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The influences of preparation and brain states on the time-course of oculomotor control in visual selection

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“..Imagine for a moment that we are nothing but the product of billions of years of molecules coming together and ratcheting up through natural selection, that we are composed only of highways of fluids and chemicals sliding along roadways within billions of dancing cells, that trillions of synaptic conversations hum in parallel, that this vast egg like fabric of micron-thin circuitry runs algorithms undreamt of in modern science, and that these neural programs give rise to our decision making, loves, desires, fears, and aspirations. To me, that understanding would be a numinous experience, better than anything ever proposed in anyone's holy text.”

David Eagleman

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Publications

Paoletti, D., Weaver, M. D., Braun, C., & van Zoest, W. (2014). Trading off stimulus salience for identity: A cueing approach to disentangle visual selection strategies. *Vision Research*. doi:10.1016/j.visres.2014.08.003

Weaver, M.D., Paoletti, D., van Zoest, W. (2014). The impact of predictive cues and visual working memory on dynamic oculomotor selection. *Journal of Vision*, 14(3). doi: 10.1167/14.3.27

Paoletti, D., Braun, C., & van Zoest, W. (under revision). The effect of pre-stimulus neural oscillatory activity on saccadic reaction times and oculomotor selection performance.

Preface

Every day our eyes are overflowed by a constant stream of visual information, however, we have the innate capacity of selecting any subset of it that is relevant for our purposes. We may scan familiar visual scenes for searching what we need: it can be a key, a lighter, our glasses or a smartphone on a probably messy desktop. Maybe we are in a hurry for our meeting, and our eyes spasmodically jump from one object to the other, without having success in the visual search. Why are we selecting certain objects instead of the one we are looking for? For example, we may want to find the small white piece of paper on which we noted down the details of a very important meeting we need to attend. However, the natural blue fluorescent lamp that our colleague bought is way too attractive for our eyes, and we may also feel kind of tired that morning. In the end, we usually find what we need, but in different ways. I am sure you agree with me that often, during searches, it happens that things other than the object of search capture your attention. Often sudden things are particularly salient and your eyes are kind of involuntary captured, and this mostly happens when you are in hurry. This search modality is known as stimulus-driven. If instead you take your time, you will realize that avoiding salient items can be extremely easy and after a while your eyes will succeed in finding what you were looking for. In this latter case you are adopting the so-called goal-driven strategy. Although there have been many studies on the influences of stimulus- and goal-driven control of attention, only few investigate the role of time in stimulus-driven and goal-driven visual selection. Moreover, as expressed above, the strategy you want to adopt may not solely depend on your intentions. It may be the case that one of the most important organ of your body that day does not feel like helping just before starting to search. In more scientific words, it can be the case that preparatory mechanisms occurring before the beginning your search may influence the search modality itself.

The goal of present thesis is twofold. Firstly, we aim to investigate if observers are able to consciously regulate the trade-off between stimulus-driven and goal-driven strategies of visual selection. Secondly, we aim to uncover how brain processes occurring before the display presentation may affect visual search modalities both in terms of response time and performance.

Chapter 1

General Introduction

Stimulus-driven and goal-driven

At any given time, the visual field is full of information that cannot be processed at once. An essential property of our brain is the capacity of selecting subsets of information that is important for us, and discard the irrelevant ones. Visual search occurs whenever we are scanning the environment to find a specific element, pattern or even a group of object. This process can be accomplished mostly in two ways: by covertly selecting the relevant subset of information, or by overtly deploying an eye movement to the target location. Thus, it becomes clear how attention and eye movement are closely connected. By means of eye movements and shifting attention individuals are able to visually explore the environment according to their needs. Attention and eye movement may be controlled by the properties of the stimulus field or by goals and intentions of the observers. Theories and models of visual search refer to these search modalities as stimulus-driven and goal-driven (Connor, Egeth, & Yantis, 2004; Corbetta & Shulman, 2002; Shipp, 2004). Bottom-up mechanisms are considered to control the selection when visual search is stimulus driven; that is, when the winner of selection corresponds to the more salient element present in the visual field. Visual saliency here refers to the physical, distinctiveness of an element, and is a relative property that is contextually dependent (Itti, Koch & Niebur, 1998). Top-down processes, instead, grant attention to those elements that match the observer's target settings and lead to goal driven selection behaviors. In the past, some researchers have argued that stimulus-driven processes dominate visual selection, (Banich et al., 2000; Nothdurft, 2002; Theeuwes, 1992, 2004) resulting in an attentional control predominantly driven by stimulus saliency. According to this bottom-up model, selection is only influenced by stimulus-driven control while goal-driven processes may only play a role in the process after an element is selected on the basis of stimulus-driven activity (Nothdurft, 2002; Jan Theeuwes, Atchley, & Kramer, 2000). In other words, endogenous modulation can only contribute to visual selection processes only after an

element is identified. Goal-driven control is assumed to occur after, and to be contingent to stimulus-driven control (Itti, L., Koch, C., Niebur, 1998; Koch & Ullman, 1987; Nothdurft, 2002; Theeuwes & Burger, 1998; VanRullen, 2003). On the other hand, other researchers have claimed that it is the goal-driven processes which control visual selection (Bacon & Egeth, 1994; Chen & Zelinsky, 2006; Folk, Remington, & Johnston, 1992). According to this top-down view of attentional selection, initial search is determined by observers' goals and intentions. However, while selection may sometimes be more stimulus driven than goal driven or vice versa, most researchers agree that stimulus-driven and goal-driven factors interact to ultimately control the allocation of attentional selection (Connor et al., 2004; Duncan & Humphreys, 1989; Serences et al., 2005; Treisman & Sato, 1990).

Evidence for stimulus-driven and goal-driven saccadic programming can be readily observed in visual search tasks in which eye movements are recorded (Hunt, von Mühlenen, & Kingstone, 2007; Wieske van Zoest, Donk, & Theeuwes, 2004). In a standard visual search task, participants are required to respond or to fixate a target item among a number of non-targets items. When saccades in these tasks are stimulus-driven, they are involuntary driven by stimulus-properties of the visual field, irrespective of the goals and intentions of the participants. Stimulus-driven saccades are also referred to as exogenous saccades and depend on an items' saliency, that is, the greater is the saliency of an object and the bigger is the amount of exogenous stimulation (Desimone & Duncan, 1995; Godijn & Theeuwes, 2002; Wolfe, 1994). The idea that oculomotor responses occurring early in time are more likely to be made to the most physically salient stimuli regardless of task-relevance is supported by recent studies on visual selection (Godijn & Theeuwes, 2002; Mulckhuyse, van Zoest, & Theeuwes, 2008). When saccades are instead goal-driven, they are voluntarily directed to those items that are in line with a current set of goals or intentions. Goal-driven eye movements are also referred to as endogenous saccades. Stimulus-driven and goal-driven saccadic selections are not mutually exclusive. Both stimulus-driven and goal-driven processes may contribute to drive the eyes to a certain location. For example, if the pre-specified target is the most salient element item in a display, both stimulus-driven and goal-driven processes may influence the saccade toward the target. In summary, goal- and stimulus-processes ultimately interact to control the allocation of attention, however, one factor that is underrated in the above cited studies, is the role of time.

Evidence for time-course

Recent studies (van Zoest et al., 2004; van Zoest & Donk, 2006) provide support for the view that stimulus-driven and goal-driven strategies influence the processing of the same visual stimuli and the executed saccade but do so via different time windows. The design adopted in these studies is based on the additional-singleton paradigm (Theeuwes, 1992). In this task, participants perform a visual search and are instructed to execute a fast saccade toward a unique target presented amongst a number of identical non-targets. A singleton distractor that differs from the target in the same dimension (i.e., orientation) is presented concurrently with the search display. This distractor can be more or less salient than the target. To analyze the time course, the oculomotor responses are binned (divided into bins) according to the saccadic reaction times. For each bin the correct proportion of eye movements are computed by dividing the number of eye movement that landed on the target by the total number of eye movement that observers made. Splitting the saccadic eye movements of observers on the basis of reaction time allows for a better understanding of the relative contribution of stimulus-driven and goal-directed control in a variety of response latencies. The typical pattern of results shows that early oculomotor responses are frequently directed toward the most salient element on the screen (i.e., singleton target or distractor) and that the effect of stimulus-saliency transiently decreases with time, even if it concerns the target. This shows that the influence of saliency and goal-directed control are independent (van Zoest & Donk, 2008) and that saccadic visual selection is initially completely saliency-driven, whereas goal-driven control dominates visual selection later in time. The findings of van Zoest and Donk are in line with former studies that have shown how stimulus-driven activity is fast and transient, while goal-driven activity arises later and is more sustained (Cheal & Chastain, 2002; Cheal & Lyon, 1991; Müller & Rabbitt, 1989; Nakayama & Mackeben, 1989). While bottom-up models of attention selection are able to account for the early effects of saliency, top-down models of attention are able to account for the absence of an effect of saliency later during selection. In turn, a bottom-up account fails to explain the absence of a saliency effect in case of slow eye movements, while a top-down control model fails to explain the large saliency effect in case of fast saccades. As a result, one or the other account per se cannot explain stimulus-driven and goal-driven control influence selection independently. This further suggests that both stimulus-driven and goal-driven selections occur, but in different time windows.

Neural correlates of visual oculomotor selection

The neural circuitry that is responsible for visual selection and saccades generation has been intensely investigated in the past decade. Researchers, employing different type of imaging technique were able to reveal a wide network underlying generation and execution of saccades (Leigh & Zee, 1982; Moschovakis, Scudder, & Highstein, 1996; Scudder, Kaneko, & Fuchs, 2002; Wurtz & Goldberg, 1989).

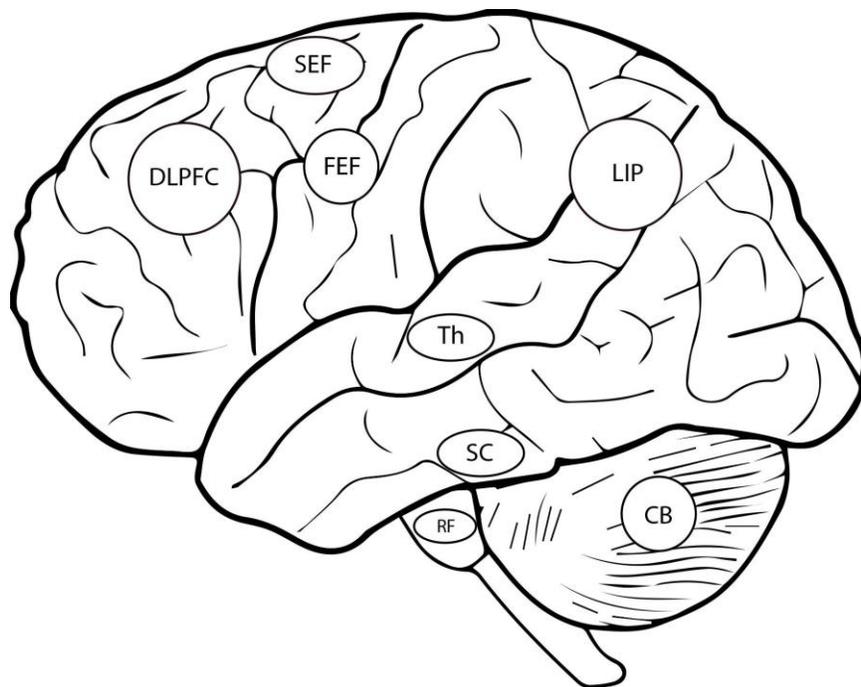


Fig. 1: Brain areas responsible for saccadic control in humans. Abbreviations: LIP, lateral intraparietal cortex; DLPFC, dorsolateral prefrontal cortex; FEF, frontal eye field; Th, thalamus; SC, superior colliculus; CB, cerebellum; RF, reticular formation. Adapted from Munoz, 2002.

Critical nodes of this extended network have been identified in the human brain and include regions in the lateral intraparietal cortex (LIP), the dorsolateral prefrontal cortex (DLPFC), the frontal eye field (FEF), the thalamus (Th), the superior colliculus (SC), the cerebellum (CB) and the brainstem reticular formation (RF).

Recent studies have accounted some of these brain areas not solely responsible for the generation of saccades. For example, Miller and Buschman (Miller & Buschman, 2013) found evidence for the involvement of the LIP in guiding observers attention in a stimulus-driven fashion. When LIP neurons respond to highly salient stimuli, the oculomotor selection seems to be biased toward the salient location. When instead the cascade of processes originates from frontal cortices such as the FEF and the DLPFC, the visual search seems to be more guided by internal values and goals. Further evidence from others studies of Buschman & Miller (Buschman & Miller, 2007, 2013) where they used a pop-out display (homogenous display with one unique singleton) and a search display (heterogeneous display with no unique singleton) to investigate the time course of bottom-up and top-down processes in the brain of primates. They concurrently recorded monkeys' eye movements and neuronal activity from multiple electrodes placed in frontal and parietal cortices. The behavioral results showed that when deploying fast saccades, the monkeys were unable to inhibit the salient distractors. On the contrary, slower saccades were characterized by more control and top-down behavioral hallmarks. When looking at neural activity, they found that fast and bottom-up signals appear first in the LIP while the signals generated from longer latency saccades and associated to more top-down control were recorded from electrodes located in the frontal cortex.

More evidence, in line with the theory of Buschman & Miller proposing an overlap between the saccade-generating network and the brain circuitry of goal-directed and stimulus-driven attention comes from the intensive work of Corbetta & Shulman (Corbetta & Shulman, 2002; Corbetta et al., 1998). According to their theory, two partially segregated systems are responsible for goal- and stimulus-driven attentional processes in the human brain. The first one, which includes parts of the intraparietal cortex and superior frontal cortex, is involved in preparing and controlling goal-directed selection for stimuli and responses (Maurizio Corbetta & Shulman, 2002). The second one instead, which includes the temporoparietal cortex and the inferior frontal cortex, is more responsible for the detection of salient and unexpected stimuli. Corbetta and Shulman, in their theory, propose that the stimulus- and the goal-driven networks interact recursively. Specifically, their idea is that the default operandi mode is based on goal-driven network, and only when highly salient stimuli appear the stimulus-driven network kicks in, granting attention to the incoming salient stimuli.

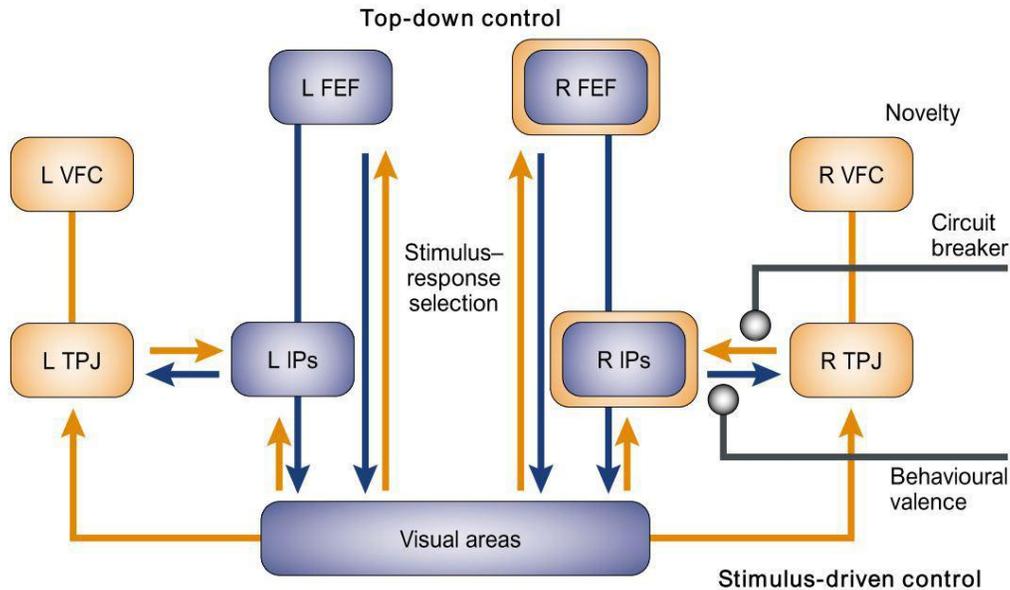


Fig. 2: Schematization of top-down and stimulus-driven control in the brain. TPJ: temporoparietal junction, IPL/SGT: inferior parietal lobule/superior temporal gyrus, VFC: ventral frontal cortex, IPs: intraparietal sulcus, FEF: frontal eye field. The IPs-FEF network is involved in the top-down control of visual processing (blue arrows). The TPJ-VFC network is involved in stimulus-driven control (orange arrows). Picture taken from Corbetta & Shulman, 2002.

The attentional oculomotor network that results from the comprehensive review of Corbetta & Shulman (Corbetta & Shulman, 2002), is derived from many experiments that implied mostly fMRI (functional magnetic resonance), PET (positron emission tomography) techniques and visual tasks where participants had to discriminate colors or motion (Corbetta, Shulman, Miezin, & Petersen, 1995; Corbetta, 1998; Shulman, D'Avossa, Tansy, & Corbetta, 2002). In summary, the above-discussed work suggests that stimulus- and goal-driven processes are controlled by different interacting networks. However, the fact that different displays have been used to make assessments regarding search strategies adopted by primates and humans (i.e., pop-out vs. serial search, color manipulation, motion discrimination, etc.) could have in principle affected the true nature of the visual search. In other words, drastic changes across conditions may also correlated with changes in reaction times, which in turn affect the relative contribution of the processes at stake. Also, in the first and second paragraph of this general introduction, we underlined the importance of time when referring to stimulus- and goal-driven processes. The question is then what could be the best technique to understand the underpinning of such phenomena as visual search is, in the brain. fMRI and PET are

not certainly optimal for their temporal resolution. After presenting and discussing the first study we are going to propose the magnetoencephalography (MEG) as a better neuroimaging tool to investigate the role of prestimulus oscillatory activity that may influence stimulus- and goal- driven processes.

Motivation experimental work: Study 1

In the first and second section of the general introduction we have outlined how the relationship between effects of stimulus salience and time course of responses seems to be critical for the understanding of the relative contribution of stimulus- and goal-driven processes in visual selection. When observers take little time to make an eye movement following the presentation of a search display, results show they are strongly driven by stimulus-salience, independent of identity of the salient item. In contrast, when people are slower to initiate the saccade, selection can be guided by the target, in line with task instructions. However, it remains unclear as to what factors determine whether observers respond fast or slow on any particular trial, resulting in the respective adoption of either stimulus-driven or goal-driven dominant strategies to produce the task-demanding behavioral output. While potentially random fluctuations in cognitive control state may contribute (Esterman, Noonan, Rosenberg, & DeGutis, 2013; A. Leber, Lechak, & Tower-Richardi, 2013), another factor that may determine response speed is individual differences in response biases. For instance, more conservative participants may be relatively slower to respond, thereby increasing the accumulation of visual evidence to allow for better discrimination of the target. More liberal participants may instead respond faster, resulting in saccades that would tend to land on the most salient element in a display. Moreover, the balance between conservative and liberal response strategies can also occur within an individual over the course of an experiment. Observers, on the basis of performance and feedback while accomplishing a visual task, can exert on-line adaptive changes in their speed of selectivity to maximize performance. This means that the accumulation of sensory evidence will vary along a continuum and lead to different outcomes in terms of accuracy. With study 1, we aim to investigate whether observers are able to control the timing of saccadic selection and, if so, whether this then regulates the trade-off between stimulus-driven and goal-driven influences. Study 2 will instead focus

on the possible difference between brain states as observed by the mean of magnetoencephalography (MEG) occurring before the stimulus onset. In details, we are going to investigate how prestimulus oscillatory activity in the alpha range (8-12 Hz) may affect visual search modalities in respect to performance and saccadic reaction times.

Chapter 2

Study 1: Trading off stimulus salience for identity: a cueing approach to disentangle visual selection strategies

Abstract

Recent studies show that time plays a primary role in determining whether visual selection is influenced by stimulus salience or guided by observers' intentions. Accordingly, when a response is made seems critically important in defining the outcome of selection. The present study investigates whether observers are able to control the timing of selection and regulate the trade-off between stimulus- and goal-driven influences. One experiment was conducted in which participants were asked to make a saccade to the target, a tilted bar embedded in a matrix of vertical lines. An additional distractor, more or less salient than the target, was presented concurrently with the search display. To manipulate when in time the response was given we cued participants before each trial to be either fast or accurate. Participants received periodic feedback regarding performance speed and accuracy. The results showed participants were able to control the timing of selection: the distribution of responses was relatively fast or slow depending on the cue. Performance in the fast-cue condition appeared to be primarily driven by stimulus salience, while in the accurate-cue condition saccades were guided by the search template. Examining the distribution of responses that temporally overlapped between the two cue conditions revealed a main effect of cue. This suggests the cue had an additional benefit to performance independent of the effect of salience. These findings show that although early selection may be constrained by stimulus salience, observers are flexible in guiding the 'when' signal and consequently establishing a trade-off between saliency and identity.

Introduction

The amount of visual information available in real world scenes goes far beyond the computational capacities of our visual system (Tsotsos, 1989, 1990). Everyday life, however, points out the innate ability of selecting from the visual stream subsets of information that are behaviourally relevant, filtering out those that are unnecessary. Information gating and distribution of attentional resources are therefore fundamental in allowing visually guided behaviour. Theories and models of visual search generally assume that two major attentional mechanisms are at the basis of visual and oculomotor selection processes (Connor et al., 2004; Corbetta & Shulman, 2002; Shipp, 2004). Bottom-up mechanisms are considered to control selection when visual search is stimulus driven (SD); that is, when the winner of selection corresponds to the more salient element present in the visual field. Visual saliency here refers to the physical, bottom-up distinctiveness of an element, and is a relative property that is contextually dependent (Itti, Koch, Niebur, 1998). Top-down processes, instead, grant attention to those elements that match the observer's target settings and lead to goal driven (GD) selection behaviours. In the past, some researchers have argued that SD processes dominate visual selection (Nothdurft, 2002; Theeuwes, 1992, 2004), resulting in an attentional control predominantly driven by saliency. On the other hand, other researchers have claimed that it is GD processes which control visual selection (Bacon & Egeth, 1994; Chen & Zelinsky, 2006; Folk, Remington, & Johnston, 1992). However, while selection may sometimes be more stimulus driven than goal driven or vice versa, most researchers agree that SD and GD factors interact to ultimately control the allocation of attentional selection (Connor, Egeth, & Yantis, 2004; Duncan & Humphreys, 1989; Serences et al., 2005; Treisman & Sato, 1990).

Moreover, recent findings (van Zoest, Donk, & Theeuwes, 2004; van Zoest & Donk, 2006) have accumulated evidence for the view that SD and GD strategies influence the processing of the same visual stimuli via different time windows. The design adopted in these studies was based on the additional-singleton paradigm (Theeuwes, 1992). In this task, participants perform a visual search and execute a fast saccade toward a unique target presented amongst a number of identical non-targets. A singleton distractor that differs from the target in the same dimension (i.e., orientation) is presented concurrently with the search display. This distractor can be more or less salient than the target. When saccadic eye movements are measured in this type of task, the typical pattern of results

shows that early oculomotor responses are frequently directed toward the most salient element in the screen (i.e., singleton target or distractor) while late saccades are more driven by the correct identification of the target. This suggests that both SD and GD control occur, but in different time windows. Further support for this view can be found in studies on attention and eye movements (Hunt, von Muhlenen, & Kingstone, 2007; van Zoest, Donk, & Theeuwes, 2004).

The entwined relationship between effects of stimulus salience and time course of responses seems critical for the understanding of the relative contribution of SD and GD processes in visual selection. However, it remains unclear as to what factors determine whether observers respond fast or slow on any particular trial, resulting in the respective adoption of either SD- or GD-dominant strategies to produce the task-demanding behavioural output. While potentially random fluctuations in cognitive control state may contribute (e.g., Leber, 2010; Esterman et al., 2013), another factor that may determine response speed is individual differences in response biases. For instance, more conservative participants may be relatively slower to respond, thereby increasing the accumulation of visual evidence to allow for better discrimination of the target. More liberal participants may instead respond faster, resulting in saccades that would tend to land on the most salient element in a display. Moreover, the balance between conservative and liberal response strategies can also occur within an individual over the course of an experiment. Observers, on the basis of performance and feedback while accomplishing a visual task, can exert on-line adaptive changes in their speed of selectivity to maximize performance. This means that the accumulation of sensory evidence will vary along a continuum and lead to different outcomes in terms of accuracy. Eventually each participant will develop a balance between speed and accuracy in order to achieve the task. With the present study, we aim to investigate whether observers are able to control the timing of saccadic selection and, if so, whether this then regulates the trade-off between stimulus-driven and goal-driven influences.

The general idea of the speed-accuracy trade-off (SAT) has been studied in the field of cognitive science for a long time (Pew, 1969; Wickelgren, 1977) and lately has been reconsidered and investigated in neuroimaging studies (Bogacz, Wagenmakers, Forstmann, & Nieuwenhuis, 2010; Forstmann et al., 2008) and in monkey physiological studies (Heitz & Schall, 2012). Even though the models underpinning these studies diverge on the individual dynamics of information gathering, they share the idea that sensory evidence accumulates over time from a baseline level until a certain threshold (Ivanoff, Branning, & Marois, 2008). Moreover, stimulus strength has been demonstrated to

directly affect the functions underlying such dynamics, leading to different outcomes in terms of time and accuracy (Palmer, Huk, & Shadlen, 2005).

However, psychophysiological tasks in SAT studies consider fast responses to range from ~300 to ~500 ms (Forstmann et al., 2008; van Veen, Krug, & Carter, 2008). In this regard, the general idea of SAT does not easily translate to the trade-off found between stimulus- and goal-driven controls in studies of oculomotor visual selection. Oculomotor responses that occur before ~300 ms are not necessarily less accurate. For example, when the target is the most salient element on the screen in a visual search task (van Zoest et al., 2004) early saccades driven by the high stimulus saliency can reach performance level of ~80% accuracy (van Zoest & Donk, 2006). In fact, accuracy in target selection decreases over response time instead of increasing as described in the typical accumulator models of SAT (Donk & van Zoest, 2008). Accumulator models of SAT are able to explain performance only when the salient element is presented as irrelevant distractor; in this case performance steadily increases with time.

As already outlined, performance and efficiency in visual tasks that rely on saccadic responses depend mostly on the interaction between stimulus saliency and the selection strategies that observers adopt. However, the degree to which differing selection strategies can be voluntarily adopted by observers is still an open question. Moreover is not clear yet if observers are able to control and regulate the trade-off between speed and accuracy in oculomotor selection tasks that involve differing levels of saliency. Finding that observers are able to control the extent to which selection is saliency-driven or guided by goal-directed intentions is in line with the general idea that overall performance depends on observer strategies. Recent evidence for early strategic influences has been reported in manual reaction time (Geyer, Müller, & Krummenacher, 2008; Thomson, Willoughby, & Milliken, 2014), eye tracking (Moher, Abrams, Egeth, Yantis, & Stuphorn, 2011) and electrophysiology (Tollner, Muller, & Zehetleitner, 2012) studies. For example, Moher et al. (2011) explored suppression of salient capture by manipulating the probability of distractor presence in the search array. They found that the degree of distractor interference decreased as distractor appearance probability increased, arguing that this was due to participants having greater incentive to apply suppression. Taken together, these studies suggest that distractor interference is under volitional control, supporting the idea that top-down expectancies can alter observer's strategies at

early stages of perceptual attentional selection. However, findings from these studies are rarely ever directly related to the time-course of performance.

The current study aimed to examine whether observers could utilize cues to produce different SAT strategies in oculomotor selection. Recent SAT studies have shown that the use of explicit cues emphasizing speed or accuracy can induce specific behavioral strategies both in humans (van Veen et al., 2008) and non-human primates (Heitz & Schall, 2012). Van Veen et al. (2008) demonstrated that, in line with cued instructions provided before a block of trials, participants could alter their manual response performance in a Simon task to emphasize speed at the cost of accuracy and vice versa. Heitz and Schall (2012) manipulated central fixation color to instruct primates to make either a fast, neutral or accurate saccadic response in a visual search task. Their findings show that primates can also proficiently adjust their behavior in line with cue instructions. The main question then is how the potential flexibility regarding when to make an eye movement may interact with the dynamic influence of stimulus salience in visual selection.

Experiment

In order to investigate whether observers are able to modulate and control visual selection strategies efficiently, trial-wise instructions emphasizing task speed or accuracy were given. Specifically, participants were cued to either make a fast or an accurate saccade to the target. The target was a uniquely oriented line element surrounded by a series of homogeneously oriented non-targets. Together with the target and non-targets an additional distractor of unique orientation was presented. The distractor was always tilted to the opposite direction of the target and could vary in orientation to be more or less salient than the target (as determined by orientation relative to the non-targets).

If it is the case that observers are able to control the timing of visual selection, we expect to find a difference in saccadic reaction times (SRTs) between the two cue conditions. More specifically, in the fast condition observers should be able to make rapid saccades and consequently be more influenced by the relative salience of the unique elements displayed. On the other hand, in the accurate condition we expect participants to slow down and so be more likely to avoid fast salient

capture, allowing them to direct a greater proportion of saccades to the target. The cue may furthermore influence the time-course of selection. In this case we expect that the entire distribution of selection responses will shift to a later moment in time in the accurate cue condition compared to the fast cue condition. The main question then, is how this shift in time will affect the time-course of accuracy performance. It may be the case that an overall slower time-course will not affect the underlying trade-off processing between stimulus- and goal-driven controls. That is, the cue will affect SRTs, but the underlying function will be same in both cue conditions: the only difference between the cues being the result of observers accessing the function at different moments in time. Alternatively, it may be that the cue has an additional effect on the time-course function. Independent of the delay in the distribution of responses, the cue may qualitatively change the information sensitivity that guides the responses. This may increase performance in the accurate-cue condition relative to the fast-cue condition, above and beyond what is to be expected on the basis of time alone.

Methods

i. Participants

Twenty young adults (11 females, average age 23.5 years, range 20-28 years) participated as paid volunteers. All subjects reported having normal or corrected-to-normal vision. Two participants were excluded from the analyses due to a high percentage of errors (> 30%, error specification in the results section). The study was conducted in accordance with ethical standards codified by the World Medical Association in the Declaration of Helsinki and written informed consent was obtained from participants before the experiment.

ii. Apparatus

A tower mount PC, (Dell Precision T1600) based on Intel Xeon (3.10 Ghz) technology with 8.00 GB of RAM coupled with a high performance 19" monitor (ViewSonic E96f+SB, display area 360 × 270 mm, refresh rate 100 Hz) were used for stimulus presentation. The experimental design was realized with Psychtoolbox 3 (Psychophysics Toolbox Version 3; Brainard, 1997; Pelli, 1997) in combination with MATLAB R2010b. Eye movements were recorded with the Eyelink® 1000 (SR research). All participants were sitting at a distance of approximately 600 mm in front of the monitor with the head supported by a chinrest. The experiment took place in a sound-attenuated lab with suffused light.

ii. Stimuli

Participants were asked to perform a visual search task (figure 1) in which they had to make a saccade to a target. For half of the participants, the target consisted of a right-tilted bar (i.e., a line segment tilted 45° to the right of a vertical axis), while the other half looked for a left-tilted bar (i.e., a line segment tilted 45° to the left). The target was embedded within a raster of non-targets (i.e., vertically oriented line segments). Together with the target and the raster of singleton non-targets, an additional distractor was presented. The distractor was always tilted to the opposite direction of the target and could vary in orientation to be more (67.5°) or less (22.5°) salient than the target, henceforth referred to as MS and LS conditions, respectively. All elements (1 target, 1 distractor, and 287 non-targets) were arranged in a 17 × 17 matrix display with a raster width of 290 × 210 mm (27.2° × 19.9° of visual angle). The target and unique distractor could appear at four different locations set on the corners of an imaginary square such that, embedded within the matrix of non-targets, targets and distractors were always presented at equal distance from fixation (7.6° of visual angle) and separated by an angular distance of 90°. All line elements had an approximate height of 0.65° and width of 0.12° of visual angle. All elements were white and superimposed on a black background.

iv. Design and Procedures

Each trial started with a drift correction whereby participants pressed the space bar while fixating a central point. A display with a central cue (“fast” or “accurate”) then appeared for 1000 ms, indicating whether participants should aim to be as fast or as accurate as possible in their response. After the cue, a display with a central fixation point was presented for 1000 ms followed by the stimulus array. The stimulus array was presented for 1500 ms. Participants were instructed to keep fixation until the appearance of the stimulus.

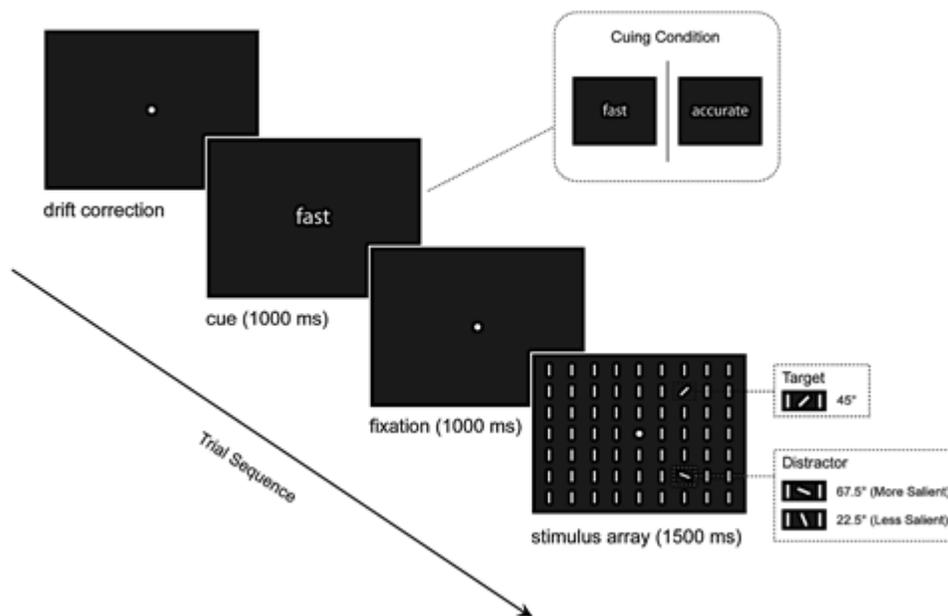


Fig. 1: Trial sequence. Participants executed a saccade to the uniquely oriented target element, depicted here as the 45° tilted segment to the right relative to vertical non-target elements. Together with the target and the raster of non-targets an additional distractor of unique orientation was presented. The distractor was always tilted to the opposite direction of the target and could vary in orientation to be more or less salient than the target. Before the stimulus array, a display with the cue (“fast” or “accurate”) was shown, indicating whether participants should be as fast or as accurate as possible in their responses. Note, stimuli not drawn to scale.

To make sure that the task was fully understood by the participants, oral and written instructions were given and a practice session of 32 trials conducted before the beginning of the experiment.

Visual feedback on SRTs and accuracy was given to participants every 32 trials to reinforce the manipulation and to keep participants motivated throughout the experiment. Participants were instructed to be faster if the SRT mean was below 300 ms and to be more accurate if accuracy was less than 70%. A factorial design was used; cue (fast vs. accurate), target positions (4), distractor orientation (LS vs. MS) and distractor positions (2, constrained by target position) were equally counterbalanced and presented in random order. The experiment consisted of 576 trials divided into three blocks of 192 trials and lasted approximately 50 minutes. The eye tracker was recalibrated after each block.

Results

i. Error and data validation criteria

Saccades were defined on the basis of minimum eye-movement velocity and acceleration thresholds ($30^\circ/\text{s}$ and $8000^\circ/\text{s}^2$, respectively). SRT was defined as the time between the onset of the stimuli and the moment in which a saccade of at least 3° of visual angle was made from the fixation point. If the first saccade landed within a distance of 4° of visual angle from target or distractor the trial was considered valid for analyses. Trials were excluded if the initial saccade went neither to the target nor to distractor (trials rejected = 6.61%, mean SRT = 325 ms), started from more than 3° of visual angle from central fixation at the onset of the search display (trials rejected = 3.12%), initiated within 80 ms of the onset of the stimuli display (trials rejected = 0.65%), or if the SRT was larger than 2.5 standard deviations from individual participant means (trials rejected = 0.23%). These specifications led to the rejection of 10.61% of trials from the 18 participants that were included in the primary analyses.

ii. SRT's and proportions to target

A two-by-two repeated measures ANOVA design was used to test the effects of the within-subject factors (cue: fast or accurate and distractor orientation: LS or MS) on the dependent variables

(proportion to target and SRTs). Figure 2 displays the overall mean proportion of saccades made to the target¹ and the average SRT as a function of cue and distractor orientation.

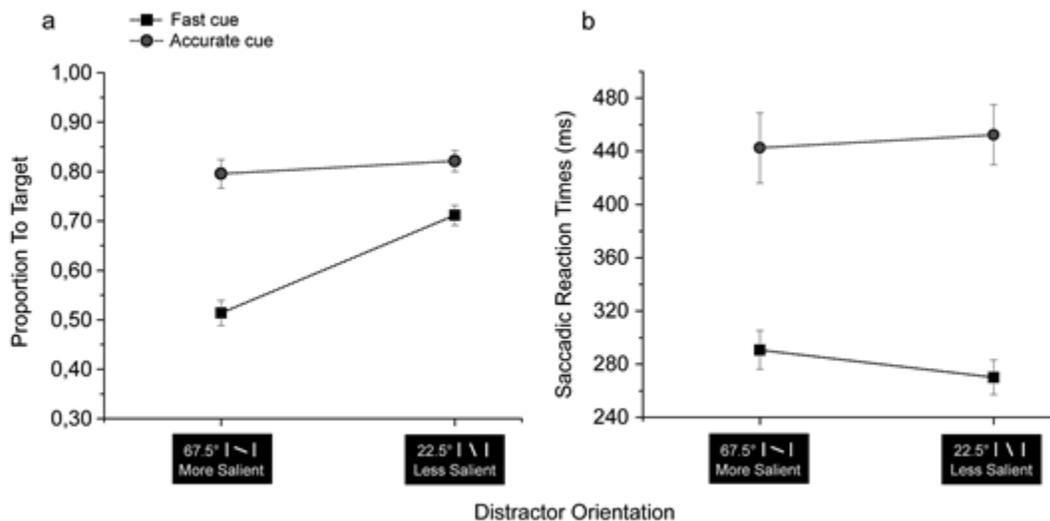


Fig. 2: Main effect of the cue on the mean proportion to target (a) and SRTs (b) as a function of distractor saliency manipulation. Error bars reflect standard errors of the mean.

The results of the ANOVA revealed a significant main effect of the cue on proportion to target, $F(1, 17) = 61.71$, $MSE = .011$, $p < .001$, $\text{partial } \eta^2 = .78$. Participants were more precise in the accurate cue condition ($M = .80$) compared to the fast cue condition ($M = .60$). A significant main effect was found for distractor orientation $F(1, 17) = 21.02$, $MSE = .010$, $p < .001$, $\text{partial } \eta^2 = .55$; saccades were directed more toward the target in the LS distractor condition ($M = .76$) when compared with the MS distractor condition ($M = .65$). A significant two-way interaction was found between cue and distractor orientation $F(1, 17) = 34.21$, $MSE = .004$, $p < .001$, $\text{partial } \eta^2 = .67$. In the fast cue condition the orientation manipulation led to a large behavioral difference in proportion to target between the MS ($M = .51$) and LS ($M = .71$) distractor conditions. In contrast, for the accurate cue condition the difference in performance between the LS ($M = .79$) and MS ($M = .81$) distractor orientations tested with Bonferroni post-hoc analyses did not show any significant difference. The ANOVA conducted on

¹ The proportion to target is computed by dividing the number of saccades landed on target by the total number of saccades that went to either the target or distractor

SRTs revealed a significant main effect of cue, $F(1, 17) = 59.38$, $MSE = 8461$, $p < .001$, $\text{partial } \eta^2 = .78$. SRTs were shorter in the fast cue condition ($M = 280$ ms) than in the accurate cue condition ($M = 447$ ms). However, the average SRT in the MS distractor condition ($M = 367$ ms) did not significantly differ from the LS condition ($M = 361$ ms), $F(1, 17) < 2.46$.

iii. Time course analyses

1. *Proportion to Target*

To explore the relative contribution of the cue in stimulus- and goal-driven control in visual search as a function of time, mean SRTs and proportions to target were computed separately for each type of cue, distractor orientation, and for each quartile of the initial SRT distributions. Figure 3 shows the mean proportions of correct saccades across participants as a function of quartile time bin separately for cue type and distractor orientations. A within-subject three-way repeated measures ANOVA was conducted on the proportion of correct saccades, with cue (fast, accurate), distractor orientation (LS, MS) and quartiles (1-4) as factors. All main effects (cue, distractor orientation, and quartiles) were significant, together with the three two-way interactions (cue \times distractor orientation, cue \times quartiles, and distractor orientation \times quartiles; all $F_s(1, 17)$ and $(3, 51) > 8.93$, $p_s < .001$). Moreover, as observable in figure 3 and crucial for the current analyses, these effects were qualified by a significant three-way interaction (cue \times distractor orientation \times quartiles), $F(3, 51) = 6.41$, $MSE = .008$, $p < .001$, $\text{partial } \eta^2 = .27$. To test for significant differences between distractor orientations in each quartile, post-hoc analyses using Bonferroni-corrected criterion were conducted for the time-course of the accurate and fast cue condition. In the fast cue condition, distractor orientation mostly modulated the responses. In the first quartile, the saccadic behavior conveyed by proportion to target between the two distractor conditions showed a significant difference ($M_s MS = .36$ vs. $LS = .81$, $p < .001$). The second and third quartiles indicated decreasing, but still significant, differences in proportion to target between distractor conditions (2nd quartile: $M_s MS = .42$ vs. $LS = .70$; 3rd quartile: $M_s MS = .54$ vs. $LS = .63$, $p_s < .001$).

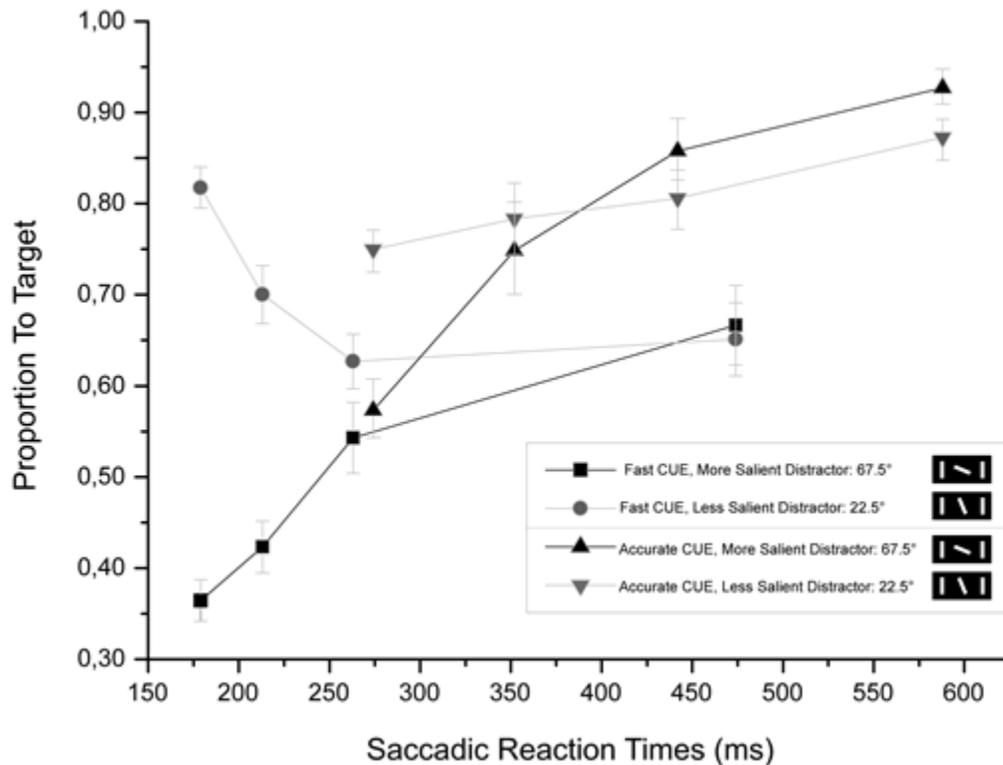


Fig. 3: Proportion of eye movements correctly directed toward the target as a function of time. Saccade latencies were divided according to cue type (fast/accurate). Fast and accurate SRT distributions were further plotted separately for each distractor condition (MS/LS) and vincentized in 4 time bins. Error bars reflect standard errors of the mean.

This difference was not significant by the fourth quartile (M_s MS = .67 vs. LS = .65, $p > .05$). The accurate cue condition, characterized by slower responses, shows initially the same (albeit minor) significant difference in proportion to target between distractor conditions for the first quartile (M_s MS = .57 vs. LS = .75, $p < .05$). In the second quartile no significant difference was found in performance between distractor orientations (M_s MS = .75 vs. LS = .75, $p > .05$). Intriguingly, the third and fourth quartiles appear to be characterized by an opposite tendency: participants were better able to discriminate the target when in presence of the MS distractor (3rd quartile $M = .85$; 4th quartile $M = .92$) than compared to when the LS distractor was present (3rd quartile $M = .80$; 4th quartile $M = .87$). However, these differences were not reliable ($p_s > .05$).

2. Saccade latency

A within-subject three-way repeated measures ANOVA was conducted on SRTs with cue (fast, accurate), distractor orientation (LS, MS) and quartiles (1-4) as main factors. Of the main effects (cue, distractor orientation, quartiles), cue: $F(1, 17) = 49.10$, $MSE = 36221$, $p < .001$, $\eta^2 = .74$, and quartiles: $F(3, 51) = 229.24$, $MSE = 3751$, $p < .001$, $\eta^2 = .93$, were significant, while distractor orientation effect was not ($F(1, 17) < 2.90$). The significant interaction of cue \times quartiles ($F(3, 51) = 18.27$, $MSE = 2686$, $p < .001$, $\eta^2 = .51$) shows that the distribution of latencies in the fast cue condition was narrower compared to the accurate cue condition (from 179 ms to 372 ms following fast cues vs. 274 ms to 588 ms following accurate cues). The significant interaction between distractor orientation and quartiles was significant ($F(3, 51) = 5.28$, $MSE = 101$, $p < .05$, $\eta^2 = .24$), with post-hoc comparisons indicating a significant difference only for the fourth quartile ($M_{MS} = 474$ vs. $M_{LS} = 486$, $p < .001$). The interaction between cue and distractor orientation ($F(1, 17) < 1.00$) was not significant, showing that there were no differences in SRT to the target in the LS or in the MS distractor as a function of the cue manipulation. Moreover, time did not modulate this pattern as evidenced from the absence of a significant three-way interaction (cue \times distractor orientation \times quartiles, $F(3, 51) < 1.00$).

An additional analysis assessed whether the large influence of salience was a common feature of rapid responding across (vs. solely within) individual SRT distributions. A correlation was performed on the relationship between an individual's 'Saliency Effect' (proportion to target in the LS – MS distractor orientation condition) and mean SRTs for each participant in the two cue conditions. If the time-course of performance also affects selection generally between participants, it was predicted that observers that were fast to respond should have a larger Saliency Effect than observers who were on average slow to respond. In contrast, if the time-course was primarily restricted to within-in subject variability, this pattern of results should not be present. The analyses revealed a negative trend between the size of the Saliency Effect and latency of SRTs in the fast-cue condition ($r(18) = -0.44$, $p = .065$) and a significant negative correlation in the accurate-cue condition ($r(18) = -0.53$, $p < .05$). These results provide partial support for the hypothesis that generally, the faster a participant is, the more likely they will be influenced by salience.

iv. Interim discussion

These results demonstrate that participants were able to utilize the cue to modulate their oculomotor responses in time and accuracy domains. Specifically, in line with the cue, the fast cue responses were faster and less accurate overall than the accurate cue responses, which were slower and more accurate. Observers were able to guide the 'when' signal (see also, Findlay & Walker, 1999). As predicted by the time-course of selection, performance in the fast-cue condition was primarily driven by stimulus saliency. Early responses in time, as expressed in the time-course analyses, were mainly directed to the most salient element, which was the target (45°) in presence of the less salient distractor (22.5°). In contrast, when the distractor was more salient (67.5°) than the target (45°), oculomotor responses landed most frequently on the distractor. This effect slowly disappeared over response time: in the last quartile, despite a general decrease of accuracy when the target was the most salient element there were no differences in proportion to target as a function of distractor saliency. The accurate-cue condition, on the other hand, was characterized by overall slower oculomotor RTs and an increase in performance accuracy. Visual search was guided to a greater extent by observers' intentions even though relatively fast responses were still affected by the distractor saliency manipulation. These results demonstrate the cue effectiveness as a top-down modulator used by participants to regulate the speed-accuracy trade-off in performing the visual search task.

However, we also observed a vast difference in the SRT distributions between the two cue conditions. The responses in the accurate-cue condition showed overall slower latencies and a wider distribution while the fast-cue condition was characterized by relatively quicker oculomotor responses and a narrower distribution. Such observations were supported by a chi-square test comparing the proportion of responses in each quadrant between the two distributions ($\chi^2(3, N = 4634) = 1375, p < .001$). Despite these differences, there was an overlap in SRT between responses of fast and accurate distributions. Thus, the question that remains is to what extent does the cue affect performance, independently of time-course differences? That is, if we match for SRT across both cue conditions, is performance qualitatively different between cue conditions? Or instead, is performance solely based on the time-course of selection? If the cue has a distinct contribution to performance, we would expect to find an overall difference in accuracy between the two cue conditions when matched

for SRT. Alternatively, if the cue no longer affects performance, the outcome of selection would be completely determined by when in time the saccade is executed.

1. Further analyses

a. Methods

For each participant, we first extracted the distribution of saccadic responses that temporally overlapped across both fast- and accurate-cue conditions. Because SRTs in the fast-cue condition occurred earlier in time than in the accurate-cue condition, this was accomplished by taking the fastest (i.e., lower limit) of the accurate cue responses and the slowest (i.e., upper limit) of the fast cue responses. This initial trimming created two response distributions within the same time range. Because the frequency distributions of trials within the selected time window were not equivalent across both cue conditions, we equalized the frequencies in each cue condition using a histogram function. Histograms (each with 10 bins) were created separately for the fast-cue and accurate-cue overlap distributions and the frequencies in each bin were then matched across cue condition, such that both had equal number of trials in each of the 10 bins. Participants were only included if they had at least 140 trials across the 10 bins; this led to the exclusion of one more participant from the further analyses. A two-tailed paired-samples t-test comparing extracted SRT means for fast- versus accurate-cue conditions was not significant ($t(16) = 1.40, p = .18$), allowing for the subsequent comparison of performance accuracy between the two cue conditions. The new SRTs, matched for time and trial-frequency, were then used to calculate the new vincentized time-course of performance (three bins, see figure 4).

b. Results

The effect of cue on performance for the SRT intersecting distributions was tested with a three-way repeated measure ANOVA (factors: cue × distractor orientation × tertiles) as shown in figure 4. The analyses revealed a significant main effect of cue ($F(1, 16) = 14.93$, $MSE = .017$, $p < .002$, $\text{partial } \eta^2 = .48$): overall performance accuracy benefited from the accurate cue ($M = 0.71$) compared to the fast cue ($M = 0.63$). The significant main effect of distractor orientation ($F(1, 16) = 9.37$, $MSE = .044$, $p < .008$, $\text{partial } \eta^2 = .37$) followed the direction of the previous analyses: despite an equivalent time-course the MS distractor (67.5°) elicited generally worse performance ($M = 0.61$) than the LS distractor (22.5° ; $M = 0.71$). In the significant two-way interaction between cue × distractor orientation ($F(1, 16) = 6.43$, $MSE = .008$, $p < .05$, $\text{partial } \eta^2 = .29$) a greater difference was observed between distractor conditions in the fast-cue ($M_s MS = 0.57$ vs. $LS = 0.69$) compared to the accurate-cue condition ($M_s MS = 0.67$ vs. $LS = 0.73$). As expected, the increase in proportion to target as a function of tertiles was also significant ($F(2, 32) = 15.36$, $MSE = .020$, $p < .001$, $\text{partial } \eta^2 = .49$).

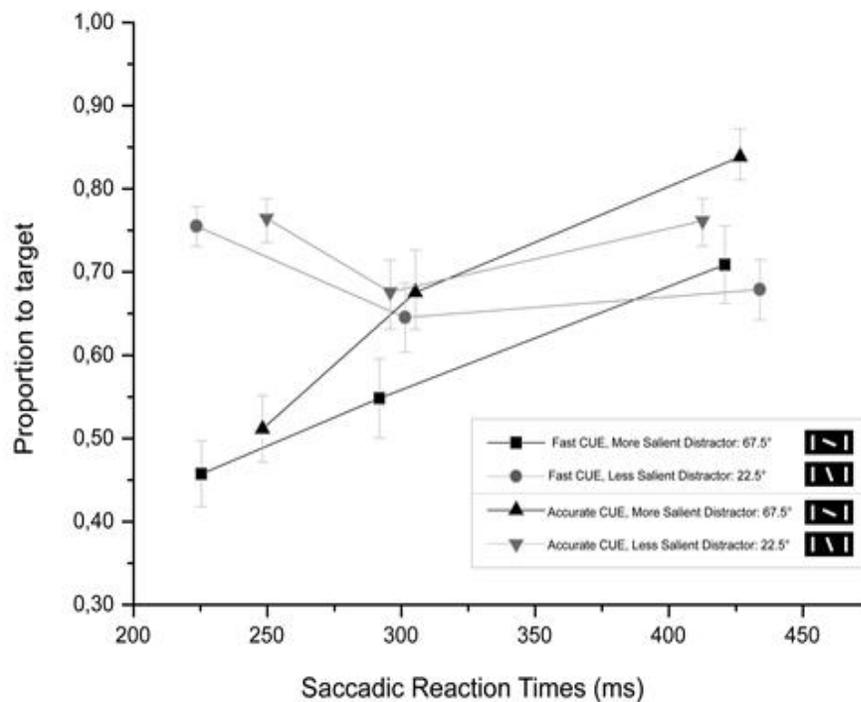


Fig. 4: New vincentized time-course of performance (3 bins) computed on the basis of the oculomotor responses that overlap in time. Error bars reflect standard errors of the mean.

There was a significant two-way interaction between distractor orientation and tertiles ($F(2, 32) = 26.52$, $MSE = .018$, $p < .001$, partial $\eta^2 = .62$). Neither the cue \times tertiles interaction ($F(2, 32) < 2.20$) or the three-way interaction between cue, distractor orientation, and tertiles ($F(2, 32) < 0.20$) were significant.

Discussion

Our results show that independent of the cue, short-latency saccades were driven by stimulus salience and long latency responses were primarily goal directed. Importantly, for the aims of the present study, we found evidence that observers are able to control the timing of saccadic visual selection by following the trial-wise instructions. Selection in the fast cue condition was characterized by rapid saccades while the accurate cue condition was characterized by overall slower oculomotor responses. Looking at the overall performance as a function of time-course, the trade-off in the fast cue primarily showed stimulus-driven selection based on saliency early in time; evidence for goal-driven control was only found in the final time bin, where stimulus salience no longer influenced selection. Instead, goal-driven processes predominantly guided the trade-off in the accurate cue condition; stimulus salience only influenced performance for the fastest responses. It appeared that observers' timing of responses based on the cue influenced this trade-off between stimulus- and goal-driven strategies. In sum, guided by the cue, observers were able to elicit faster or slower eye movements thereby consequently exerting adaptive changes in their visual search strategies, making selection relatively more stimulus- or goal-driven.

The present results suggest that the ability to elicit either a fast or slow response is flexible: participants are able to adopt a 'fast' or 'accurate' strategy before each trial, depending on the task instructions. This has a consequent effect on whether search processes are primarily stimulus- or goal-driven. Specifically in the fast-cue condition participants may have been prompted into a cognitive state that allowed rapid attentional deployment characterized by fast and salient captures; goal-driven control was severely limited in this case. On the other hand, in the accurate-cue condition, participants appeared to refrain from fast responding and so were able to avoid salient capture; observers were more accurate in making correct eye movements to the designated target. These

results indicate that while performing the task, participants were able to optimize their internal states to guide behavior, that is, observers were able to enter a state of cognitive control in which performance was optimized to accomplish the task in the given situation (Miller, 2000). Our results thus illustrate an important role of an observer's preparedness in solving a task. Interestingly, a negative association between the magnitude of the Saliency Effect and individual SRTs suggests that the trade-off between stimulus- and goal-driven selection as a function of response time is not solely explained by intra-subject variability. Observers who were faster overall to respond showed a larger effect of saliency than those who were generally slower.

Critically, however, when SRTs were matched between cue conditions, while there were no longer any differences in the trade-off between stimulus-driven and goal-driven selection, overall performance accuracy in the accurate-cue condition was better than in the fast-cue condition. This finding suggests that the cue may have qualitatively changed the sensitivity related to the accrual of information that guided the visual selection process. The performance enhancement in the accurate-cue condition relative to the fast-cue condition suggests that mechanisms of selection can alter sensitivity prior to saccadic execution depending on a given strategy.

The present findings are in line with a SAT study on monkey physiology (Heitz & Schall, 2012) where primates were instructed to perform a visual search task where they had to saccade to a specific target (L or T shapes) presented concurrently with distractors (L or T shapes). Before each trial, monkeys were cued to either make a fast, neutral, or accurate saccade. Monkeys were able to produce saccades in line with the cue and moreover, Heitz and Schall found that activity for visual salience neurons started to differ 300 ms before the onset of the stimuli for fast and accurate cues. Specifically, the neuron discharge rate was significantly greater and increased more rapidly over time in the fast, than in the accurate, cue condition. These results suggest that fast saccades are rapidly engaged from pools of visually responsive neurons that encode stimulus salience. Visually responsive neurons in the frontal eye field (FEF), superior colliculus (SC), and posterior parietal cortex (PPC) can modulate their firing rate according to top-down guidance instructions (i.e., cue and stimuli's physical properties).

The overall performance benefit that we observed in the accurate cue condition when SRTs were matched between cue conditions, suggest that mechanisms of selection can be more sensitive prior to saccadic execution. Pre-stimulus effects of preparation have also been reported for feature-specific instructions in a recent fMRI study from Serences and Boynton (Serences & Boynton, 2007) and in a monkey physiology study (Hayden & Gallant, 2005). The results of these studies suggest that feature-based attention can be enhanced before the stimulus presentation by increasing sensitivity to certain features (i.e., orientation, color) facilitating the perception of behaviorally pertinent stimuli. Although the above studies do not directly refer to saccadic selection, these mechanisms seem to affect the oculomotor system as well. A recent study (Weaver, Paoletti, & van Zoest, 2014) reported an increase of performance in very early saccades when a feature-informative cue (color) regarding the target was given to participants rather than a neutral cue. However, the results of the present study differ in that the enhancement concerned a general feature-independent improvement in performance. As far as we are aware, this study is the first to show that this type of aspecific information can affect saccadic efficiency in humans. However, unlike the feature-specific preparation benefit apparent from the fastest saccadic responses under 200 ms (Weaver, Paoletti, & van Zoest, 2014), the general benefit in the present study seemed to take more time to be established. The benefit from the accurate cue was only observable after 250 ms, the time it typically takes for goal-driven strategies in orientation search to be expressed (van Zoest, Donk, & Theeuwes, 2004). Still, the present data are limited to this respect because of the absence of data before 250 ms in the accurate-cue condition. Based on the present data, it cannot be determined whether the general enhancement following the cue can also be established for the fastest oculomotor responses.

However, while not necessarily related to the speed of saccadic selection, Moher et al. (2011) showed that advanced a specific information concerning the likelihood of distractor appearance affects oculomotor performance. In their study, the proportion of distractor to no-distractor trials was manipulated while participants performed an additional-singleton task. Their results showed that the degree of distractor interference varied as a function of distractor appearance probability: oculomotor capture was reduced when the probability of distractor appearance was increased. This finding was taken to suggest that distractor interference is under volitional control, in that observers could voluntarily and flexibly adopt top-down attentional control settings to ignore rapidly salient

distractors. However, one caveat to consider when probabilities of conditions are varied is that intertrial repetitions co-vary with probability. Specifically, intertrial priming is more likely to occur when the probability of distractor presence is increased. This then may have affected the ability to ignore the distractor and reduce oculomotor capture (see also Theeuwes, 2013). Moreover, it is unclear how this type of cueing is related to the time-course of performance. For example, in relation to the potential intertrial priming, it may be the case that observers were relatively slow to respond when the probability of distractor appearance was high. This SRT decrease could have increased the relative goal-driven control compared to a situation where observers were relatively fast to respond when distractor probability was low.

The time window between the cue presentation and the stimulus appearance, also known as pre-stimulus phase, has recently gained importance among the scientific community and has been shown to impact stimuli perception not only in psychophysiological experiments (Hanslmayr et al., 2007), but also in the specific context of visual search studies (Mazaheri, DiQuattro, Bengson, & Geng, 2011). Interestingly, a recent study by Leber (2010) revealed that different degrees of distraction could be predicted by specific pre-trial activity in the middle frontal gyrus (MFG) as recorded by fMRI. Non-invasive physiology techniques with better temporal resolution than fMRI such as electroencephalography (EEG) and magnetoencephalography (MEG) may be able to provide more insight on the mechanisms that underlie changes in sensitivity before stimulus presentation. Irrespective of any cue, it may be that brain states themselves could also impact the strategy that participants adopt on any particular trial. Future investigation on visual selection strategies based on brain-state dependent stimulation (Jensen et al., 2011; Silvanto, Muggleton, & Walsh, 2008) may open new ways to assess how brain signatures proper of specifics and different attentional states affect saccadic control in humans.

The present results differ in an important way from traditional SAT studies that typically account for a linear relation between accuracy and speed with which a task is solved. Based purely on stimulus saliency, performance does not need to be inaccurate when responses are speeded. Specifically, performance was initially very accurate when the target was salient and the distractor not salient (accuracy > 80%). As control increased, performance decreased as a function of saccade latency. It is presently poorly understood how neurons that encode stimulus-saliency are related to

this negative slope found in the fast-cue condition (see also, Donk & van Zoest, 2008; van Zoest & Donk, 2008). A possible explanation is that independent of stimulus identity, observers suppress salience activity. While this strategy is counterintuitive when the target is the most salient element, it eventually leads to selection that is in accordance with the required task. Based on this explanation, stimulus-driven processes would impact oculomotor responses only when the responses are made before the active inhibitory processes take place (Godijn & Theeuwes, 2002; McSorley, 2006). Alternatively, it may be the case that independent of goal-driven strategies, saliency related activity rapidly decays over time in a passive fashion (Cheal & Lyon, 1991; Donk & van Zoest, 2008; Nakayama & Mackeben, 1989; Nothdurft, 2002). As a consequence, later selection would become less and less influenced by the early stimulus-driven activity elicited by highly salient targets.

In order to distinguish between these accounts using data from the present study, we conducted an additional analysis to test whether active suppression of the target occurred when appearing at a former distractor location. If there is an active suppression of saliency, then we would expect that the location of suppressed distractor saliency would inhibit selection of a target presented at the same location on a subsequent trial. Alternatively, if saliency rapidly (i.e., within a trial) and passively fades, then we would not expect previous location of a salient distractor to influence performance on a subsequent trial. Participants were observed to be significantly slower and less accurate to select a target when it was presented in the same location as a distractor on a previous trial². This finding is consistent with that of a recent study showing that singleton distractors elicit location-specific inhibition (Gaspar & McDonald, 2014). Although these results do not rule out the account that stimulus influence rapidly and passively fades out, the analysis provides evidence supporting an active suppression of distractor location from one trial to the next.

² A two-way ANOVA was conducted on proportion to target and SRT, using within-participants factors of Cue and Previous Location (target at previous distractor location vs. target at previous neutral location; TD vs TN). Previous trial location only included subsequent trials of an identical cue condition and the neutral location referred to a location containing a vertically oriented non-target line. The analyses revealed a significant main effect of previous trial location for both SRT ($F(1,17) = 14.79$, $MSE = 569$, $p < .01$, $\text{partial } \eta^2 = .47$) and accuracy ($F(1,17) = 19.87$, $MSE = .007$, $p < .001$, $\text{partial } \eta^2 = .54$) performance. Participants were slower (M_s TD = 370 ms vs. TN = 348 ms) and less accurate (M_s TD = 0.59 vs. TN = 0.68) to select a target when it was presented in the same location as a distractor on a previous trial. There was no significant interaction between previous trial location and cue ($F_s < 3.80$).

The present study revealed that individual observers are relatively flexible regarding the extent to when a response is triggered. This 'when' signal in turn, determined the degree to which participants were more or less driven by stimulus salience or identity. Thus, when investigating whether visual selection is primarily stimulus or goal driven, the present work demonstrates the critical importance of taking into account the trade-off between the influence of stimulus salience and target identity over time.

2.1 Motivation experimental work: Study 2

In summary, the results of study 1 suggest that the time window before the stimulus onset plays an important role in defining the timing of response, which in turn become crucial for the behavioral outcome of the visual search. Our first study demonstrates that participants were able to adopt a 'fast' or 'accurate' strategy before each trial, depending on the task instructions. This had a consequent effect on whether search processes were primarily stimulus- or goal-driven. Specifically in the fast-cue condition participants may have been prompted into a cognitive state that allowed rapid attentional deployment characterized by fast and salient captures; goal-driven control was severely limited in this case. On the other hand, in the accurate-cue condition, participants appeared to refrain from fast responding and so were able to avoid salient capture; observers were more accurate in making correct eye movements to the designated target. These results indicate that while performing the task, participants were able to optimize their internal states to guide behavior, that is, observers were able to enter a state of cognitive control in which performance was optimized to accomplish the task in the given situation (Miller, 2000). This preparatory period, in the following also referred to as prestimulus phase and consisting of a time window between the cue presentation and the stimulus appearance has recently gained interest within the scientific community. It has been shown to impact stimulus perception not only in psychophysiological experiments (Hanslmayr et al., 2007), but also in the context of visual studies (Jensen, Bonnefond, & Van Rullen, 2012; Thut, Miniussi, & Gross, 2012; Mazaheri, DiQuattro, Bengson, & Geng, 2011). The results of these studies suggest that neural oscillations occurring in the prestimulus period may be functionally important for visual control and processing (Jensen, Bonnefond, & Van Rullen, 2012; Thut, Miniussi, & Gross, 2012). Neural oscillatory activity comes from rhythmic spikes of neuronal populations at the level of post-synaptic potentials, and can be easily recorded by the means of electroencephalogram (EEG) or magnetoencephalography (MEG). For example, prestimulus oscillations in the alpha band (8-12 Hz) have been proposed to play a functional role in stimulus perception. General increases in alpha power have been associated with lower probabilities of consciously processing visual stimuli close to perception thresholds (Babiloni, Vecchio, Bultrini, Romani, & Rossini, 2006; Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014; Linkenkaer-Hansen, Vadim, Palva, Ilmoniemi, & Palva, 2004) and poor perceptual performance (Hanslmayr et al.,

2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Alpha modulations have additionally been associated to spatial control of attention, where it has been suggested that different patterns of alpha power modulations over posterior brain areas may provide an index of voluntary shifting or maintenance of attention (Rihs, Michel, & Thut, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006). However, most of these studies focus on covert and spatial attention and uses different designs other than visual search displays. We propose to make use of concurrent eye movement and MEG recordings to investigate the role of prestimulus oscillatory activity in the context of oculomotor overt selection and especially in the study of stimulus- and goal-driven control time-course.

In the paragraph “Neural correlates of visual selection” we outlined how Buschman & Miller and Corbetta & Shulman (Buschman & Miller, 2007,2013; Corbetta, Shulman, Miezin, & Petersen, 1995; Corbetta, 1998; Shulman, D’Avossa, Tansy, & Corbetta, 2002) mostly utilized fMRI and PET to study the neural underpinning of stimulus- and goal-driven processes. However, in the General introduction we pointed out the importance of time when studying the interaction between these competing visual strategies. We find that fMRI and PET techniques lack of the right temporal resolution to investigate processes where time plays such an important role. This is why in study 2 we propose to combine the eye tracking device with the MEG to investigate how possible different brain states may impact on oculomotor selection strategies. A certain brain state, as for example expressed by alpha oscillatory activity in a specific brain area, may be a signature of a certain type of oculomotor control. The good spatial resolution of MEG may give us the possibility to identify the source of activity in the brain that is determinant of a more goal-driven strategy rather than stimulus-driven. In addition, the MEG temporal resolution of milliseconds, combined with the high temporal resolution of the eye tracking, may allow us to follow the cortical stages of visual processing just before the saccade is deployed. In visual search experiments where eye movements are recorded, saccadic reaction times range usually between 100 to 300 ms. Given his high temporal and spatial resolution, to us MEG is the best neuroimaging method to combine with the eye tracking for the study of oculomotor selection in visual search.

One drawback of a concurrent eye tracking and MEG recordings can derive from spikes and artifacts generated by eye movement and blinks. However latest advance in the Independent Component Analyses (ICA) method may help to identify the artifactual features of blinks and eye

movement (Bell & Sejnowski, 1995; Makeig, Bell, Jung, & Sejnowski, 1996). Once identified, ICA would allow removing them from the recordings without any threat for subsequent data analyses.

Chapter 3

Study 2: The effect of pre-stimulus neural oscillatory activity on saccadic reaction times and oculomotor selection performance

Abstract

When in time a response is made seems critically important in defining whether visual selection is driven by physical stimulus-salience or goal-driven control. In study 1 we investigated whether observers are able to control the timing of selection and regulate the trade-off between stimulus- and goal-driven influences. Participants were instructed to make a saccade to an orientation target while a cue instructed them to do so either 'fast' or 'accurate'. Relative salience of the target and an irrelevant distractor was manipulated. Performance in the fast-cue condition appeared to be driven by stimulus salience, while in the accurate-cue condition saccades were guided by the search template. A main effect of cue suggests that preparation can bias mechanisms of selection prior to saccadic execution. In study 2, using spontaneous response time variability, we tested the hypothesis that alpha-oscillations (8-12 Hz) occurring in the prestimulus period may influence performance and saccadic reaction times in a visual search task. Using a similar design, MEG and eye movements were measured concurrently. Results revealed that slow oculomotor reaction times in the non-salient target condition were predicted by an overall increase of power in the alpha range. Additionally, higher alpha pre-stimulus activity seems to predict erroneous response similarly for fast and slow saccadic reaction times. When further decomposing the source of the difference between correct and incorrect responses for fast and slow saccadic reaction times, analyses revealed two main sources of activity. Wrong responses for fast saccadic reaction times were anticipated by higher alpha activity occurring in the parietal regions, with sources located in the lateral intraparietal area. The source of

alpha activity for the errors occurring in the slow responses was instead located more in the frontal lobes and specifically around the dorsolateral prefrontal cortex.

Introduction

Picture yourself arriving late in a busy conference hall, searching for a free seat. Suddenly, the presenter announces that the talk is going to start, and you need to rapidly find among the crowded room a free seat. To succeed in this situation, your brain needs to select and process task-relevant sensory information required to find the free spot, filtering out the unnecessary. In this example, goal-related mechanisms needed to find the desired seat are in competition with interfering processes related to task-irrelevant salient information, like perceiving the bright yellow shirt of a colleague, or the starting up of the presentation on the big screen. The literature refers to these competing mechanisms of visual control as goal-driven, when top-down processes grant attention to those stimuli that are in line with the intention of the observer (Bacon & Egeth, 1994; Chen & Zelinsky, 2006; Folk et al., 1992); and stimulus-driven, when instead bottom-up mechanisms lead to the selection of salient information (Nothdurft, 2002; Theeuwes, 1992, 2004). However, whether these mechanisms are available might also depend on the brain state of the observer and on how much in a hurry he or she is moving through the auditorium. The present work aims to investigate how brain states influence control and timing of responses in visual selection.

According to Corbetta & Shulman, goal-driven and stimulus-driven mechanisms are organized into two distinct and partially segregated brain networks (Maurizio Corbetta & Shulman, 2002). One system, composed by the intra parietal and superior frontal cortex is supposed to be mostly responsible for goal-driven processes. Stimulus-driven control instead engage a secondary network composed by the temporoparietal and the inferior frontal cortex.

In addition to the idea that different brain areas are responsible for different functions, neural oscillations occurring in the prestimulus period may be functionally important for visual control and processing (Jensen, Bonnefond, & Van Rullen, 2012; Thut, Miniussi, & Gross, 2012). Neural oscillatory activity is generated by rhythmic spikes of neuronal ensembles at the level of post-synaptic potentials, and can be easily recorded by the means of electroencephalogram (EEG) or magnetoencephalography

(MEG). For example, prestimulus neural oscillations in the alpha band (8-12 Hz) have been proposed to play a functional role in stimulus perception. General increases in alpha power have been associated with lower probabilities of consciously processing visual stimuli close to perception thresholds (Babiloni, Vecchio, Bultrini, Romani, & Rossini, 2006; Lange, Keil, Schnitzler, van Dijk, & Weisz, 2014; Linkenkaer-Hansen, Vadim, Palva, Ilmoniemi, & Palva, 2004) and poor perceptual performance (Hanslmayr et al., 2007; van Dijk, Schoffelen, Oostenveld, & Jensen, 2008). Alpha modulations have additionally been associated to spatial control of attention, where it has been suggested that different patterns of alpha power modulations over posterior brain areas may provide an index of voluntary shifting or maintenance of attention (Rihs, Michel, & Thut, 2009; Thut, Nietzel, Brandt, & Pascual-Leone, 2006).

More directly relevant for the present work is the finding that prestimulus alpha power as recorded by EEG could predict performance in a task that directly investigated stimulus-driven and goal-driven control. Mazaheri & al. designed a visual search paradigm in which they concurrently measured eye movements and EEG (Mazaheri et al., 2011). Participants were instructed to make an eye movement to a lateralized target that could appear alone or together with a lower or higher contrast distractor. The EEG recordings showed that goal-driven and stimulus-driven strategies could be predicted by prestimulus neural activity. Specifically, frontal oscillations in the alpha band (8-12 Hz) timed to the presentation of the display were higher when a salient distractor captured attention, reflecting the adoption of a stimulus-driven behavior. Trials in which observers were able to correctly detect the target, ignoring the salient distractor, were instead characterized by a transient pre-saccadic increase in the posterior-parietal low alpha band (7-8 Hz). This latter finding depended on saccade-locked analysis of the data. These results show that the combination between oscillations and their location is critically important in the distinction between stimulus- and goal-driven selections. However, the lack of spatial resolution of EEG sensor space analyses made it hard to assess which specific brain network could account for one or the other selection strategy. Moreover, the saliency of the distractor was predictive of the target location, potentially benefitting the selection and discrimination of the target. In addition, differences between saccadic response times to the target and distractor may have been directly related to stimulus- and goal-directed processes, making ambiguous the subsequent alpha power comparisons.

Specifically, response time has been shown to be critically important in determining whether selection is stimulus- or goal-driven (van Zoest, Hunt, & Kingstone, 2010; van Zoest, Donk, & Theeuwes, 2004; Van Zoest & Donk, 2006). When observers take little time to make an eye movement following the presentation of a search display, results show they are strongly driven by stimulus-salience, independently from the identity of the salient item. In contrast, when people are slower to initiate the saccade, selection can be guided by the target, in line with task instructions. Moreover, recent evidence suggests that although early selection may be constrained by stimulus salience, observers are flexible in guiding the 'when' signal and consequently establishing a trade-off between saliency and identity (Paoletti, Weaver, Braun, & van Zoest, 2014). In this study, participants were instructed to respond either 'fast' or 'accurate' in the prestimulus period. Depending on the cue, the results showed people responded fast and driven by saliency or responded much more slowly guided by the target features. In other words, observers may be prompted into a state of preparation that allows rapid deployment to salient elements or a state that results in slower selection that optimizes the use of goal-driven control. The idea that we want to investigate in the present work is to what extent the variations in timing and consequent control are driven by variations in prestimulus alpha oscillations. Whereas our previously discussed work employed an explicit cue to prompt these different strategies (Paoletti et al., 2014), the present study will rely on the natural variation of the distribution of oculomotor selection. Indeed, using spontaneous response time variability, Bompas and colleagues have demonstrated a relationship between oculomotor reaction times and prestimulus alpha power, presenting evidence that broadband higher prestimulus oscillatory amplitude in occipital, parietal and temporal areas is a predictor of slower reaction times (Bompas, Sumner, Muthumaraswamy, Singh, & Gilchrist, 2015). Thus, the contribution of the present investigation is to further detail how alpha prestimulus oscillatory mechanisms are related to response time and importantly to consequent oculomotor performance. This potential interaction between saccade reaction time, control of strategies and oscillatory activity may come about in two different ways. First, an increase in alpha power in specific frontal and parietal brain regions may increase reaction times and consequently leave more time for goal-directed visual search. Second, an increase in alpha may induce a shift towards goal directed search, which in turn takes longer to implement and thus leads to longer reaction times. In order to differentiate between these two

possibilities we concurrently record of eye movements and MEG brain activity while subjects will perform a visual search task.

Based on the idea that increased alpha band modulations reflect functional inhibition or a specific task disengagement (Hanslmayr, Gross, Klimesch, & Shapiro, 2011; Klimesch, Sauseng, & Hanslmayr, 2007) we expect stronger frontal alpha activity being related to less control, such that performance will be driven by stimulus salience. Vice versa, stronger alpha in posterior areas should be related to the inhibition of the salient distractor, reflecting more control and better oculomotor performance. At the same time, based on the idea that stronger alpha activity is related to slower oculomotor reaction times (Bompas et al., 2015), we expect to find different levels of alpha modulations depending on whether participants will respond quickly or more slowly following the presentation of the search display. Note that these predictions based on previous literature are seemingly in contrast with each other when stronger alpha predicts both poor performance and slower reaction times. Slower reaction times for the most part imply more accurate performance.

Methods and Materials

i. Participants

Sixteen healthy participants (9 females, average age 24.7 years, range 21-28 years) participated as paid volunteers. All subjects reported having normal or corrected-to-normal vision. The study was conducted in accordance with ethical standards codified by the World Medical Association in the Declaration of Helsinki and written informed consent was obtained from participants before the experiment.

ii. Design

Participants were asked to perform a visual search task (see Figure 1) in which they had to make a saccade to a target. For half of the participants, the target consisted of a right-tilted bar (i.e., a line segment tilted to the right of a vertical axis), while the other half looked for a left-tilted bar (i.e., a line segment tilted to the left). The target was always embedded within a raster of non-targets

singleton elements (i.e., vertically oriented line segments). Together with the target and the raster of singleton non-targets an additional distractor was present on the screen. The distractor was always tilted to the opposite direction of the target. Elements were either tilted 67.5° or 22.5° . Relative to the vertical background items, the larger difference in the degree of tilt of the 67.5° element made it perceptually more salient than the 22.5° element. The experiment comprised 4 sessions: in the 1st and 3rd session the target was tilted by 67.5° while the distractor consisted in a 22.5° tilted bar, i.e., salient target, non-salient distractor condition. In the 2nd and 4th sessions the target bar was tilted by 22.5° and the distractor by 67.5° , i.e., non-salient target, salient distractor condition. For half of the participants the sessions order was reversed. All elements (1 target, 1 distractor, and 287 non-targets) were arranged in a 17×17 matrix display with a raster width of 290×210 mm (height \times width, corresponding to $27.2^\circ \times 19.9^\circ$ of visual angle). Target and distractor could be placed at four different locations set on the corners of an imaginary square such that, embedded within the matrix of non-targets, targets and distractors were always presented at equal distance from fixation (7.6° of visual angle) and separated by an angular distance of 90° . To avoid potential inter-hemifield effects, the distractor was always presented to the opposite visual hemifield in respect to the target. All line elements had an approximate height of 0.65° and width of 0.12° of visual angle. All elements were white and superimposed on a grey background. The experimental design was realized using Psychtoolbox 3 (Brainard, 1997; Pelli, 1997) in combination with MATLAB R2010b (The MathWorks, Inc., Natick, MA).

iii. Procedure

Each trial began with a drift correction of the eye tracking signal to ensure that participant's gaze was at the fixation point before stimuli onset. A display with a central fixation point was presented for 1800 ms plus a jittering interval of ~ 200 ms (total fixation duration: min 1800 ms, max 2000 ms) to avoid possible expectancy effects. The stimulus array was then presented for 1500 ms. Participants were instructed to make a saccade to the tilted element defined as the target as soon as the search display was presented. To make sure that the task was understood by the participants, oral and written instructions were given and a practice session of 32 trials was conducted before the

beginning of the experiment. A factorial design was used: target positions (4) and orientations (2) were equally counterbalanced and presented in random order. Distractor position was always constrained by target location. The experiment consisted of 448 trials divided into four blocks of 112 trials each and lasted approximately 50 minutes. The eye tracker was re-tuned at the beginning of each session.

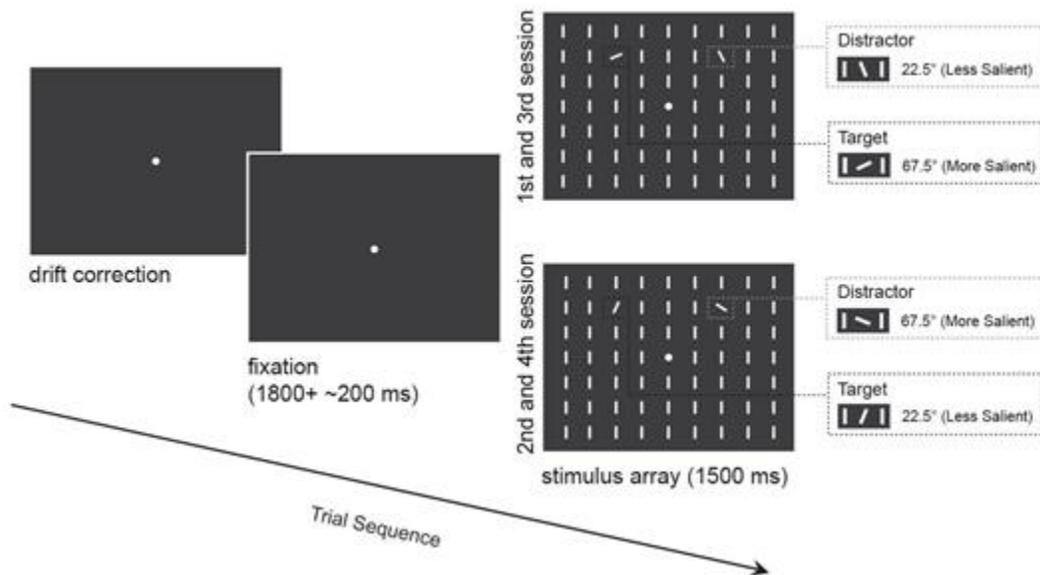


Fig. 1: Trial sequence. Participants executed a saccade to the singleton target element, depicted here as the 67.5° or the 22.5° tilted segment to the right relative to vertical non-target elements. Additionally, a uniquely oriented distractor line element was presented together with the target and the raster of non-targets. The unique distractor was always tilted to the opposite direction of the target and was more or less salient in dependence of the target orientation Note, stimuli not drawn to scale.

iv. Eye movement and MEG recordings

Eye movements and magnetic fields were recorded simultaneously in a magnetically shielded room while participants were performing the task comfortably seated on the height-adjustable chair of the MEG unit. To minimize head movements and to maintain participants in the focal range of the eye-tracking camera, subjects were resting their head on an MEG compatible chin support. Participant's head position relative to the MEG sensors was monitored at the beginning and at the end of each recording session. Eye movements were recorded using an Eyelink 1000 (SR research Ltd., Mississauga, ON, Canada) in combination with the MEG compatible *Long Range Mount* (remote infrared camera) and the *Fiber Optic Camera Upgrade*. The non-ferromagnetic remote infrared camera was connected through the optic fiber directly to the MEG acquisition console and was intended to reduce electromagnetic noise that would adulterate the MEG recordings. Neuromagnetic brain activity was recorded continuously by a 275-channel MEG system (CTF MEG by MISL, Coquitlam, BC). Electromagnetic activity and eye movement data were sampled at 1171 Hz. In order to avoid aliasing magnetic brain signals, data were filtered with a hardware low-pass filter at 293 Hz.

Analyses strategy

i. Eye movement analyses

During offline analyses, saccades were defined on the basis of minimum eye-movement speed and acceleration threshold ($30^\circ/s$ and $8000^\circ/s^2$ respectively). Saccade reaction time (SRT) was measured as the time between the onset of the stimuli and the moment in which the eye moved at least 3° of visual angle from fixation point. Trials were considered valid if the first saccade landed within 4° of visual angle from target or distractor. Trials were instead excluded when the initial saccade went neither to the target nor to distractor (trials rejected = 5.27%), started from more than 3° of visual angle from central fixation at the onset of the search display (trials rejected = 2.23%), was anticipative (<80 ms, trials rejected 0.33%) or if the SRT was larger than 2.5 standard deviations from individual participant means (trials rejected = 3.82%). Combined, these criteria led to the rejection of 11.65% of trials from the 16 participants that were included in the primary analyses. For each

participant an individual distribution of SRTs was calculated and split into two bins (fast and slow), containing an equal number of trials. For each bin, we then computed the percentage of initial eye movements correctly directed to target and the average SRTs. Repeated measurement ANOVA was used to test the effect of saliency on performance and SRTs.

ii. MEG data analyses

1. *Preprocessing*

All MEG recordings were analyzed using Matlab R2014a (The MathWorks, Inc., Natick, MA) in combination with the Fieldtrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011). Firstly, data were band-pass filtered between 1 and 45 Hz. Artifact rejection related to muscle activity, eye-movements and outlier channels was managed by a semi-automatic procedure individually for each subject. Specifically, eye-movements and cardiac activity were identified and removed using Independent Component Analyses (ICA) technique (Bell & Sejnowski, 1995; Makeig, Bell, Jung, & Sejnowski, 1996). Additionally, the identification of artifactual components deriving from eye movement was facilitated by comparing ICA time courses with saccades reaction time information coming from the eye-tracking device. Lastly, data were visually inspected to find any residual eye movement or muscular artifact that was not correctly identified and removed in the previous steps. MEG data were then epoched starting from 2000 ms before the stimulus onset to 1500 ms after for a total epoch time of 3500 ms. Stimulus onset timing, target position and target saliency were obtained from the triggering system of the MEG acquisition console. Additional information on single trial SRTs bin and first saccade landing position was derived from the analyses of the eye tracking data. With this process we finally categorized and split the MEG data into four different conditions: target salient and target not-salient, each one having a fast and slow condition according to SRT bin and correct (to target) or incorrect (to distractor) saccades.

2. Time-frequency analyses

For each of these conditions we computed the time-frequency representations (TFRs) applying nonparametric Morlet wavelets between 5 and 40 Hz with an adaptive sliding time window in steps of

50 ms between -500 ms and 0 ms with respect to the stimulus onset. Before computing the TFRs, we calculated the planar gradiometer representation of the data using a nearest-neighbor approach (Bastiaansen & Knösche, 2000). This method, by showing maximal activity over the neural sources, simplifies the interpretation of sensor-level data. Spectral power was then estimated firstly across trials for each participant and then grand-averaged across participants. For the Target salient condition and Target not-salient condition separately, we compared the TFRs maps between fast and slow SRTs and correct and incorrect responses respectively to investigate different predictive neuronal oscillatory mechanisms that could occur in the prestimulus period.

3. Statistical test of TFRs

After sorting the trials, changes in power between the above-described conditions were statistically assessed using a cluster-based permutation test. This nonparametric randomization method effectively corrects for errors deriving from multiple comparison over sensors in within-subject comparisons (Maris & Oostenveld, 2007; Nichols & Holmes, 2002). When comparing two different conditions, clusters are identified by grouping adjacent sensors that show a t statistics exceeding $p < .05$. Since this comparison is only used to identify sensors for the subsequent cluster analyses, the power values are not required to be normally distributed. The clusters of channels that survive this first step are then forwarded to the cluster-level statistic, defined as the sum of t statistics of the sensors in a cluster. To control Type-I error rate for the complete set of 272 MEG channels, cluster-level test statistic is checked under the randomization null distribution of the maximum cluster-level statistic. This process is accomplished by randomly permuting the data coming from the two-experimental conditions within every participant. In our analyses, we created a reference distribution from 1000 random sets of permutations and the p values were defined as the proportion of elements exceeding the observed maximum cluster-level statistical test in the null randomized distribution.

4. Frequency-domain source analyses

The reconstruction of sources for the pre-selected frequency bands based on the results of sensor level analyses was performed applying a frequency–domain beamforming technique called dynamic imaging of coherent sources (DICS). This technique, using an adaptive spatial filters, has been demonstrated to be particularly capable of localizing oscillatory neuronal sources originating from specific frequency bands in the whole brain (Gross et al., 2001; Liljeström, Kujala, Jensen, & Salmelin, 2005). Since individual MRIs could not be obtained, head sensors positions of each participant were used to match individual brain to a standard structural MRI template (Steinstraeter et al., 2009). The resulting brain volume was then discretized to a 0.5 grid resolution and lead fields were evaluated for each grid point. To estimate the source of the difference, we calculated common filters for all the conditions, and then applied it to the data separately for the individual conditions. The estimated source location were plotted on a standard MNI brain template.

Results

i. Behavioral

1. Time-course analyses, proportion to target

In order to examine performance as a function of time, for each participant an individual distribution of SRTs was calculated and split into two bins (fast and slow) containing an equal number of trials. For each bin we then computed the percentage of initial eye movements correctly directed to target and the average SRTs (see Figure 2). A two-ways repeated measurement ANOVA was conducted on the proportion of correct eye movement using within-participants factors of target saliency (salient and not-salient), and SRT bin (fast and slow). All main effects (target saliency and SRT bin) were significant (target saliency: $F(1, 15) = 12.13$, $MSE = .015$, $p < .001$, partial $\eta^2 = .46$; SRT bin: $F(1, 15) = 28.56$, $MSE = .017$, $p < .001$, partial $\eta^2 = .67$), together with the two-way interaction target saliency \times SRT bin: $F(1, 15) = 38.86$, $MSE = .005$, $p < .001$, partial $\eta^2 = .74$. These results showed that fast bin responses were mostly driven by target saliency (mean correct target salient = .69, mean correct target not-salient = .39): participants were better able to select the target when it was salient

compared to when it was not-salient. Slow bin responses were instead characterized by equal performance in both target saliency condition (mean correct target salient = .68, mean correct target not-salient = .62).

2. Time course-analyses, saccadic reaction times

A two-ways repeated measurement ANOVA was performed on saccade latencies with target saliency (67.5° and 22.5°) and SRT bin (fast and slow) as within factors. The result disclosed a significant main effect of SRT bin ($F(1, 15) = 119,17$, $MSE = 1147$, $p < .001$, partial $\eta^2 = .89$). Target saliency effect showed instead to be not significant ($F(1, 15) < 1.00$) as well as the interaction between target saliency and SRT bin ($F(1, 15) < 1.00$): there were no differences in SRT to the target in the 67.5° and 22.5° condition as a function of fast and slow time bins.

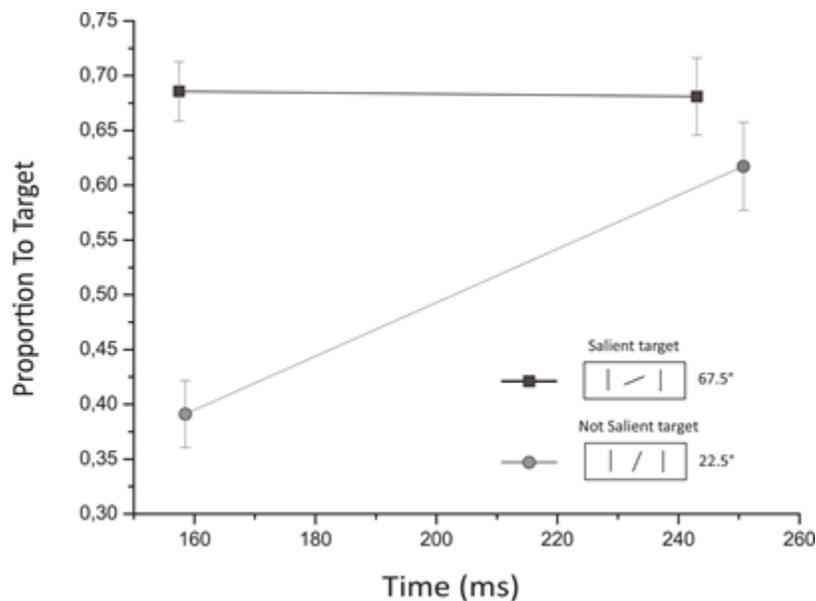


Fig. 2. Proportion of saccades correctly deployed on the target as a function of fast and slow SRT. Error bars reflect standard errors of the mean.

ii. MEG results

1. Time-frequency results and source analyses

In order to investigate how alpha modulation influenced saccadic performance as a function of time we computed the TFR of power for all the MEG sensors time courses after calculating the planar gradiometer representation of the data. We then compared these TFR maps between fast and slow responses, based on SRTs information and separately for salient and non-salient target conditions (see methods). In the salient target condition, there was no evidence to suggest that alpha modulation influenced differences between fast and slow SRTs (Figure 3A). This result was in line with the behavioral result showing no modulation in performance as a function of time in presence of a salient target. On the contrary, the not-salient target condition showed vast differences in alpha power level depending on whether responses were fast or slow (Figure 3C). The whole brain cluster-corrected permutation test disclosed a significant alpha modulation between fast and slow trials (main effect collapsed over correct/incorrect trials, $p = .002$).

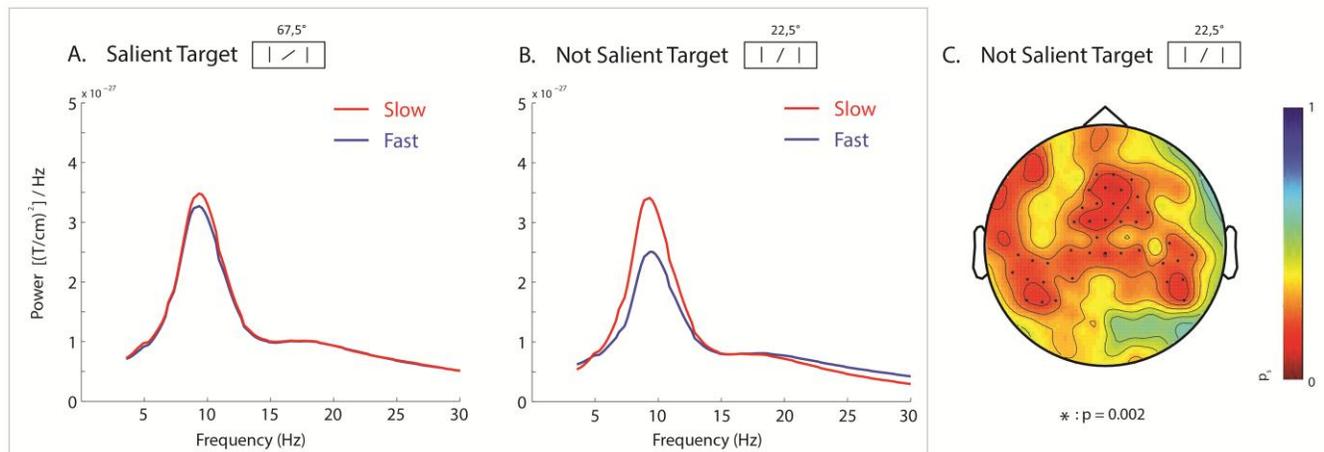


Fig. 3. Prestimulus averaged spectra of the 275 MEG CTF channels (planar gradiometers) for fast and slow SRTs respectively for **A.** salient target and **B.** non salient target condition. **C.** Cluster of significant channels in the prestimulus period ($t = -0.5$ to 0 s) for slow SRTs compared to fast SRTs ($p = 0.002$, corrected for multiple comparison) in the power alpha range (8-12 Hz).

Specifically, overall alpha power was stronger for slower responses compared to fast responses (Figure 3B). In addition, to investigate how alpha mechanisms specifically interact with performance under non-salient target condition, we divided the fast and slow trials as a function of correct (i.e., when the eye movement was directed toward the non-salient target) and incorrect selection (i.e., when saccade landed on the salient distractor). We then conducted separate contrasts comparing incorrect to correct for the fast (Figure 4A) and slow responses (Figure 4B). For fast responses, alpha power was higher for incorrect compared to correct responses. A whole brain cluster-corrected permutation test disclosed a significant alpha modulation in the fast responses between incorrect and corrects trials (main effect trials, $p = .002$).

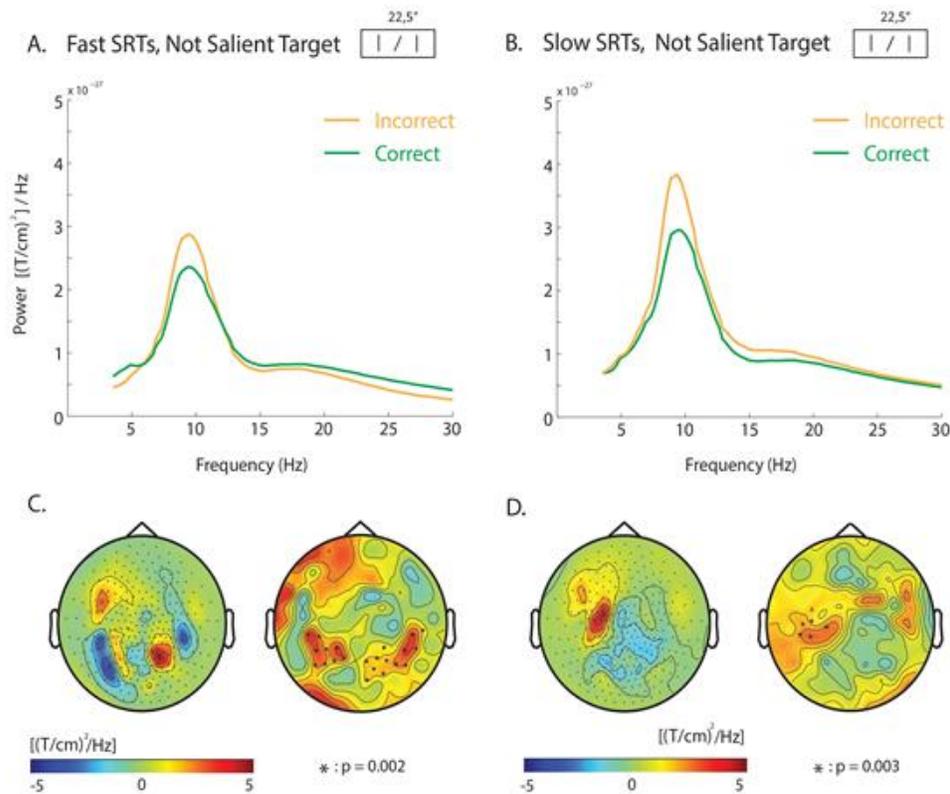


Fig. 4. Separate contrast for slow and fast SRTs in the non salient target condition. Average spectra for correct and incorrect saccades in **A.** fast SRTs and **B.** slow SRTs. **C.** Topographic plot showing prestimulus ($t = -0.5$ to 0 s) alpha power (8-12 Hz) and significant cluster respectively for **C.** fast and **D.** slow SRTs. Bar graph showing alpha power intensity.

This contrast was also reliable for the slower responses (main effect trials, $p = .003$). To identify the sources producing the oscillatory activity that modulates timing of responses and performance in the non-salient target condition, we applied a beamforming technique. We subtracted the source activity of incorrect and correct saccades in the fast and slow SRTs condition.

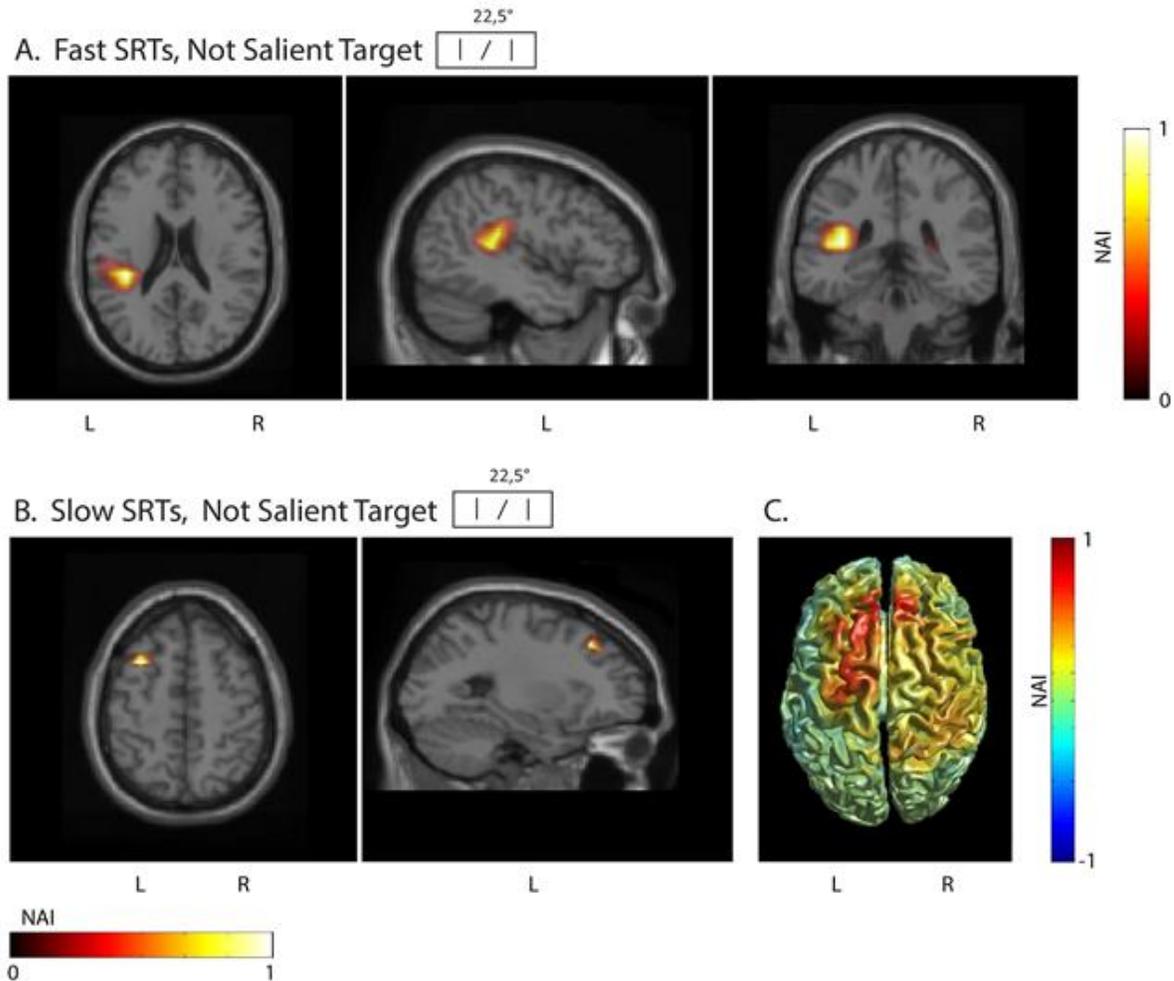


Fig. 5. Neuronal sources of alpha power differences between incorrect and correct saccades for slow and fast SRTs in the non-salient target condition. **A.** fast SRTs and **B.** slow SRTs. **C.** Projection of the difference between incorrect and correct responses for slow SRTs on the cortex. Bar graph showing Neural Activity Index as computed by the DICS beamformer.

Consistently with the topographic maps in figure 4C, the sources representing the alpha power difference in the fast responses were identified in posterior areas, around the lateral intraparietal

cortex and intraparietal sulcus (LIP/IPS), with stronger activity lateralized to the left side of the brain (Figure 5A). The source of alpha modulations accounting for the difference between correct and incorrect in slow SRTs was instead located more in frontal regions, and specifically around the dorsolateral prefrontal cortex (DLPFC; Figure 5B, 5C). Also in this condition there was a tendency toward a left lateralization.

Discussion

In line with our previous study (Paoletti et al., 2014), we showed that short-latency saccades are primarily driven by stimulus salience while long latency saccade are mainly directed to the target, strengthening the idea that performance and SRTs are strongly related to each other. Looking at alpha prestimulus oscillatory power, the results showed that in presence of a salient target, prestimulus alpha power did not affect saccadic SRTs. This is in line with the behavioral results showing no modulation in performance for fast and slow responses. Instead, when participant were asked to find the non-salient target we observed reliable differences in broadband alpha power depending on oculomotor response time. Specifically, slower SRTs were predicted by overall stronger alpha power in the 500 ms time window preceding the stimulus onset, while weaker alpha power was a signature of faster responses.

We then looked at alpha power separately for the fast and slow responses to see whether different levels of alpha power helped to further explain correct and more goal-driven performance. The follow-up analyses showed that relative stronger alpha power predicted incorrect responses similarly for fast and slow oculomotor reaction times. In other words, the relationship between alpha power for correct and incorrect was alike irrespective of saccadic response time and irrespective of the overall proportion of eye movements directed to the target.

Thus, we find evidence for two main influences of prestimulus alpha power on selection performance. First, stronger alpha power found in frontal and parietal areas helped to predict overall slower response time. Second, when this overall activity was further decomposed, we found evidence for specific alpha activity from two different sources that predicted correct versus incorrect responses

independent of time. Specifically, topographic maps revealed an alpha power difference for correct and incorrect saccades in fast responses that appeared to be more posterior in contrast to slow responses that appeared to be more in frontal areas. In more detail, the source analyses disclosed that the ~ 10 Hz difference for the fast saccades was located around the LIP/IPS areas. In contrast, the source for the slow responses was located close to the DLPFC.

These results are in line with existing works concerning control of goal-directed and stimulus-driven attention in the brain. For instance, Miller and Buschman (Miller & Buschman, 2013) have suggested that LIP and DLPFC are part of the oculomotor network that control bottom-up and top-down attentional processes (see also Buschman & Miller, 2007; Corbetta & Shulman, 2002). Specifically, The LIP is known to be involved in saccadic preparation (Andersen, Bracewell, Barash, Gnadt, & Fogassi, 1990; Curtis & Connolly, 2008; Platt & Glimcher, 1997; Wardak, Olivier, & Duhamel, 2002) and in resolving competition between stimulus elicited activity and endogenous saccade planning (Anderson, Husain, & Sumner, 2008). Instead, many studies have identified the left DLPFC as a key structure for top-down attentional control that dynamically adjust performance and control according to contextual demands (Banich et al., 2000; MacDonald, Cohen, Stenger, & Carter, 2000; Milham, Banich, & Barad, 2003; Siltan et al., 2010).

More importantly for the present study is the notion that the DLPFC play a crucial role in saccadic inhibition, helping to prevent reflexive eye movements toward distracting stimuli (McDowell, Dyckman, Austin, & Clementz, 2008; C. Pierrot-Deseilligny et al., 2003; Charles Pierrot-Deseilligny, Milea, & Müri, 2004; Ptak, 2012). For example in their study Buschman & Miller (Buschman & Miller, 2007) used a pop-out display and a search display to investigate the time course of bottom-up and top-down processes in primates brain. They concurrently recorded monkey's eye movements and neuronal activity from multiple electrodes placed in frontal and parietal cortices. The behavioral results showed that when deploying fast saccades, the monkey were unable to inhibit the salient distractors. On the contrary, slower saccades were characterized by more control and top-down behavioral hallmarks. When looking at neural activity, they found that fast and bottom-up signals appear first in the LIP while the signals generated from longer latencies saccades and associated to more top-down control were recorded from electrodes located in the frontal cortex.

Though this previously discussed work did not directly look at a prestimulus brain state, our results suggest that alpha power occurring in the prestimulus period in those same areas may influence the forthcoming visual process and the subsequent oculomotor behavior. For example, an increase of alpha power in LIP/IPS may reflect a preparatory mechanism mostly responsible for fast deployment of overt attention toward salient stimuli. Vice versa, prestimulus increases of alpha power in the DLPFC may match a preparatory set more prone for a better oculomotor control, leading to a more goal-directed behavior. This idea is in line with the hypothesis proposed from Buschman and Miller (Miller & Buschman, 2013), suggesting that parietal areas are mostly responsible for fast and stimulus-driven target selection, whereas longer latency top-down selection occurs in the frontal cortex. In this present work, these ideas are supported by looking at the overall behavioral difference in the proportion of eye movements. Figure 2 shows that when people made a quick saccades in the presence of a salient distractor they were much more likely to end up incorrectly at the location of the salient item. When people instead took more time, they were more likely to make a goal-driven saccade to the target. Based on the overall proportion eye movements in fast and slow eye movements, we can infer the relative contribution of stimulus-driven and goal-directed control. However, when considering the subset of quick saccades and comparing them to the subset of slow saccades, we found no evidence for an interaction between SRT and correct versus incorrect eye movements. Stronger alpha power predicted incorrect saccades similarly for fast and slow saccades, suggesting that alpha power did not directly relate to the overall proportion of stimulus-driven selection in our study.

In the introduction, we outlined two ways in which the interaction between saccade reaction time, control of strategies and oscillatory activity could come about. First, an increase in alpha power in specific frontal and parietal brain regions may increase reaction times and consequently leave more time for goal-directed visual search; second, an increase in alpha may induce a shift towards goal directed search, which in turn takes longer to implement and thus leads to longer reaction times. Our results are in line with the former hypothesis suggesting that prestimulus alpha power does not directly predict stimulus- or goal-driven selections. Specifically, the relationship between alpha power for correct and incorrect was comparable irrespective of response time and irrespective of the overall proportion of eye movements directed to the salient distractor. Instead, a general alpha increase was

related to a slowing down of responses, which indirectly predicted better control and a more accurate selection behavior.

Our general results of finding that alpha power predicts slower saccadic reaction times is in line with Bompas et al. study (Bompas et al., 2015). However, we found a relationship between alpha power and saccadic reaction time only when the task was difficult, i.e.: when the target was more difficult to select because of distractor competition. Our results are in contrast with Mazaheri et al. (Mazaheri et al., 2011) where stronger prestimulus frontal alpha was found under bottom-up salient captures and pre-saccadic posterior transient alpha reflected salient distractor inhibition. In the present study, stronger alpha in frontal areas was related to slower overall responding, allowing observers to have more control in line with goal-driven behaviors. Stronger posterior alpha was instead a signature of faster response that promoted salient captures and led to more stimulus-oriented behaviors. The discrepancy between the results of Mazaheri et al. and the present study may be partly explained by differences in the design and methods. Specifically in Mazaheri et al. study, because the target was presented either in isolation or accompanied by one sole distractor, the question is whether the task adopted was a true visual search task. Because the target and distractor always appeared at one of two locations, the salient distractor location could predict the target location. In other words, when a salient distractor was presented, it automatically cued the location of target item where the target discrimination was to be made. In the present study target and distractor position were unpredictable. Furthermore, analyses in the Mazaheri et al. study were based on saccadic responses that were averaged over all trials; correct saccade to the target were much slower than incorrect saccades to the salient distractor. However the role of time in establishing this control and its relationship to alpha power was unclear. The present study was designed to enable investigation of selection performance and alpha power separately for quick and slow responses, making it possible to look at prestimulus brain state in relation to response time and selection performance together.

General conclusions

In our first study we showed that independently from a pre-given cue, short-latency saccades were driven by stimulus salience and long latency responses were primarily goal directed. More importantly, we showed that participants were capable of following the cue instructions and therefore to control the timing of saccadic visual selection. The fast cue condition visual search was characterized by short timing saccades while in the accurate cue condition we observed slower oculomotor responses. The overall performance as a function of time-course showed that the trade-off in the fast cue was mainly stimulus-driven, thus selection was based on saliency early in time. Goal-driven control was only found in the final time bin, where stimulus salience no longer influenced selection. Instead, goal-driven strategies mostly directed the trade-off in the accurate cue condition; stimulus salience only influenced performance for the fastest responses. It appeared that observers' timing of responses based on the cue influenced this trade-off between stimulus- and goal-driven strategies. Following the cue, observers were able to elicit faster or slower eye movements and consequently exerting adaptive changes in their visual search strategies, making selection relatively more stimulus- or goal-driven. These results suggest that the ability to elicit either a fast or slow response is flexible: participants are able to adopt a 'fast' or 'accurate' strategy before each trial, depending on the task instructions. This has a consequent effect on whether search processes are primarily stimulus- or goal-driven. Specifically in the fast-cue condition participants may have been prompted into a cognitive state that allowed rapid attentional deployment characterized by fast and salient captures; goal-driven control was severely limited in this case. On the other hand, in the accurate-cue condition, participants appeared to refrain from fast responding and so were able to avoid salient capture; observers were more accurate in making correct eye movements to the designated target. These results indicate that while performing the task, participants were able to optimize their internal states to guide behavior, that is, observers were able to enter a state of cognitive control in which performance was optimized to accomplish the task in the given situation (Miller, 2000). Our results thus illustrate an important role of an observer's preparedness in solving a task. The prestimulus effects of preparation have also been reported for feature-specific instructions in a recent fMRI study from Serences and Boynton (2007) and in a monkey physiology study (Hayden & Gallant, 2005). The results of these studies suggest that feature-based attention can be enhanced

before the stimulus presentation by increasing sensitivity to certain features (i.e., orientation, color) facilitating the perception of behaviorally pertinent stimuli. Although the above studies do not directly refer to saccadic selection, these mechanisms seem to affect the oculomotor system as well. A recent study (Weaver, Paoletti, & van Zoest, 2014) reported an increase of performance in very early saccades when a feature-informative cue (color) regarding the target was given to participants rather than a neutral cue. Study one revealed that individual observers are relatively flexible regarding the extent to when a response is triggered. This 'when' signal in turn, determined the degree to which participants were more or less driven by stimulus salience or identity. Thus, when investigating whether visual selection is primarily stimulus or goal driven, the present work demonstrates the critical importance of taking into account the trade-off between the influence of stimulus salience and target identity over time.

In our second study, we aimed to investigate how prestimulus brain state could influence oculomotor visual search in relation to saccadic reaction times and performance. In line with study 1 (Paoletti et al., 2014), we showed that short-latency saccades were primarily driven by stimulus salience while long latency saccades were mainly directed to the target, strengthening the idea that performance and SRTs are strongly related to each other. Looking at alpha prestimulus oscillatory power, the results showed that in presence of a salient target, prestimulus alpha power did not affect saccadic SRTs. This is in line with the behavioral results showing no modulation in performance for fast and slow responses. Instead, when participant were asked to find the non-salient target we observed reliable differences in broadband alpha power depending on oculomotor response time. Specifically, slower SRTs were predicted by overall stronger alpha power in the 500 ms time window preceding the stimulus onset, while weaker alpha power was a signature of faster responses.

We then looked at alpha power separately for the fast and slow responses to see whether different levels of alpha power helped to further explain correct and more goal-driven performance. The follow-up analyses showed that relative stronger alpha power predicted incorrect responses similarly for fast and slow oculomotor reaction times. In other words, the relationship between alpha power for correct and incorrect was alike irrespective of saccadic response time and irrespective of the overall proportion of eye movements directed to the target. Thus, we find evidence for two main influences of prestimulus alpha power on selection performance. First, stronger alpha power found in

frontal and parietal areas helped to predict overall slower response time. Second, when this overall activity was further decomposed, we found evidence for specific alpha activity from two different sources that predicted correct versus incorrect responses independent of time. Specifically, topographic maps revealed an alpha power difference for correct and incorrect saccades in fast responses that appeared to be more posterior in contrast to slow responses that appeared to be more in frontal areas. When people made a quick saccades in the presence of a salient distractor they were much more likely to end up incorrectly at the location of the salient item. When people instead took more time, they were more likely to make a goal-driven saccade to the target. Based on the overall proportion of eye movements to the target in fast and slow eye movements, we can infer the relative contribution of stimulus-driven and goal-directed control. However, when considering the subset of quick saccades and comparing them to the subset of slow saccades, we found no evidence for an interaction between SRT and correct versus incorrect eye movements. Stronger alpha power predicted incorrect saccades similarly for fast and slow saccades, suggesting that alpha power did not directly relate to the overall proportion of stimulus-driven selection in our study. As stated in the paper reported above, we proposed two ways in which the interaction between saccadic reaction time, control of strategies and oscillatory activity could come about. First, an increase in alpha power in specific frontal and parietal brain regions may increase reaction times and consequently leave more time for goal-directed visual search; second, an increase in alpha may induce a shift towards goal directed search, which in turn takes longer to implement and thus leads to longer reaction times. Our results are in line with the former hypothesis suggesting that prestimulus alpha power does not directly predict stimulus- or goal-driven selections. Specifically, the relationship between alpha power for correct and incorrect was comparable irrespective of response time and irrespective of the overall proportion of eye movements directed to the salient distractor. Instead, a general alpha increase was related to a slowing down of responses, which indirectly predicted better control and a more accurate selection behavior. One drawback of the present work is that we didn't find a clear direct relationship between alpha power and stimulus-driven and goal-directed control. Whereas one might be inclined to associate the correct eye movement selection of the non-salient target to goal-directed control and incorrect selection of salient distractor to stimulus-driven selection, this reductionist approach does not seem to fit with our results. Previous work that has suggested that stimulus- and goal-driven processes are controlled by different networks, have typically used different displays to make

assessments regarding search strategies adopted by observers (i.e., pop-out vs. serial search, salient distractor absent vs. salient distractor present). However, these drastic changes across condition are also correlated with changes in reaction times, which in turn affects the relative contribution of the processes at stake. The strength of the current work is that we used the exact same display and employing saccadic reaction time at the behavioral level to disentangle stimulus-driven from goal-directed responses.

Previous works on alpha prestimulus role primarily concerned studies of covert spatial attention and temporal attention. Our second study is the first to look at alpha power in relation to overt selection and dynamic control in saccadic eye movements. We have demonstrated how an overall increase of alpha power in the prestimulus period can be a predictor of slow responses that consequently allows more time for goal-directed control. Stronger alpha power also was found to predict incorrect performance, but was not directly related to stimulus-driven or goal-directed selection. Again, we have demonstrated that reaction times, oculomotor performance and prestimulus oscillatory mechanisms are interacting. Addressing these topics in a dichotomist way (i.e.: interaction between performance and prestimulus period) and looking at different dimensions in isolation (saliency, prestimulus period, performance and reaction times) does not tell the whole story. Future studies investigating possible implications of prestimulus oscillatory mechanisms in oculomotor strategies will need to consider the tangled relation between saccadic reactions time and performance.

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