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Short-term and long-term plasticity in the visual-attention system: Evidence from habituation of attentional capture

Massimo Turatto [a,b,*], David Pascucci [c]

[a] Center for Mind/Brain Sciences, University of Trento, Italy
[b] Department of Psychology and Cognitive Sciences, University of Trento, Italy
[c] Department of Neurological Sciences, Section of Physiology and Psychology, University of Verona, Italy

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ABSTRACT

Attention is known to be crucial for learning and to regulate activity-dependent brain plasticity. Here we report the opposite scenario, with plasticity affecting the onset-driven automatic deployment of spatial attention. Specifically, we showed that attentional capture is subject to habituation, a fundamental form of plasticity consisting in a response decrement to repeated stimulations. Participants performed a visual discrimination task with focused attention, while being occasionally exposed to a distractor consisting of a high-luminance peripheral onset. With practice, short-term and long-term habituation of attentional capture emerged, making the visual-attention system fully immune to distraction. Furthermore, spontaneous recovery of attentional capture was found when the distractor was temporarily removed. Capture, however, once habituated was surprisingly resistant to spontaneous recovery, taking from several minutes to days to recover. The results suggest that the mechanisms subserving exogenous attentional orienting are subject to profound and enduring plastic changes based on previous experience, and that habituation can impact high-order cognitive functions.

1. Introduction

Plasticity and selectivity are two fundamental characteristics of the central nervous system. Plasticity is exemplified by the brain's ability to retain and integrate new information from past experience, namely by learning. Selectivity is expressed whenever the limited resources of analysis are deployed to certain stimuli or locations and not to others, a function accomplished by selective attention. Although attention and learning are independent processes, as common experience suggests they are also strongly related: for example, we all know that to learn the name of a person just met, or the lyric of a new poem, we must pay attention to this information. Attention is often important for learning, and particularly with respect to an important instance of cortical plasticity known as perceptual learning (Fahle & Poggio, 2002). The research in this area has shown that attention plays a major role in controlling this form of experience-dependent plasticity (Ahissar & Hochstein, 1993). Much less obvious, instead, is the possibility that plasticity might have an impact on selectivity, or in other words, that some form of learning could affect attentional selection. To address this issue, we decided to explore the role of habituation in the mechanisms of exogenous attentional capture.

Habituation is the simplest and most basic form of experience-dependent plasticity, and consists in a decrement of response following repeated irrelevant stimulation (Thompson, 2009). It is present in virtually all animals, from amoeba to humans, which suggests that it must have great survival value for the organism. Obviously, the type of habituation occurring in single-celled organisms lacking a central nervous system must be different from that observed in higher vertebrates, whose behavioral responses are for a large part controlled by the brain. In particular, we are interested in a cerebral form of habituation possibly affecting higher cognitive functions like attention. Since the pioneering work of Thompson and Spencer (1966) habituation is known to present nine specific features, among which the most relevant for the present study are the first four: (#1) given that a particular stimulus elicits a response, repeated applications of the stimulus result in decreased response (habituation); (#2) if the stimulus is withheld, the response tends to recover over time (spontaneous recovery); (#3) other things being equal, the more rapid the frequency of stimulation, the more rapid and/or more pronounced is habituation; (#4) if repeated series of habituation training and spontaneous recovery are given, habituation becomes successively more rapid (potentiation of habituation). Finally, it is useful to consider that short-term

* Corresponding author at: Center for Mind/Brain Sciences, University of Trento, Italy.

E-mail address: massimo.turatto@unitn.it (M. Turatto).

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(within session) and long-term (across sessions) mechanisms of habituation have been described (Thompson & Spencer, 1966; Thompson, 2009).

As for the orienting of attention, it can be controlled either endogenously or exogenously. The former occurs when attention is voluntary controlled by the observer's will and goals, whereas the latter occurs automatically, with the deployment of attention controlled by some salient properties of the sensory input, regardless of the observers' intentions (Egeth & Yantis, 1997). In particular, high-contrast sudden onsets are among the most powerful attentional-grabbing events (Jonides & Yantis, 1988; Yantis & Jonides, 1984), likely because they signal the visual system that a new object has appeared in the scene. However, as to whether the capture of attention triggered by visual onsets is mandatory, the results of two studies seemed to indicate that when attention was fully focused in advance on the upcoming target location, onsets no longer captured attention (Theeuwes, 1991; Yantis & Jonides, 1990). The notion emerging from these studies was that when attention is unfocused, onsets do have a distracting power; but if attention is completely focused prior to onsets appearance, onsets do not capture focused attention.

This conclusion, however, has been challenged by the results of a more recent study by Neo and Chua (2006). The authors showed that if irrelevant onsets are infrequent events they do capture attention in an automatic fashion, even when attention is fully focused. But if irrelevant onsets are presented too frequently (i.e. in the majority of the trials), onsets fail to capture attention, likely because the exogenous orienting of attention is suppressed as a result of habituation (Sokolov, 1963). This would explain why previous studies, in which the irrelevant onset was presented almost in every trial, did not find evidence of capture (Theeuwes, 1991; Yantis & Jonides, 1990). That infrequent onset distractors do capture focused attention in a mandatory fashion was also confirmed in a recent study by Pascucci and Turatto (2015), who showed that while a single or two onsets captured attention, a longer series of onsets did not. Hence, the frequency with which an irrelevant peripheral onset is presented across trials seems to play a crucial role in modulating the onset's strength in capturing focused attention (Neo & Chua, 2006; Pascucci & Turatto, 2015).

Two features of sudden onsets make them particularly suitable to study whether plasticity has any modulatory effect on attention: first, onsets exert a strong influence on the mechanism controlling the orienting of attention, often triggering an automatic attentional capture, and thus creating the most challenging condition for the habituation of attentional capture to occur; second, attentional capture driven by onsets takes place also when onsets are completely irrelevant (Jonides, 1981), a typical characteristic of the stimuli for which habituation can be observed.

Whether or not habituation can affect the automatic attentional capture is something that has not been specifically and systematically addressed. However, the fact that different visceral and motor responses of the orienting reflex have long been shown to habituate (Barry, 2009; Sokolov, 1963), suggests that this might be the case. Hence, to establish whether habituation could specifically modulate the capture of spatial attention we engaged our participants in a speeded visual discrimination task with focused attention. Crucially, 200 ms before the occurrence of a visual target the sudden onset of a bright annulus serving as distractor was occasionally presented (Fig. 1). Attentional capture is found if the presence of the distractor increases the response times (RTs) and/or the errors for target discrimination. Habituation emerges if the amount of capture diminishes with repeated exposition to the distractor; by contrast, spontaneous recovery is observed if capture is to some extent restored after the distractor is withheld for a certain time.

2. General method

2.1. Participants

Overall, 121 participants (85 females) were recruited in the study, and were divided as follows: 13 in Experiment 1, and 18 in each of the remaining experiments (Experiment 2, 3a, 3b, 4, 5, 5b). Participants were undergraduate students of the University of Trento (Italy), recruited from the Department of Psychology and Cognitive Sciences for course credits. Their ages ranged from 19 to 39 yeas old. 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, and 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, University of Trento, Italy).

2.2. Apparatus

The apparatus was identical in all of the experiments. Stimuli were presented on a ViewSonic Graphic Series G90fB 19″ (1024×768, 100 Hz) and generated with a custom made program written in MATLAB and the Psychophysics Toolkbox (Pelli, 1997) running on a Dell Precision T1600 machine (Windows 7 Enterprise). Eye fixation was monitored with an Eyelink 1000 Tower Mount system (sampling rate: 1000 Hz; SR Research, Ontario, Canada).

2.3. Stimuli and procedure

The same visual stimuli were used in all experiments. All trials started with the presentation of a central fixation spot (0.5° of visual angle in diameter, 19.5 cd/m^2) displayed for 500 ms on a uniform gray background (35.3 cd/m^2). This was followed by the appearance of four placeholders (four annuli with inner diameter of 4° and outer diameter of 4.15°) centered on the four corners of an imaginary square around fixation (diagonal of 22.62°). Three of the placeholders were gray (17.5 cd/m^2) indicating task-irrelevant locations, while the remaining one was red (7 cd/m^2), serving as visual cue for the position of the upcoming target. The position of the red annulus was randomly assigned on each trial. The four placeholders remained on screen for 1300 ms. In the last 100 ms of presentation, the visual target, a gray Landolt C (1.5°, 30.8 cd/m^2) with a 0.5° gap on the right or left side, appeared at the center of the cued location. In distractor-present trials, 200 ms before the target a high-luminance light-gray annulus frame (inner diameter of 3.75°, outer diameter of 4.25°, 88.9 cd/m^2) was superimposed for 100 ms to one of the irrelevant placeholders, thus creating a sudden visual onset distractor. The position of the distractor relative to the target position was balanced across trials.

Participants were instructed to maintain fixation on the central spot while focusing their attention exclusively on the location cued by the red annulus. The task was to report as quick as possible the position of the target's gap (left vs. right) by pressing the corresponding arrow on the computer keyboard. Response times were recorded for 1500 ms starting from the appearance of the target. Trials in which participants did not respond within this time window were excluded from the analysis (less than 1% in total). Incorrect target discriminations were followed by an error message presented on the screen for 500 ms at the end of each trial.

Eye position was monitored starting from 800 ms before the target, and until the target disappeared. When eye movements or blinks were detected in the first 500 ms, the trial was interrupted