970). Effects of interstimulus interval length and variability on startle-response habituation in the rat. *Journal of Comparative and Physiological Psychology*, 72(2), 177-192. https://doi.org/10.1037/h0029472
- De Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, *1204*, 102-111. https://doi.org/10.1016/j.brainres.2008.01.105
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4

- Ditchburn, R. W., & Ginsborg, B. L. (1953). Involuntary eye movements during fixation.

 The Journal of Physiology, 119(1), 1–17.

 https://doi.org/10.1113/jphysiol.1953.sp004824
- Dixon, M. L., Ruppel, J., Pratt, J., & de Rosa, E. (2009). Learning to ignore: Acquisition of sustained attentional suppression. *Psychonomic Bulletin and Review, 16*(2), 418–423. https://doi.org/10.3758/PBR.16.2.418
- Dukewich, K. R. (2009). Reconceptualizing inhibition of return as habituation of the orienting response. *Psychonomic Bulletin & Review*, *16*(2), 238-251. https://doi.org/10.3758/PBR.16.2.238
- Dukewich, K. R., & Boehnke, S. E. (2008). Cue repetition increases inhibition of return. *Neuroscience Letters*, 448(3), 231-235. https://doi.org/10.1016/j.neulet.2008.10.063
- Elliott, E. M., & Cowan, N. (2001). Habituation to auditory distractors in a cross-modal, color–word interference task. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27*(3), 654-667. https://doi.org/10.1037/0278-7393.27.3.654
- Engbert, R. (2006). Microsaccades: a microcosm for research on oculomotor control, attention, and visual perception. *Progress in Brain Research*, *154*, 177–192. https://doi.org/10.1016/S0079-6123(06)54009-9
- Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research*, 43(9), 1035–1045. https://doi.org/10.1016/S0042-6989(03)00084-1
- Eriksen, C. W., & Colegate, R. L. (1971). Selective attention and serial processing in briefly presented visual displays. *Perception & Psychophysics*, *10*(5), 321-326.
- Eriksen, C. W., & Hoffman, J. E. (1972). Some characteristics of selective attention in visual perception determined by vocal reaction time. *Perception & Psychophysics*, *11*(2), 169-171.

- Ezzeddine, Y., & Glanzman, D. L. (2003). Prolonged habituation of the gill-withdrawal reflex in Aplysia depends on protein synthesis, protein phosphatase activity, and postsynaptic glutamate receptors. *The Journal of Neuroscience*, *23*(29), 9585–9594. https://doi.org/23/29/9585
- 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.
- Fischer, H., Furmark, T., Wik, G. & Fredrikson, M. (2000). Brain representation of habituation to repeated complex visual stimulation studied with PET. *NeuroReport*, *2*, 123-126.
- Folk, C. L., & Remington, R. (1998). Selectivity in distraction by irrelevant featural singletons: evidence for two forms of attentional capture. *Journal of Experimental Psychology: Human perception and performance*, 24(3), 847.
- Folk, C. L., & Remington, R. W. (2015). Unexpected abrupt onsets can override a top-down set for color. *Journal of Experimental Psychology: Human Perception and Performance*, 41(4), 1153–1165. http://dx.doi.org/10.1037/xhp0000084
- 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,* 1030–1044.

 http://dx.doi.org/10.1037/0096-1523.18.4.1030
- 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.
- Forster, S., & Lavie, N. (2008). Attentional capture by entirely irrelevant distractors. *Visual Cognition, 16,* 200–214. http://dx.doi.org/10.1080/13506280701465049
- Fuchs, A. F., Kaneko, C. R. S., & Scudder, C. A. (1985). Brainstem Control of Saccadic Eye Movements. *Annual Review of Neuroscience*, 8(1), 307–337. https://doi.org/10.1146/annurev.ne.08.030185.001515

- Galfano, G., Betta, E., & Turatto, M. (2004). Inhibition of return in microsaccades. *Experimental Brain Research, 159*(3), 400–404. https://doi.org/10.1007/s00221-004-2111-y
- Gaspelin, N., & Luck, S. J. (2018). The role of inhibition in avoiding distraction by salient stimuli. *Trends in Cognitive Sciences*, *22*(1), 79-92. https://doi.org/10.1016/j.tics.2017.11.001
- Gati, I., & Ben-Shakhar, G. (1990). Novelty and significance in orientation and habituation: A feature-matching approach. *Journal of Experimental Psychology: General*, 119(3), 251–263. doi:10.1037/0096-3445.119.3.251
- Geng, J. J. (2014). Attentional mechanisms of distractor suppression. *Current Directions in Psychological Science*, 23(2), 147–153.
 https://doi.org/10.1177/0963721414525780
- Geyer, T., Müller, H. J., & Krummenacher, J. (2008). Expectancies modulate attentional capture by salient color singletons. *Vision Research, 48,* 1315–1326. http://dx.doi.org/10.1016/j.visres.2008.02.006
- Girard, B., & Berthoz, A. (2005). From brainstem to cortex: Computational models of saccade generation circuitry. *Progress in Neurobiology*, *77*(4), 215–251. https://doi.org/10.1016/j.pneurobio.2005.11.001
- Godijn, R., & Kramer, A. F. (2008). Oculomotor capture by surprising onsets. *Visual Cognition*, *16* (2/3), 279–290. https://doi.org/10.1080/13506280701437295
- Godijn, R., & Theeuwes, J. (2002a). Oculomotor capture and Inhibition of Return: Evidence for an oculomotor suppression account of IOR. *Psychological Research*, 66(4), 234–246. https://doi.org/10.1007/s00426-002-0098-1
- Godijn, R., & Theeuwes, J. (2002b). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology. Human Perception and Performance*, *28*(5), 1039–1054. https://doi.org/10.1037/0096-1523.28.5.1039

- 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.
- Groves, P. M., & Thompson, R. F. (1970). Habituation: A dual-process theory. *Psychological Review*, 77(5), 419–450. https://doi.org/10.1037/h0029810
- Groves, P. M., & Thompson, R. F. (1973). A dual-process theory of habituation: Neural mechanisms. In *Physiological substrates* (pp. 175-205). Academic Press.
- Hafed, Z. M., & Clark, J. J. (2002). Microsaccades as an overt measure of covert attention shifts. *Vision Research*, 42(22), 2533–2545. https://doi.org/10.1016/S0042-6989(02)00263-8
- Hannula, D. E., & Ranganath, C. (2009). The eyes have it: Hippocampal activity predicts expression of memory in eye movements. *Neuron*, *63*(5), 592–599. doi:10.1016/j.neuron.2009.08.025
- Harris, J. D. (1943). Habituatory response decrement in the intact organism. *Psychological Bulletin*, 40(6), 385–422. doi:10.1037/h0053918
- Havermans, R. C. (2012). Stimulus specificity but no dishabituation of sensory-specific satiety. *Appetite*, *58*(3), 852–855. https://doi.org/10.1016/j.appet.2012.02.009
- Havermans, R. C., Hermanns, J., & Jansen, A. (2010). Eating without a nose: Olfactory dysfunction and sensory-specific satiety. *Chemical Senses*, *35*(8), 735–741. https://doi.org/10.1093/chemse/bjq074
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, *57*(6), 787–795. https://doi.org/10.3758/BF03206794
- Houck, R. L., & Mefferd, R. B. (1969). Generalization of GSR habituation to mild intramodal stimuli. *Psychophysiology*, *6*(2), 202–206. https://doi.org/10.1111/j.1469-8986.1969.tb02900.x

- Huang, Y., & Rao, R. P. N. (2011). Predictive coding. *WIREs Cognitive Science*, *2*, 580–593. http://dx.doi.org/10.1002/wcs.142
- Hunt, A. R., & Kingstone, A. (2003a). Covert and overt voluntary attention: linked or independent? *Cognitive Brain Research*, *18*(1), 102–105. https://doi.org/10.1016/j.cogbrainres.2003.08.006
- Hunt, A. R., & Kingstone, A. (2003b). Inhibition of return: Dissociating attentional and oculomotor components. *Journal of Experimental Psychology: Human Perception and Performance*, 29(5), 1068–1074. https://doi.org/10.1037/0096-1523.29.5.1068
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, *7*(1), 56–64. https://doi.org/10.1038/nn1169
- 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*, 1443–1458. https://doi.org/10.1016/S0042-6989(00)00030-4
- James, W. (1890). The principles of psychology (vol. 1) New York: Henry Holt & Co.
- Jonides, J., & Yantis, S. (1988). Uniqueness of abrupt visual onset in capturing attention. *Perception & Psychophysics*, 43(4), 346–354. https://doi.org/10.3758/BF03208805
- Jordan, W. P., Strasser, H. C., & McHale, L. (2000). Contextual control of long-term habituation in rats. *Journal of Experimental Psychology: Animal Behavior Processes,* 26(3), 323–339. doi:10.1037/0097-7403.26.3.323
- Kagan, J., Linn, S., Munt, R., Reznick, J. S., & Hiatt, S. (1979). Asymmetry of inference in the dishabituation paradigm. *Canadian Journal of Psychology*, *33*(4), 288–305. https://doi.org/10.1037/h0081727
- Kelley, T. A., & Yantis, S. (2009). Learning to attend: Effects of practice on information selection. *Journal of Vision*, 9(7):16, 1–18. http://journalofvision.org/9/7/16/, doi:10.1167/9.7.16

- Kimble, D. P., Bagshaw, M. H., & Pribram, K. H. (1965). The GSR of monkeys during orienting and habituation after selective partial ablations of the cingulate and frontal cortex. *Neuropsychologia*, *3*(2), 121-128.
- Klein, R. M. (2000). Inhibition of return. *Trends in cognitive sciences*, *4*(4), 138-147. https://doi.org/10.1016/S1364-6613(00)01452-2
- Klein, R. M., & Pontefract, A. (1994). Does oculomotor readiness mediate cognitive control of visual attention? Revisited! In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 333–350). The MIT Press.
- Klein, R.M. (1980). Does oculomotor readiness mediate cognitive control of visual attention? In R.S. Nickerson (Ed.), *Attention and performance VIII* (pp. 259–276). Hillsdale, NJ: Erlbaum.
- Koch, C., & Ullman, S. (1985). Shifts in selective visual attention: Towards the underlying neural circuitry. *Human Neurobiology*, *4*, 219–227.
- Kohn, A. (2007). Visual adaptation: Physiology, mechanisms, and functional benefits. *Journal of Neurophysiology, 10461,* 3155–3164. https://doi.org/10.1152/jn.00086.2007.
- Konorski, J. (1967). *Integrative activity of the brain*. Chicago, IL: University of Chicago Press.
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research*, *35*(13), 1897–1916. https://doi.org/10.1016/0042-6989(94)00279-U
- Krauskopf, J., Cornsweet, T. N., & Riggs, L. A. (1960). Analysis of eye movements during monocular and binocular fixation. *Journal of the Optical Society of America*, *50*(6), 572–578. https://doi.org/10.1364/JOSA.50.000572

- Kraut, A. G., & Smothergill, D. W. (1978). A two-factor theory of stimulus-repetition effects. *Journal of Experimental Psychology: Human Perception and Performance*, *4*(1), 191-197. https://doi.org/10.1037/0096-1523.4.1.191
- Laubrock, J., Engbert, R., & Kliegl, R. (2005). Microsaccade dynamics during covert attention. *Vision Research*, *45*(6), 721–730. https://doi.org/10.1016/j.visres.2004.09.029
- Laubrock, J., Engbert, R., Rolfs, M., & Kliegl, R. (2007). Microsaccades Are an Index of Covert Attention: Commentary on Horowitz, Fine, Fencsik, Yurgenson, and Wolfe (2007). *Psychological Science*, *18*(4), 364–366. https://doi.org/10.1111/j.1467-9280.2007.01904.x
- Leber, A. B., & Egeth, H. E. (2006a). Attention on autopilot: Past experience and attentional set. *Visual Cognition*, *14*, 565–583. http://dx.doi.org/10.1080/13506280500193438
- Leber, A. B., & Egeth, H. E. (2006b). It's under control: Top-down search strategies can override attentional capture. *Psychonomic Bulletin & Review, 13,* 132–138. http://dx.doi.org/10.3758/BF03193824
- Leber, A. B., Gwinn, R. E., Hong, Y., & O'Toole, R. J. (2016). Implicitly learned suppression of irrelevant spatial locations. *Psychonomic Bulletin & Review, 23,* 1873–1881. http://dx.doi.org/10.3758/s13423-016-1065-y
- Logan, G. D. (1988). Toward an instance theory of automatization. *Psychological Review*, 95(4), 492–527. doi:10.1037/0033-295X.95.4.492
- Lord, M. P. (1951). Measurement of binocular eye movements of subjects in the sitting position. *The British Journal of Ophthalmology*, *35*(1), 21–30.
- Ludwig, C. J. H., Ranson, A., & Gilchrist, I. D. (2008). Oculomotor capture by transient events: A comparison of abrupt onsets, offsets, motion, and flicker. *Journal of Vision*, 8(14):11, 1–16. https://doi.org/10.1167/8.14.11

- Lupiáñez, J., Martín-Arévalo, E., & Chica, A. B. (2013). Is Inhibition of Return due to attentional disengagement or to a detection cost? The Detection Cost Theory of IOR. *Psicológica*, *34*(2), 221-252.
- Mackworth, J. F. (1969). Vigilance and habituation. Penguin Books.
- 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), 906–922. https://doi.org/10.1037/a0029905
- 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.

 https://doi.org/10.1523/JNEUROSCI.2966-15.2016
- Marlin, N. A., & Miller, R. R. (1981). Associations to contextual stimuli as a determinant of long-term habituation. *Journal of Experimental Psychology: Animal Behavior Processes*, 7(4), 313.
- Marr, D. (1982). Vision. A computational investigation into the human representation and processing of visual information. San Francisco: W. H. *H. Freeman*.
- Martinez-Conde, S., Otero-Millan, J., & Macknik, S. L. (2013). The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nature Reviews Neuroscience*, *14*(2), 83–96. https://doi.org/10.1038/nrn3405
- McCamy, M. B., Otero-Millan, J., Macknik, S. L., Yang, Y., Troncoso, X. G., Baer, S. M., ... Martinez-Conde, S. (2012). Microsaccadic Efficacy and Contribution to Foveal and Peripheral Vision. *Journal of Neuroscience*, *32*(27), 9194–9204. https://doi.org/10.1523/JNEUROSCI.0515-12.2012
- Moher, J., Lakshmanan, B. M., Egeth, H. E., & Ewen, J. B. (2014). Inhibition drives early feature-based attention. *Psychological Science*, *25*, 315–324. http://dx.doi.org/10.1177/0956797613511257

- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, *98*(3), 1273-1276.
- Moschovakis, A. K. (1996). The superior colliculus and eye movement control. *Current Opinion in Neurobiology*, 6(6), 811–816. https://doi.org/10.1016/S0959-4388(96)80032-8
- 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), 1–16. doi:10.1037/0096-1523.35.1.1
- Müller, H. J., von Mühlenen, A., & Geyer, T. (2007). Top-down inhibition of search distractors in parallel visual search. *Perception & Psychophysics*, 69(8), 1373–1388. https://doi.org/10.3758/BF03192953
- Munneke, J., Heslenfeld, D. J., Usrey, W. M., Theeuwes, J., & Mangun, G. R. (2011).

 Preparatory effects of distractor suppression: Evidence from visual cortex. *PLoS ONE*, 6 (12), e27700. http://dx.doi.org/10.1371/journal.pone.0027700
- Müri, R. M., & Nyffeler, T. (2008). Neurophysiology and neuroanatomy of reflexive and volitional saccades as revealed by lesion studies with neurological patients and transcranial magnetic stimulation (TMS). *A Hundred Years of Eye Movement Research in Psychiatry*, 68(3), 284–292. https://doi.org/10.1016/j.bandc.2008.08.018
- Neo, G., & Chua, F. K. (2006). Capturing focused attention. *Perception & Psychophysics,* 68(8), 1286–1296. https://doi.org/10.3758/BF03193728
- Otero-Millan, J., Troncoso, X. G., Macknik, S. L., Serrano-Pedraza, I., & Martinez-Conde, S. (2008). Saccades and microsaccades during visual fixation, exploration, and search: Foundations for a common saccadic generator. *Journal of Vision, 8*(14), 21–21. https://doi.org/10.1167/8.14.21
- Otero-Millan, Jorge, Macknik, S. L., Serra, A., Leigh, R. J., & Martinez-Conde, S. (2011). Triggering mechanisms in microsaccade and saccade generation: a novel proposal:

- Otero-Millan et al. *Annals of the New York Academy of Sciences, 1233*(1), 107–116. https://doi.org/10.1111/j.1749-6632.2011.06177.x
- Pascucci, D., & Turatto, M. (2015). The distracting impact of repeated visible and invisible onsets on focused attention. *Journal of Experimental Psychology: Human Perception and Performance*, 41(3), 879–892. http://dx.doi.org/10.1037/xhp0000025
- Pavlov, I. P. (1927). Conditioned reflexes. Oxford University Press.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision*, *10*, 437–442. https://doi.org/10.1163/156856897X00366
- Peterson, M. S., Kramer, A. F., & Irwin, D. E. (2004). Covert shifts of attention precede involuntary eye movements. *Perception & Psychophysics*, *66*(3), 398–405. https://doi.org/10.3758/BF03194888
- Posner, M. I. (1980). Orienting of attention. *The Quarterly Journal of Experimental Psychology*, *32*, 3–25. http://dx.doi.org/10.1080/00335558008248231
- Posner, M.I., & Petersen, S.E. (1990). The attention system of the human brain. *Annual Review of Neuroscience*, *13*, 25–42.
- Ramaswami, M. (2014). Network plasticity in adaptive filtering and behavioral habituation. *Neuron*, *82*(6), 1216–1229. https://doi.org/10.1016/j.neuron.2014.04.035
- Rankin, C. H. (2000). Context conditioning in habituation in the nematode Caenorhabditis elegans. *Behavioral Neuroscience*, *114*(3), 496-505. https://doi.org/10.1037/0735-7044.114.3.496
- Rankin, C. H., & Carew, T. J. (1988). Dishabituation and sensitization emerge as separate processes during development in Aplysia. *The Journal of Neuroscience, 8,* 197–211.
- Rankin, C. H., Abrams, T., Barry, R. J., Bhatnagar, S., Clayton, D. F., Colombo, J., ... Thompson, R. F. (2009). Habituation revisited: An updated and revised description of

- the behavioral characteristics of habituation. *Neurobiology of Learning and Memory,* 92(2), 135–138. https://doi.org/10.1016/j.nlm.2008.09.012
- Reder, L. M., Weber, K., Shang, J., & Vanyukov, P. M. (2003). The adaptive character of the attentional system: Statistical sensitivity in a target localization task. *Journal of Experimental Psychology: Human Perception and Performance*, *29*, 631–649. http://dx.doi.org/10.1037/0096-1523.29.3.631
- Rizzolatti, G., Riggio, L., Sheliha, B.M. (1994). Space and selective attention. In C. Umiltà & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing*. 231–265.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, *25*(1A), 31-40.
- Robinson, D. A. (1968). Eye Movement Control in Primates. *Science*, 161(3847), 1219–1224.
- Röer, J. P., Bell, R., & Buchner, A. (2014). Evidence for habituation of the irrelevant-sound effect on serial recall. *Memory & Cognition*, *42*(4), 609-621. https://doi.org/10.3758/s13421-013-0381-y
- Röer, J. P., Bell, R., & Buchner, A. (2015). Specific foreknowledge reduces auditory distraction by irrelevant speech. *Journal of Experimental Psychology: Human Perception and Performance*, 41, 692–702. http://dx.doi.org/10.1037/xhp0000028
- Rolfs, M., Engbert, R., & Kliegl, R. (2004). Microsaccade Orientation Supports Attentional Enhancement Opposite a Peripheral Cue: Commentary on Tse, Sheinberg, and Logothetis (2003). *Psychological Science*, *15*(10), 705–707. https://doi.org/10.1111/j.0956-7976.2004.00744.x
- Rolfs, M., Kliegl, R., & Engbert, R. (2008). Toward a model of microsaccade generation: The case of microsaccadic inhibition. *Journal of Vision, 8*(11), 5–5. https://doi.org/10.1167/8.11.5

- Rolfs, M., Laubrock, J., & Kliegl, R. (2006). Shortening and prolongation of saccade latencies following microsaccades. *Experimental Brain Research*, 169(3), 369.
- Rolfs, M., Engbert, R., & Kliegl, R. (2005). Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Experimental Brain Research*, *166*(3), 427–439. https://doi.org/10.1007/s00221-005-2382-y
- Ruz, M., & Lupiáñez, J. (2002). A review of attentional capture: On its automaticity and sensitivity to endogenous control. *Psicológica*, *23*, 283–309.
- Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological Review*, 84(1), 1–66. doi:10.1037/0033-295X.84.1.1
- Schreij, D., Owens, C., & Theeuwes, J. (2008). Abrupt onsets capture attention independent of top-down control settings. *Community Eye Health Journal, 70*(2), 208–218. https://doi.org/10.3758/PP
- Schupp, H. T., Stockburger, J., Codispoti, M., Junghöfer, M., Weike, A. I., & Hamm, A. O. (2006). Stimulus novelty and emotion perception: the near absence of habituation in the visual cortex. *Neuroreport*, *17*(4), 365-369.
- Scudder, C. A., Kaneko, C. R., & Fuchs, A. F. (2002). The brainstem burst generator for saccadic eye movements. *Experimental Brain Research*, *142*(4), 439–462. https://doi.org/10.1007/s00221-001-0912-9
- Sharpless, S. & Jasper H. (1956). Habituation of the arousal reaction. *Brain*, 79, 655-680.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*(3), 507–522. https://doi.org/10.1007/BF00233988
- Shiffrin, R. M., & Schneider, W. (1977). Controlled and automatic human information processing: II. Perceptual learning, automatic attending and a general theory. *Psychological review*, 84(2), 127.

- Smith, D. T., & Schenk, T. (2012). The premotor theory of attention: time to move on?. *Neuropsychologia*, *50*(6), 1104-1114.
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous Orienting of Attention

 Depends upon the Ability to Execute Eye Movements. *Current Biology*, *14*(9), 792–795. https://doi.org/10.1016/j.cub.2004.04.035
- Sokolov, E. N. (1960). Neuronal models and the orienting reflex. In M. A. B. Brazier (Eds.), *The central nervous system and behaviour: III*. New York: Macy Foundation.
- Sokolov, E. N. (1963). Higher nervous functions: The orienting reflex. *Annual Review of Physiology*, *25*, 545–580.
- Sörqvist, P. (2010). High working memory capacity attenuates the deviation effect but not the changing-state effect: Further support for the duplex-mechanism account of auditory distraction. *Memory & Cognition*, *38*, 651–658. http://dx.doi.org/10.3758/MC.38.5.651
- Sörqvist, P., & Rönnberg, J. (2014). Individual differences in distractibility: An update and a model. *PsyCh Journal*, *3*(1), 42–57. doi:10.1002/pchj.47
- Sörqvist, P., Nöstl, A., & Halin, N. (2012). Working memory capacity modulates habituation rate: Evidence from a cross-modal auditory distraction paradigm. *Psychonomic Bulletin and Review, 19*(2), 245–250. doi:10.3758/s13423-011-0203-9
- Steiner, G. Z., & Barry, R. J. (2011). Exploring the mechanism of dishabituation. *Neurobiology of Learning and Memory*, 95(4), 461–466. https://doi.org/10.1016/j.nlm.2011.02.007
- Steiner, G. Z., & Barry, R. J. (2014). The mechanism of dishabituation. *Frontiers in Integrative Neuroscience*, *8*, 1–8. https://doi.org/10.3389/fnint.2014.00014
- Stephenson, D., & Siddle, D. A. T. (1983). Theories of habituation. In D. Siddle (Ed.), *Orienting and habituation: Perspectives in human research* (pp. 183–236). Chichester: Wiley.

- Stilwell, B. T., & Vecera, S. P. (2019). Learned and cued distractor rejection for multiple features in visual search. *Attention, Perception, & Psychophysics*, 81(2), 359-376.
- Theeuwes, J. (1991 a). Exogenous and endogenous control of attention: The effect of visual onsets and offsets. *Perception & Psychophysics*, 49, 83–90. http://dx.doi.org/10.3758/BF03211619
- Theeuwes, J. (1991 b). Cross-dimensional perceptual selectivity. *Perception & Psychophysics*, *50*(2), 184–193. https://doi.org/10.3758/BF03212219
- Theeuwes, J. (1992). Perceptual selectivity for color and form. *Perception & psychophysics*, *51*(6), 599-606.
- Theeuwes, J. (1994). Endogenous and exogenous control of visual selection. *Perception,* 23(4), 429–440.
- Theeuwes, J., Kramer, A. F., Hahn, S., & Irwin, D. E. (1998). Our Eyes do Not Always Go Where we Want Them to Go: Capture of the Eyes by New Objects. *Psychological Science*, *9*(5), 379–385. https://doi.org/10.1111/1467-9280.00071
- 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(6), 1595–1608.

 https://doi.org/10.1037/0096-1523.25.6.1595
- Theeuwes, J. (2010). Top–down and bottom–up control of visual selection. *Acta psychologica*, 135(2), 77-99. https://doi.org/10.1016/j.actpsy.2010.02.006
- Thompson, P., & Burr, D. (2009). Visual aftereffects. *Current Biology, 19,* R11–R14. http://dx.doi.org/10.1016/j.cub.2008.10.014
- Thompson, R. F. (2009). Habituation: A history. *Neurobiology of Learning and Memory,* 92(2), 127–134. https://doi.org/10.1016/j.nlm.2008.07.011
- Thompson, R. F., & Spencer, W. A. (1966). Habituation: A model phenomenon for the study of neuronal substrates of behaviour. *Psychological Review*, *73*(1), 16–43.

- Tomsic, D., Pedreira, M. E., Romano, A., Hermitte, G., & Maldonado, H. (1998). Context-US association as a determinant of long-term habituation in the crab chasmagnathus. *Animal Learning and Behavior*, *26*(2), 196–209. https://doi.org/10.3758/BF03199212
- Trappenberg, T. P., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A Model of Saccade Initiation Based on the Competitive Integration of Exogenous and Endogenous Signals in the Superior Colliculus. *Journal of Cognitive Neuroscience*, 13(2), 256–271. https://doi.org/10.1162/089892901564306
- Turatto, M., & Pascucci, D. (2016). Short-term and long-term plasticity in the visual-attention system: Evidence from habituation of attentional capture. *Neurobiology of Learning and Memory*, *130*, 159–169. https://doi.org/10.1016/j.nlm.2016.02.010
- Turatto, M., Bonetti, F., & Pascucci, D. (2018a). Filtering visual onsets via habituation: A context-specific long-term memory of irrelevant stimuli. *Psychonomic Bulletin & Review, 1-7.* https://doi.org/10.3758/s13423-017-1320-x
- Turatto, M., Bonetti, F., Chiandetti, C., & Pascucci, D. (2019). Context-specific distractors rejection: contextual cues control long-term habituation of attentional capture by abrupt onsets. *Visual Cognition*, 1–14. https://doi.org/10.1080/13506285.2019.1580233
- Turatto, M., Bonetti, F., Pascucci, D., & Chelazzi, L. (2018b). Desensitizing the attention system to distraction while idling: A new latent learning phenomenon in the visual attention domain. *Journal of Experimental Psychology: General, 147*(12), 1827–1850. https://doi.org/10.1037/xge0000503
- Vatterott, D. B., & Vecera, S. P. (2012). Experience-dependent attentional tuning of distractor rejection. *Psychonomic Bulletin & Review*, *19*(5), 871-878. https://doi.org/10.3758/s13423-012-0280-4
- Vatterott, D. B., Mozer, M. C., & Vecera, S. P. (2018). Rejecting salient distractors:

 Generalization from experience. *Attention, Perception, and Psychophysics*, 80(2), 485–499. doi:10.3758/s13414-017-1465-8

- Vecera, S. P., & Farah, M. J. (1994). Does visual attention select objects or locations? *Journal of Experimental Psychology: General, 123*(2), 146–160. https://doi.org/10.1037/0096-3445.123.2.146
- Vecera, S. P., Cosman, J. D., Vatterott, D. B., & Roper, Z. J. (2014). The control of visual attention: Toward a unified account. In *Psychology of learning and motivation*, *60*, 303-347. https://doi.org/10.1016/B978-0-12-800090-8.00008-1
- Vissers, M. E., van Driel, J., & Slagter, H. A. (2016). Proactive, but not reactive, distractor filtering relies on local modulation of alpha oscillatory activity. *Journal of Cognitive Neuroscience*, *28*, 1964–1979. http://dx.doi.org/10.1162/jocn_a_01017
- Wagner, A. R. (1976). Priming in STM: An information-processing mechanism for self-generated or retrieval-generated depression in performance. In T. J. Tighe, & R. N. Leaton (Eds.), *Habituation: Perspectives from child development, animal behavior, and neurophysiology* (pp. 95–128). Hillsdale, NJ: Erlabaum.
- Wagner, A. R. (1978). Expectancies and the priming of STM. In S. H. Hulse, H. Fowler, & R. Honig (Eds.), *Cognitive processes in animal behavior* (pp. 177–209). Hillsdale, NJ: Erlabaum. doi:10.1101/lm.77504.ing
- Wagner, A. R. (1979). Habituation and memory. *Mechanisms of learning and motivation*, 53-82.
- Walker, R., & McSorley, E. (2006). The parallel programming of voluntary and reflexive saccades. *Vision Research*, 46(13), 2082–2093. https://doi.org/10.1016/j.visres.2005.12.009
- Wang, B., & Theeuwes, J. (2018). Statistical regularities modulate attentional capture. *Journal of Experimental Psychology: Human Perception and Performance, 44,* 13–17. http://dx.doi.org/10.1037/xhp0000472
- Waters, W. F., McDonald, D. G., & Koresko, R. L. (1977). Habituation of the orienting response: A gating mechanism subserving selective attention. *Psychophysiology*, *14*(3), 228–236. https://doi.org/10.1111/j.1469-8986.1977.tb01166.x

- Webster, M. A. (2012). Evolving concepts of sensory adaptation. *F1000 Biology Reports,* 4, 21.
- Yantis, S., & Jonides, J. (1984). Abrupt visual onsets and selective attention: Evidence from visual search. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(5), 601–621. https://doi.org/10.1037//0096-1523.10.5.601
- Yantis, S., & Jonides, J. (1996). Attentional capture by abrupt onsets: New perceptual objects or visual masking? *Journal of Experimental Psychology: Human Perception and Performance*, 22(6), 1505–1513. https://doi.org/10.1037/0096-1523.22.6.1505
- Zuber, B. L., Stark, L., & Cook, G. (1965). Microsaccades and the Velocity-Amplitude Relationship for Saccadic Eye Movements. *Science*, 150(3702), 1459–1460. https://doi.org/10.1126/science.150.3702.1459