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# Just before eye movement execution: the link between processing of visual objects and allocation of attention

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# ABSTRACT

Our visual system is fovea-heavy, which means that in-depth processing occurs only in the centre of the retina, forcing the eyes to make constant movements in order to bring visual elements into focus. Despite this, eye movements go largely unnoticed and the environment is perceived as visually stable. Pre-saccadic shifts of attention might be guaranteeing this stability by easing the transition from one foveated image to another. Before an eye movement attention shifts to the location where the eyes will land and visual elements presented there are preferentially processed. A similar mechanism, also based on the allocation of attention in eye-centred coordinates, is known as remapping. It allows attention to be maintained on locations of interest across eye movements, while accounting for the retinal displacement caused by each upcoming movement. In the current thesis, we are concerned with how the visual elements present in the environment shape the allocation of attention before eye movements.  We first aimed to determine whether pre-saccadic shifts of attention are a precondition of all saccades, irrespective of goals. We showed that whether the saccade was goal-directed, to the intended target, or involuntary, erroneously directed to a capturing distractor, made little difference to the pre-saccadic shift of attention. Retinal displacement cause by involuntary saccades was also accounted for by the visual system. Next the project focused on how the presented visual elements affect the programming of eye movements, by investigating how the decision to make an eye movement is affected by the number of target alternatives. We saw evidence that a larger set-size can reduce saccadic reaction times without increasing the error rate, a finding not predicted by a popular model. Further, whether the presence of visual elements in and around the saccade landing point influences the shifts of attention was investigated. We demonstrate that objects and their arrangement shape the distribution of attention, and that the effect is not driven by saccade metrics alone. Finally, we look at the spatial and temporal distribution of visual attention when a saccade target is removed shortly before the eye movement.

# Content

This thesis is divided into 6 Chapters. All cited material is listed in a reference section at the end of the entire thesis manuscript.

## Introduction

Chapter 1 is separated into sections.

## Body of Thesis

Chapters 2-5 present the author's own research material, either published or in preparation.

## Discussion

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**Résumé**

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# Chapter 1

# Introduction

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## 1.1 Introduction to saccadic eye movements

The human visual system is an extraordinary and complex tool, widely regarded as the most important of all these senses. It has the largest number of dedicated areas in the brain and the largest amount of neurons firing away to offer a final product that is vision. The priority that is put on visual processing is not specific to humans, rather it is a characteristic of a large number of mammals. In fact, Sprague (1996) explains that the neuronal processing in the visual cortex is extensively distributed and involves approximately half of the brain of many mammalian creatures, the ones most intensely studied in laboratory being rat, gerbil, hamster, tree shrew, cat, bush baby, owl, monkey and macaque. In the cat, 20 dedicated visual areas have been identified in the cortex, many of which are retinotopically organized containing spatial maps that range from coarse to fine-grained, in terms of representation acuity of the environment's structure. This means that visual information is assimilated from the individual's surroundings and is organized in many "maps", or basic structures, across the brain, each differing in level of detail. Central to the overall enquiry we are dealing with is how this information is obtained. The eyes initially receive the visual input and their physiology forces the visual system to function in very specific ways, in order to compensate for its weaknesses and to exploit its strong points. The highest level of clarity is offered only in the central one or two degrees of the visual field. This drives humans to shift their gaze at regular intervals, typically 3 or 4 times every second, in order to process and make sense of the visual environment (Findlay & Gilchrist, 2003). Saccadic eye movements therefore primarily serve to bring images of elements of interest into the fovea. They are, as explained by Reddi & Carpenter, (2000), often triggered by the sudden appearance of a visual stimulus in the periphery and reach velocities of 900 degrees per second, with a notably stereotyped time course. They are, in fact, the fastest of all body movements. There are three muscles that generate movement of the eye bulb: the lateral and medial rectus (left and right), the superior and inferior rectus (up and down) and the superior and inferior oblique (primarily for oblique rotational movements) (see Figure 1). Saccades are known as ballistic, in that, once planned, their destination has been set out. While this held true for many years recent discoveries by Mathôt, Melmi, & Castet (2015) based on previous work by Castet, Jeanjean, & Masson (2002) proved that perception remains active during saccadic motion, in turn, affecting pupil dilatation.

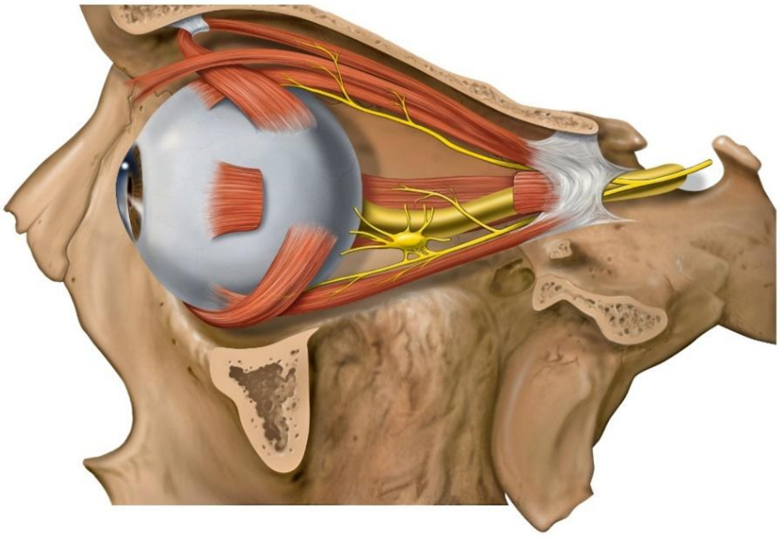

Figure 1. Image of the human eye from the side, illustrating the muscles that control movement. Author of the medical illustration is Patrick J. Lynch.

## 1.2 Neurophysiology of Saccadic Eye Movements

Saccades' main function is that of bringing detailed visual info to cortical regions for analysis. We will briefly examine various cortical regions among the most important in relation to eye movements, and particularly those which related more closely to the information present in the presented papers.

### 1.2.1 Frontal Eye Field

The frontal eye field (FEF) appears to have a central role in relation to highly deliberate and goal-directed eye movements. It has been found to be involved in the preparation and triggering of all intentional saccades towards visual targets across a whole battery of tasks (Pierrot-Deseilligny, Müri, Ploner, Gaymard, & Rivaud-Péchoux, 2003). In antisaccade tasks, where a saccade has to be made in the direction opposite to a suddenly appearing target, using fMRI the FEF was seen to be active during movement preparation, whereas the posterior eye field was not (Connolly, Goodale, Menon, & Munoz, 2002). Worth noting that antisaccades require a high level of control and intentionality, as their execution is intuitive, confirming the role of FEF in clear goal-directed saccades. On the other hand, FEF is barely called upon for the triggering of involuntary saccades, which are more reflexive and externally induced, as could be a flash of light that suddenly appears and captures gaze.

### 1.2.2 Superior Colliculus

A cortical structure particularly important for saccadic eye movements is the superior colliculus (SC). The SC is not particularly active during the execution of the saccade, but it is highly active during the planning phase, when a target or targets are presented (Glimcher & Sparks, 1992). By examining the build-up activity of neurons in the SC it was shown that the neuronal firing begins shortly after a potential saccade target is presented and that activation in the area was predictive of saccade choice (Glimcher & Sparks, 1993). Activity in the SC therefore represents the selection of a saccade target and, along with this, the required information about saccade metrics (Glimcher & Sparks, 1992). It has been suggested that the SC is responsible for sensory-motor conversions (Schneider, 1969). Kojima, Matsumura, Togawa, & Hikosaka (1996) confirmed this, proving that cognitive signals in the SC, presumably related to short-term memory and visual attention, are transformed into motor information. The saccades that result from heightened SC activity are usually fast and straight to target (Dorris, Paré, & Munoz, 1997). In fact, it is known to be involved in the generation of prosaccades, while its activity is attenuated, possibly by FEF, in antisaccade tasks (Everling, Dorris, Klein, & Munoz, 1999). Because the SC is involved in target selection activity of collicular saccade-related neurons has been investigated in relation to preparatory set. Basso & Wurtz (1997) proved that not only is the SC involved in the selection process, but its activity is also modulated by target uncertainty derived from the number of stimuli from which the target must be selected. When the set size was large, and there was increased target uncertainty, activity in the SC was reduced. The opposite pattern of results was seen when a small set size decreased target uncertainty. In a follow-up study Basso & Wurtz (1998) found that SC activity could predict changes in saccade latency, with increased activity associated to shorter latencies. Lastly, it is emerging that the role of the SC is not simply to transform sensory signals into motor signals to code the selected target, but it plays an active role in selecting strategic saccades based on probabilities and gains (Thevarajah, Mikulić, & Dorris, 2009), activities previously thought to be confined to the higher executive areas. These findings further emphasize the distinct role SC has in the planning and selection phase of saccadic movements.

### 1.2.3 Corticospinal pathway

Growing evidence in the field of cognitive neuroscience points to voluntary eye movements being prepared through widespread and complex modulation in multiple brain centres (Riehle & Requin, 1995). In particular, it has been shown that when movements are being prepared the corticospinal pathway is highly involved in activating inhibitory components which assure execution is not triggered prematurely (for a review see Cohen, Sherman, Zinger, Perlmutter & Prut, 2010). This means that when a movement has been prepared, but external sensory information is still being gathered, the motor system is in a state of readiness due to the activation of the motor plan. At this point the movement is temporarily blocked so as to release it at the appropriate moment, once the accumulation of sensory information has been completed. An example of this is an individual with their thumbs positioned on two different switches. An external signal will cue the correct switch to press, but before that happens, both motor plans (thumb presses) will be prepared and blocked, while awaiting further sensory information. The temporary blocking of movement has been labelled *global inhibition*, as it seems to produce global effects across the whole body. Research into the corticospinal pathway has revolved entirely around limb movements but in recent years it has become increasingly apparent it may also play a role in eye movements. A study on saccades found increased activity in the subthalamic nucleus of the basal ganglia, an area with direct connections to the corticospinal pathway, in saccade-countermanding and NoGo tasks (Isoda & Hikosaka, 2008). Just as stopping or controlling limb movements has been shown to lead to a global suppression of all motor output (Badry et al., 2009; Majid et al., 2012) Wessel, Reynoso, & Aron (2013) showed that rapidly stopping eye movements produces what seemed to be a global halt of the motor system (reduced corticospinal activity of hands and legs). There is therefore increasing evidence that this pathway is common to eye movements and limb movements alike.

## 1.3 Visual Stability

It has been discussed so far that eye movements are primarily made in order to foveate objects, rapidly bringing these into the area of highest resolution for in-depth processing. This, however, opens to a potential design flaw, that will be made clear by the following video camera analogy. We can think of our eyes as a videocamera filming the world, held by a cameraman. Every shift of the camera to a now object of interest, and every shake of the hand, correspond to an eye movement. Even with the highest resolution videocameras and the steadiest hands the quality of the visual information appears jerky at best, and often results in a smeared image. While technology has yet to overcome these limitations the human visual system succeeded long ago. Despite every saccade rapidly shifting the image across our retinas the world appears to remains stable. We perceive the world as a steady and continuous flow of visual information, and not a sequence of snapshots of foveated objects. This topic, of how visual stability is achieved given what we know of the visual system, has sparked scientific enquiry for centuries. In the 19th century, Herrmann von Helmholtz proposed that for each eye movement, an efference copy is created (a copy of the motor command; also referred to as corollary discharge). The efference copy allows us to anticipate the sensory changes of the movement, and thus distinguish between self-induced retinal motion and motion in the external world. More recently, neurophysiological experiments provided strong evidence for this idea (summarized in Sommer & Wurtz, 2008a, 2008b). A neural pathway from a subcortical saccade-related area SC to the FEF has been identified, whose neurons show a discharge pattern fulfilling the criteria for an efference copy signal. This means that the signal originated in a motor structure, it was time-locked to the eye movement but did not lead to the triggering of the saccade. The concept of efference copy, with oculomotor activity just prior to an eye movement providing information about the predicted location of a relevant object on the retina following a saccade, is therefore a prime candidate to explain how the visual system goes beyond snapshots to achieve visual stability.

## 1.4 Visual Attention

### 1.4.1 Preferential Processing

The amount of visual information received by the brain at a given time is too large for the visual system to process it all. A selection is thus required to process only the information most relevant to the current behaviour. This selection mechanism is called visual attention. It is important to first provide a definition of visual attention. We define visual attention as the preferential processing of parts of our visual environment. We therefore observe visual attention in its manifestation that is preferential processing, which leads to the in-depth processing of one location and not of another. This take on visual attention bares only minor semantic differences from that of Rizzolatti, Riggio, & Sheliga (1994), who state: “Spatial attention is the consequence of a facilitation of neurons in the spatial pragmatic maps”. Spatial pragmatic maps are simply neuronal circuits that represent space in a given coordinate system and spatial attention is bound to locations in that space and emerges from its manifestation, which is facilitation. Preferential processing is not always dependent on one’s volition, with countless examples in the literature of observers acting much like passive detectors of brightness and salience (Theeuwes, 1992, 1993; 2010) and even reward (B. a Anderson, Laurent, & Yantis, 2011). Here visual attention is allocated to locations in apparent automatic fashion and is defined as bottom-up driven. When visual attention is actively allocated by the observer the process is instead called top-down driven. Bottom-up and top-down factors are thought to jointly influence the distribution of covert attention (Cave & Wolfe, 1990; J M Wolfe, 1994). In this view, objects' low-level visual features, as well as their task relevance, shape attention allocation. For example, a salient bright red object between green objects will attract attention. Likewise, when we are told to find triangles in a display, covert attention will be allocated primarily to objects that match the description. The objects are therefore compared to a particular top-down set, with those bearing greater similarity to the search target attracting greater attention (Ansorge, Kiss, Worschech, & Eimer, 2011; Eimer & Kiss, 2008; Folk et al., 1992). Selectively allocating attention, allows us to overcome our system's inability to efficiently deal with many targets simultaneously by structuring the intake of the environment. Whether the visual system is able to attend to multiple distinct locations simultaneously has interested researchers for many years. Kramer & Hahn (1995) provided the initial insight into the topic by proving that attention could be allocated to two non-contiguous regions, whereas attention could not be split across onset stimuli. Müller, Malinowski, Gruber, & Hillyard (2003) built upon these results and proved that attention could be allocated to spatially separate locations for extended periods of time. Importantly, they show that the locations in between the attended ones were not encompassed by the spread of attention and that there was no cost associated with attending to two separate locations compared to two adjacent ones.

### 1.4.2 Pre-saccadic Shifts of Attention

A tight link has been shown time and time again between eye movements and visual attention, which is not surprising since eye movements have the primary purpose of gathering information from the world by means of a fovea-heavy tool. One of the most reliable and highly investigated effects in vision science is the shift attention makes, just before the eye movement is made, to the location where the eyes will land (Duebel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995). This has been shown to lead to preferential processing at the location where the eyes will land (Duebel & Schneider, 1996), with attention therefore anticipating the imminent eye movement. It is as if the eyes begin seeing before they see, meaning high levels of perceptual acuity at the location where they will land, even though the eyes have yet to move. Also, the deployment of visual attention follows a relatively strict temporal dynamic, gradually increasing, starting from several hundred milliseconds before the movement (250 ms in Deubel, 2008, 170 ms in Rolfs et al, 2010) and reaching its peak just before execution. Visual attention is therefore time-locked to the onset of the saccade. Only a handful of papers to date have provided evidence of decoupling (most notably Belopolsky & Theeuwes, 2009), and with the strongest version of a highly popular theory, the “premotor” theory of attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987; Rizzolatti, Riggio, & Sheliga, 1994), suggesting that both moving the eyes and orienting attention are coded identically in brain structures. It has, in fact, been argued that attention and eye movements may be part of the same system. It is worth noting that the location-specific shift of attention preceding a goal-direct saccade differs from distributed covert attention in that it is narrow (Zimba & Hughes, 1987) and centred almost exclusively around the target location (Kowler, Anderson, Dosher, & Blaser, 1995). There is widespread acceptance that when a target-directed saccade is programmed, non-target locations receive little or no enhancement (see Kowler, Anderson, Dosher, & Blaser, 1995), just as it is not possible to perform a saccade towards a known target whilst actively shifting attention to another location (Deubel & Schneider, 1996). The link between saccades and attention is seen not only in behaviour but also at the neurophysiological level, particularly in FEF, a cortical region discussed previously in the neurophysiology section. Moore & Fallah (2001) chose a microstimulation approach to investigate the link between FEF and visual attention. They observed that when the microstimulations were administered to a site related to the location of the associated movement field, and kept below saccadic threshold, contrast sensitivity greatly increased. This meant that, despite the microstimulations being insufficient to trigger the saccade, activity in this area was intimately tied to visual attention. Similarly, Wardak et al., (2006) injected the drug muscimol at various locations around FEF, simulating a lesion in the area. Dramatic changes in saccadic behaviour were accompanied by impaired allocation of visual attention, following the inactivation of the region. With saccadic eye movements and visual attention being tightly linked, many have tried to establish the role this mechanism plays in shaping vision. It has been argued that preferential processing of the about-to-be-foveated object is connected to perception of visual stability. In this view, the pre-saccadic attention shift provides a preview template of the saccade target, and this template may then be compared to the post-saccadic visual input. Information at the saccade target seems to play a special role in detecting external stimulus displacements (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000). A number of researchers, in fact, believe that pre-saccadic shifts of attention may facilitate the maintenance of perceptual stability and continuity across saccades (Deubel, Schneider, & Paprotta, 1998; Currie et al., 2000; Melcher, 2009). This mechanism might be the bridge between foveated snapshots of the world and visual stability, with each image being "eased" into the visual system before the eye movement is triggered.

### 1.4.3 Predictive Remapping

We have seen that locations of interest in the visual field draw considerable attention to themselves and that before an eye movement, attention shifts to the location where the eyes are expected to land. What happens to the attention allocated at a location of interest when an eye movement, which will inevitably shift the image across the retina, is made? It turns out the visual system can maintaining preferential processing at locations of interest in a way that accounts for the upcoming eye movement. This is called remapping and relates to the change in spatial profile of the receptive fields of neurons at the time immediately preceding the saccade (Hall & Colby 2011; Wurtz, Joiner & Berman, 2011). This transfer of activity between retinotopically organized neurons was first documented by Duhamel, Colby, & Goldberg (1992) and allows us to keep track of interesting parts of a scene while compensating for eye movements (for overview see Mathot & Theeuwes, 2011). When movements to saccade targets are being programmed and attention shifts to the upcoming saccade destination, approximately 80 milliseconds before saccade initiation, attention located at the locations of interest is predictively remapped. This means that attention re-adjusts itself just before the eye movements is made as that preferential processing continues to be at the locations of interest even after the saccade was been executed. This is achieved by temporarily shifting attention from the attended locations in the opposite direction of the upcoming saccade. In other words, a shift of attention will occur away from the locations of interest, and it will be the same size as the planned saccade. Perceptual enhancement has been found at this novel location (Rolfs et al., 2010). By shifting attention from a point of interest to a novel location in the direction opposite the saccade, our system can anticipate the consequences of the upcoming eye movement, and guarantee that attention will be at the location of interest once the saccade is completed (Cavanagh, Hunt, Afraz & Rolfs, 2010).

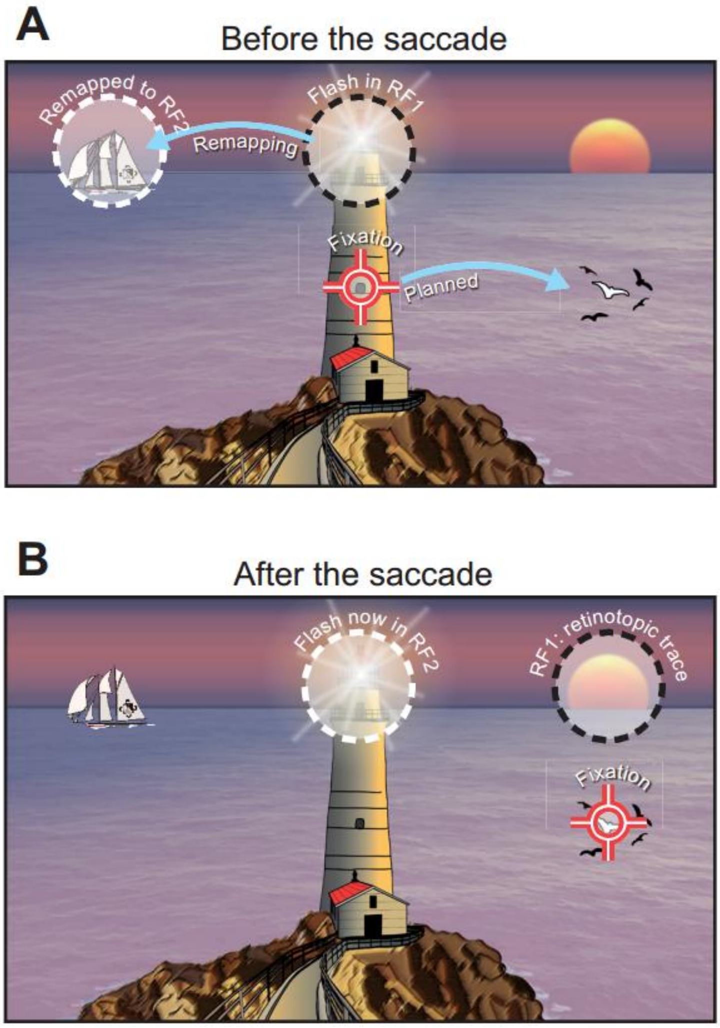

Figure 2. While fixating the lighthouse, a saccade is planned to the seagulls flying by, as the light on the lighthouse is flashing, attracting considerable attentional resources to itself. The flash is registered by a population of neurons with receptive fields at that location (RF1 in the image). In order to maintain this activation on the flash, even after the saccade the visual system shift the activation, or predictively remap it. This occurs just before the eye movement attention is maintained on the flash once the eye movement to the seagulls is completed. Were this not to

happen, activation at the flashed location would be shifted to an irrelevant location (the sun in the image) after the eye movement. Image is taken from Jonikaitis, Szinte, Rolfs, & Cavanagh (2013).

While the research has focused on the predictive remapping of the saccade target or of future saccade targets Jonikaitis, Szinte, Rolfs & Cavanagh (2013) document the remapping of a salient (non-target) object. They find that once a saccade has been programmed to a saccade target, a salient object in the display can be attended and remapped, so as to keep track of it even once the saccade has been completed. More recently Szinte, Carrasco, Cavanagh, & Rolfs (2015) showed that attentional resources are in fact temporarily removed from the locations of interest during the remapping process. Furthermore, Sommer & Wurtz (2006) could also successfully link the described efference copy signal to another phenomenon proposed to serve visual stability. Their data suggest that the signal triggers the receptive fields (RFs) of neurons in the FEF to predictively shift in direction of the saccade vector. These predictive remapping studies give clear indication of attention being once again tightly tied to saccadic eye movements, where the upcoming eye movement causes attention to shift in a seemingly mechanical way. In a very similar vein to the pre-saccadic shift of attention to the saccade target, the predictive remapping of attended locations has been suggested as a mechanism assuring visual stability is attained (Hall & Colby, 2011; Sebastiaan Mathôt & Theeuwes, 2011) in order to anticipate the perceptual consequences of the eye movement and maintain the post-saccadic processing of the visual surroundings consistent with how it was before the saccade.

### 1.4.4 Attentional Capture

We have so far seen that the allocation of visual attention can lead to the in-depth processing of locations of interest and it can begin preferentially processing the location where the eyes will land before the movement is actually executed. However, visual attention can also enhance the processing of useless or detrimental information that happens to attract attentional resources to itself. The world is filled with distractions, ranging from flashy advertisement banners to the sudden appearance of an

Internet pop-up. A primary purpose of attention is to restrict processing to items relevant to our current behaviour, and to minimize interference from irrelevant distractors. The attentional-control literature has focused on the mechanisms attraction of distractors, with instances where visual attention efficiently overcomes distraction being the obvious opposite side of the coin. Mainly two accounts have been proposed, and they stand in stark contrast. One proposes that attention is stimulus-driven and that salient distractors capture attention irrespective of one's goals or attentional set (Theeuwes, 1992, 2010). This conceptualizes attentional distraction, mainly referred to as *attentional capture*, as an almost entirely reflexive process. The other account proposes that visual attention is driven by the observer's goals and that attentional capture is contingent on one's attentional set (e.g., Folk, Remington, & Johnston, 1992). This means that only distractors that bear a certain visual similarity to an object, or objects of interest, therefore matching a current attentional set, will capture attention. While there has been an ongoing debate for the past 20 years as to when attention is captured and when attention overcomes distraction, there is a general agreement that when multiple objects are displayed along with a search target, a competition for attentional resources arises, with salient objects causing substantial interference (Bacon & Egeth, 1994; Becker, 2007; Fecteau, 2007; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Lamy, Tsal, & Egeth, 2003; Theeuwes, 1991, 1992; Yantis & Hillstrom, 1994) and that each perceived object attracts a certain amount of covert attention (Müller & Krummenacher, 2006; Zehetleitner, Krummenacher, et al., 2011). The effect is strongest when the distractor is closely positioned to the target (Bahcall & Kowler, 1999), it can occur even when the distractor is completely irrelevant to the task at hand (Theeuwes, 1994) and has been observed in settings where participants were explicitly instructed to ignore the distractor (Remington et al., 1992).

### 1.4.5 Inhibition

Just as certain locations or features can be perceptually enhanced, the visual system has the ability to inhibit the processing of particular visual elements. Also, just as for perceptual enhancement, there are varying degrees of intentionality surrounding the process. At a purely mechanical level (i.e.

void of intention) inhibition can be found around a region of enhanced visual processing (Cutzu & Tsotsos, 2003; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005; Serrano-pedraza, Gamonoso-cruz, & Derrington, 2013). It has in fact been shown that inhibition forms a suppressive annulus in the immediate vicinity of an attended item. This is known as surround suppression and has been shown to be stronger for items attended in the periphery (Xing & Heeger, 2000). Müller et al. (2005) added insight into the specific shape of the suppressive annulus. The authors manipulated the difficulty of a visual task and observed that a larger amount of attentional resources allocated to a target (i.e. higher peak of facilitation) led to a deeper dip of inhibition surrounding the target. On the other hand, when the target was easy to discriminate it was also less enhanced and led to a shallower inhibitory dip in its surrounds. Inhibition here appears to demark the location where the facilitation ends. In a very similar vein, inhibition is often called upon to alter the balance of attentional resources allocated to stimuli in competition with each other. The competition can in fact be biased by inhibiting the competing distractors so as to favour a particular target stimulus (Desimone & Duncan, 1995; Mathôt, Hickey, & Theeuwes, 2010). Salient distracting objects can in fact be efficiently ignored, in order to attend to a less salient target. Does the visual system achieve this by actively suppressing the distractors or by assigning increased weight to the target features? Gaspar & McDonald (2014) observed that salient distractors were suppressed even when they were both colour singletons, meaning that their dimensional weight would not enable selection of the target. The authors concluded that irrelevant salient distractors are actively suppressed and that this occurs only when the distractor has failed to gain access to working memory. Active suppression was seen to not only prevent the allocation of attention, but also terminate activation of a previously attended item (Sawaki, Geng, & Luck, 2012). This collection of findings shows that inhibition plays an integral part in shaping the allocation of attention to intended targets. Lastly, just as the term *facilitation* relates equally to both visual attention and motor processes, the same applies to inhibition. It was recently shown that inhibiting a particular motor response in a stop task did not carry any consequences on the selected response (Xu, Westrick, & Ivry, 2015), suggesting that inhibitory processes are independent from facilitative processes.

## 1.5 Experimental Paradigms

We will now turn to examine the experimental paradigms used to investigate the aforementioned concepts within the literature, which were also the chosen method of enquiry for the current investigations.

### 1.5.1 Singleton Search

In tasks investigating overt (i.e. saccades) or cover shifts of attention, a popular paradigm is called singleton search, where a number of objects is displayed along with a target object, which has at least one unique visual feature. A simple example of this is a task where participants are required to shift their gaze from a central fixation point to the diamond shape presented among a certain number of circles in the periphery. Singleton search, as described above, is mainly used to assess target detection. The large majority of studies has applied the paradigm to assess the encoding of target features and, more broadly, the topic of target selection, such as whether *diamond shape* or *different shape* drives the search in the example (see Bacon & Egeth, 1994). To do so, a second object with a unique visual feature is introduced (i.e. distractor), and this object enters into direct competition with the target object either by sharing one or more of the target's features or by virtue of its increased salience. Some believe that target selection will be impeded by a distractor that doesn't share any of the target features (Theeuwes, 1992), even when searching for a target onset and the distractor is visually stable (Theeuwes, 1994). Others have proposed that a degree of sharing of features or dimensions between target and distractor is necessary for interference to occur (Folk, Remington, & Johnston, 1992). A more spatial alternative account is proposed by (Kumada & Humphreys, 2002a) who suggest that the target-distractor competition, on a given trial, is a result of target selection being accompanied by positional distractor inhibition in the previous trial. This paradigm proves to be a fruitful platform, offering a multitude of investigative slants that varying cognitive approaches can make use of, in attempting to iron out the fine details of target selection and target-distractor competition.

### 1.5.2 Oculomotor Capture

When the competition for attentional resources, outlined in the previous section, is won by the distractor, gaze may be inadvertently driven to this location. This occurrence is known as *oculomotor capture*, and the name applies also to the paradigm that makes use of the effect. An intended saccade to the target (i.e. corrective saccade), is performed only after the initial involuntary saccade to the capturing object. This paradigm is used primarily to investigate the distribution of attention and the modulation of saccade trajectories. Oculomotor capture has been observed irrespective of top-down set (Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Theeuwes, Kramer, Hahn, & Irwin, 1998) mirroring the attentional capture findings. However, Theeuwes, De Vries, & Godijn (2003) found that top-down set may play a role in shaping the effect. The authors found that gaze was consistently captured when the target was a shape singleton and the distractor was a unique colour-singleton. When, instead, participants were instructed to shift their gaze to a specific shape singleton, while in the presence of a specific colour-singleton distractor, only attentional capture occurred at the distractor location, without oculomotor capture. The findings indicated that the prior knowledge (i.e. top-down set) of the features of both target and distractor meant that the attentional resources initially allocated to the distractor could rapidly be re-allocated to the target, thus preventing an unnecessary eye movement. Moher, Abrams, Egeth, Yantis & Stuphorn (2013) sought out to better understand how top-down set can modulate the oculomotor capture effect. By manipulating the probability of a distractor being displayed, they were able to see that the frequency of capture saccades decreased as the probability of distractor appearance increased. This proved that when the likelihood of a distractor being present on a given trial was high, participants could take the necessary precautions, leading to less capture and faster target-directed saccades. Recently, it was shown that non-salient objects that signal the availability of reward were able to induce oculomotor capture

(Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015), in a way that is not driven by physical salience nor can it be easily labelled as task-relevant top-down set.

### 1.5.3 Dual-Task

Most of the time, where people look is also where they're attention is. By recording saccadic eye movements, it is possible to figure out what attracts an observer's attention, or, at the very least, .get an indication. This can be important for basic research, in knowing what features attract attention, and can tell us what kind of visual information we use to make sense of the world around us. However, simply observing the parts of a visual scene visited by the eyes is not enough to clearly outline the locations that are preferentially processed, nor is it wise to assume a visual element has been attended to, simply because it has been foveated. For these reasons researchers in the field of visual science have had to devise creative methods to quantify levels of visual attention before, during and after the production of eye movements. Attentional facilitation can be gauged by briefly displaying a perceptual stimulus and requiring participants to make a forced judgement regarding its visual features (i.e. an oblique grid slanted to the left or right). If attention is measured while the observer is carrying out a particular motor task, it begins to be possible to describe attentional performance at a particular location *during* a particular action. Experiments requiring the concurrent execution of two independent tasks are called dual-task, and are particularly popular in relation to eye movements and attention. The findings, whereby attention visits and hones in on a saccade target, prior to the saccade being performed (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995), outlined in section 1.4.2, could only be achieved by briefly flashing a discrimination stimulus at the saccade target and observing attentional performance in relation to the upcoming eye movement. Through dual task paradigms, it is therefore possible to view the build-up perceptual enhancement at a saccade target location, by measuring attention at many different moments, in the time leading up to the execution of the movement. This paradigm applies to a broad range of enquiries. While we have seen that dual-tasks can be employed to assess the allocation of attention to the saccade target or attentional build-up over time, they can be used to explore the spread of attention over multiple locations. While a great number of locations can be measured over an entire experiment, researchers generally choose to measure one location per trial, and take the average performance for each location over a large number of trials. In section 1.4.3 we discussed the predictive remapping of attention to novel locations. The ground breaking study by Rolfs, Jonikaitis, Deubel, & Cavanagh (2011) employed this precise method to quantify performance at the saccade target locations (observers made sequences of two saccades) and at the remapped location of the second target.

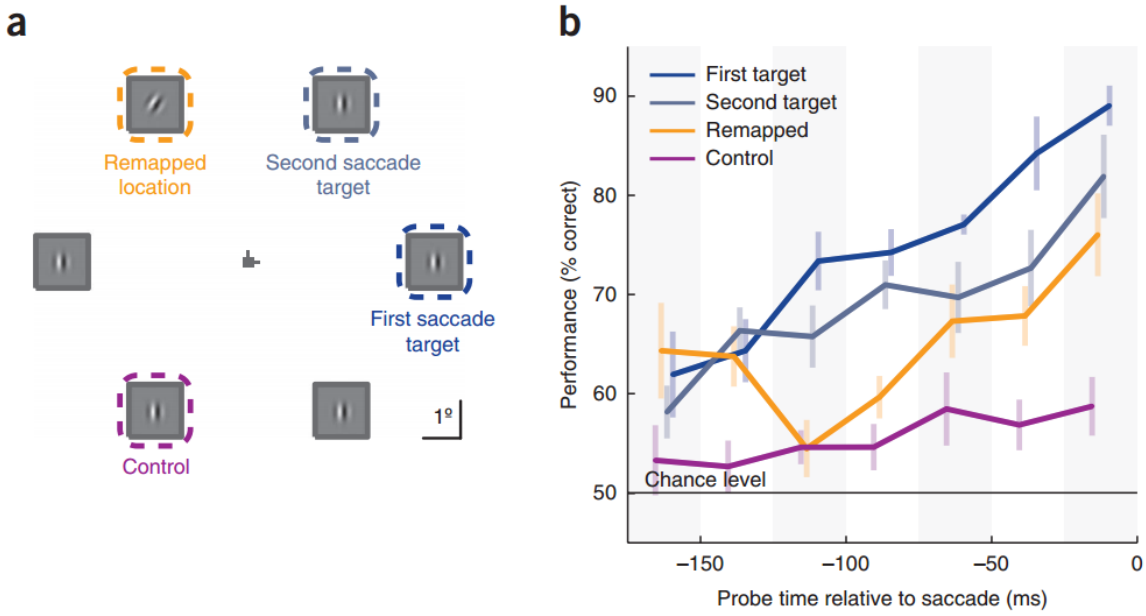

Figure 3. In the left panel (a) the stimulus arrangement is displayed. Participants performed a sequence of two saccades to the locations indicated at fixation by the directional cue. First saccade was left or right, second saccade was up or down. Perceptual enhancement was measured at the various locations (at one location per trial) by flashing a black and white grating (i.e. gabor) tilted either to the left or to the right, prior to the eye movements. Participants indicated at the end of the trial the direction of the slant of the oblique grating. In right panel (b) performance at the locations of interest is displayed. Preferential processing of the two saccade targets and the remapped location of the second target can be seen in the time leading up to the saccades. The Image is taken from (Rolfs et al., 2011).

The authors measured attention at four locations; the two saccade targets, a location coinciding with the remapped location of the second target (i.e. remapped location), and a non-relevant location disregarded by the predictive remapping hypothesis. Perceptual enhancement was observed, and increased over time, at the two saccade target locations and at the remapped location, peaking in the last tens of milliseconds before the eye movement. This confirmed behaviourally that the visual system does account the retinal displacement caused by the eye movement and remaps attention at future saccade targets, so attention will continue to be at these locations even after the eye movement. By using this method, attention can therefore be quantified at a number of locations, and temporal-dynamics can be obtained, while participants perform an independent task such as a saccadic eye movement.

### 1.5.4 Accumulator Model Framework

Accumulator models are a popular class of mathematical models that act as an elegant bridge between the fields of decision making and motor preparation. As the name suggests, they centre around an incremental decision process, often involving the accumulation of sensory information, which ultimately leads to a motor output when a threshold is reached (Gold & Shadlen, 2001). The accumulation model framework shares certain key features with signal detection theory (SDT) and with diffusion models. As in SDT, a value is sampled from a normal distribution of amounts of evidence equally spaced in time, with the distribution having a standard deviation of 1.0 and a mean that depends on the quality of the incoming stimulus information. A criterion, termed the sensory referent (Ratcliff & Smith, 2004), is set on the underlying evidence dimension and equates to the drift criterion in the diffusion models. These models have been used to explain decision making in relation to a wide range of movements, from button pressing (Ratcliff & Smith, 2004; Tandonnet, Garry, & Summers, 2013) and eye movements (Hanes & Schall, 1996). The accumulator framework applies elegantly to the study of eye movements because an accumulation of information striving to reach a threshold is, based on what we currently know, appears to take place before each saccade. Reddi & Carpenter

(2000) explains how the electrical stimulation for saccade generation, based on the neural circuits, should take approximately 40 ms, but the average eye movement takes over 200 ms. This process of procrastination, as the authors call it, is needed for the higher levels of the brain to decide where exactly to foveate, while resolving possible ambiguities derived from competing stimuli. Studies investigating eye movements within the accumulator model framework, have found evidence of the race to threshold, by comparing two or four-alternative choice tasks. A heightened planning-related activation was observed for the two choice-alternatives, which lead to more accurate movements that were initiated quicker (Churchland, Kiani, & Shadlen, 2008; Churchland & Ditterich, 2012). This framework can prove particularly fruitful in trying to understand how underlying decision-making processes relate to differences in saccadic reaction time.

## 1.6 Summary of the state of research and overview of the current thesis

The topics discussed so far will feature in the scientific papers listed in the following chapters. Some topics will not only be featured, but will be the supporting pillars of the enquiry. Focus will be placed on the perceptual processes that occur prior to eye movements, in order to better understand the link between processing of visual objects and allocation of attention. This means establishing whether the pre-saccadic shift of attention is sensitive to visual objects present in the environment and how these visual objects might shape the distribution of attention. This requires first determining whether the pre-saccadic shifts of attention is specific to deliberate eye movements directed toward an established target, or whether they appear to have a higher degree of generalizability. After all, eye movements performed freely throughout daily life are likely to be far less goal directed and more explorative, compared to their laboratory counterparts. Once established this, it will be important to assess whether eye movement preparation is always beneficial for motor performance. It has been shown that the visual system is sensitive to visual objects, automatically encoding these before eye movements as potential targets. We will explore how the differing number of presented elements affects saccade planning and movement errors. Furthermore, the project aims to understand how top-down and bottom-up signals, associated with visual objects, contribute to the distribution of attentional resources before eye movements. These differing signals may affect pre-saccadic shifts differently, depending on whether they revolve around the saccade target or non-saccade target objects. Establishing the sensitivity of the visual system to visual objects, in the time leading up to the saccade, seems of central importance, given that saccades are described as the tool that brings objects of interest into the fovea for closer inspection.

The introduction has touched upon the longstanding debate about how the visual system achieves the perception of a coherent and stable flow of information, despite visual exploration being carried out by eye movements having high clarity only in the fovea. Shifts of attention to the saccade target have been observed prior to eye movements, and it has been suggested that they ease the transition between each foveated “snapshot”, bridging the pre- and post-saccadic image. It has been documented that visual attention is predictively remapped from attended locations, just before an eye movement is executed, in order to maintain attention at these locations across eye movements. We first aim to determine whether these attentional processes occur only for goal-directed movements, where the intention to move the eyes may induce the described shifts and remapping of attention. Alternatively, these attentional processes could be a defining feature of all saccades, regardless of intentionality. This possibility would be a prerequisite for a collection of tightly linked processes in charge of achieving, or at least aiding, visual stability. Whereas previous research has successfully assessed the shift of attention prior to a voluntary goal-directed saccade to a target location, our initial study will examine whether oculomotor capture leads to the same perceptual benefits at a capturing distractor location. We also aim to determine whether the predictive remapping of attended objects is carried out also when involuntary saccades are made, signifying that the perceptual consequences of an involuntary saccade are also accounted for. A large portion of the project will aim to determine whether the shifts of attention are a signature of all saccadic eye movements, where attention is allocated to the landing point of the upcoming saccade. On the other hand, the visual environment, as in the spatial relationship between the visual objects present at and around the saccade landing point, might shape the shifting of attentional resources. If this is the case, it will be of interest to map the spread of pre-saccadic attention when an object is present and when it is not. Differences in attentional spread could help determine behaviourally the memory-degradation time-course of the visual attention associated with the stimulus location. As the entire investigation revolves around processes occurring at the time leading up to the eye movement, part of the project will be aimed at assessing how the planning of saccades is affected by the varying number of presented stimuli. The investigation will therefore touch upon the topic of pre-saccadic accumulation of information, as a link between planning and execution of saccadic eye movements.

In sum, the current state of research postulates that the planning of saccades is tightly coupled with attention. This is based on the fact that attention is spatially and temporally time-locked to the up-coming eye movement; a mechanism proposed as an explanation of how the visual system links the continuous foveated snapshots. However, we do not know whether this process occurs for all saccades, if it is influenced by the presented visual elements, whether targets present only in memory lead to a different shift of attention, nor whether the planning of saccades occurs automatically when targets are presented. In the following chapters four studies will be presented:

- *Study 1: Perceptual Enhancement prior to Intended and Involuntary Saccades*
  This study investigated pre-saccadic shifts of attention made to an intended target or made to a capturing distractor. Evidence was obtained that shifts of visual attention are relatively unconcerned by saccade goals, and that sequences of capture-corrective saccades also lead to attentional remapping. The study has been published in Journal of Vision (Puntiroli, Kerzel, & Born, 2015).

- *Study 2: Race to accumulate evidence for saccade decision: an exception to speed-accuracy trade-off*

  This study investigated the planning of saccades in large and small set sizes. We found that executing saccades to a target in a large set size can lead to reduced latencies compared to a small set size. This difference did not come at the expense of accuracy and is not predicted by a popular accumulator model. The study has been submitted for publication, and minor revisions are required.

- *Study 3: Objects and their arrangement affect Visual Attention before Eye Movements*

  This study investigated whether preferential processing found at the location where the eyes will land is purely dictated by saccade metrics. To this end, we presented differing numbers of placeholders at and around the saccade target location. The findings show that visual objects and their arrangement influence the locations selected for preferential processing. The study is being prepared for submission.

- *Study 4: Malleable pre-saccadic shifts of attention*

  This study investigated the pre-saccadic shift of attention when the saccade target object was present and when it had disappeared shortly before the movement (i.e. present only in visual working memory). Detailed maps of the spread of attention were obtained in both conditions. The finding show that when a target object is present attention shifts specifically to this location and when the target object is no longer present attention spreads away from the landing point and further to the surrounding locations. The study is being prepared for submission.

## 1.7 Publications:

Puntiroli, M., Kerzel, D., & Born, S. (2015). Perceptual enhancement prior to intended and involuntary saccades, *Journal of Vision, 15*(4)*,* 1–20.

Puntiroli, M., Tandonnet, C., Kerzel, D., & Born, S. (minor revisions). Race to accumulate evidence for saccade decision: an exception to speed-accuracy trade-off, *Journal of Exp Brain Res*.

Puntiroli, M., Kerzel, D., & Born, S. (in preparation). Objects and their arrangement affect Visual Attention before Eye Movements.

Puntiroli, M., Deubel, H., & Szinte, M. (in preparation). Malleable presaccadic shift of attention.

Some of the work has been presented at international peer-reviewed conferences:

Puntiroli, M., Kerzel, D., & Born, S. (2013). Dynamics of pre-saccadic attention allocation in the presence of an abrupt onset distractor. Poster presented at the European Conference on Eye movements (ECEM), Lund, Sweden.

Puntiroli, M., Kerzel, D., & Born, S. (2014). Remapped & Captured Pre-Saccadic Attention produce perceptual facilitation at non-target locations. Poster presented at the Annual Meeting of the Vision Sciences Society (VSS), St. Pete Beach, Florida.

Puntiroli, M., Kerzel, D., & Born, S. (2015). Motor preparation and attentional benefits: dependencies on the number of possible saccade targets. Poster presented at the Annual Meeting of the Vision Sciences Society (VSS), St. Pete Beach, Florida.

Puntiroli, M., Kerzel, D., & Born, S. (2015). Eye movement preparation towards potential targets. Poster presented at the European Conference on Eye movements (ECEM), Vienna, Austria.

Puntiroli, M., Kerzel, D., Born, S., Deubel, H., & Szinte, M. (2016). Malleable presaccadic shifts of attention. Poster to be presented at the Annual Meeting of the Vision Sciences Society (VSS), St. Pete Beach, Florida.

# Chapter 2

# Study 1: Perceptual Enhancement prior to Intended and Involuntary Saccades

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Prior to an eye movement, attention is gradually shifted towards the point where the saccade will land. Our goal was to better understand the allocation of attention in an oculomotor capture paradigm for saccades that go straight to the eye movement target and for saccades that go to a distractor and are followed by corrective saccades to the target (i.e., involuntary saccades). We also sought to test facilitation at the future retinotopic location of target and non-target objects, with the principal aim of verifying whether the remapping process accounts for the retinal displacement caused by involuntary saccades. Two experiments were run employing a dual-task design, primarily requiring participants to perform saccades towards a target while discriminating an asymmetric cross presented briefly before saccade onset. The results clearly show perceptual facilitation at the target location for goal-directed saccades and at the distractor location when oculomotor capture occurred. Facilitation was observed at a location relating to the remapping of a future saccade landing point, in sequences of oculomotor capture. In contrast, performance remained unaffected at the remapped location of a salient distracting object, which was not looked at. The findings are taken as evidence that pre-saccadic enhancement occurs prior to involuntary and voluntary saccades alike and that the remapping process also indiscriminately accounts for the retinal displacement caused by either.

Puntiroli, M., Kerzel, D., & Born, S. (2015). Perceptual enhancement prior to intended and involuntary saccades, *Journal of Vision, 15*(4), 1–20.

## Introduction

Vision science strives to determine how attention is distributed over objects in our surroundings, the relation this distribution has with upcoming eye movements, and the information that is extracted during the process. The allocation of covert attention is a competitive process jointly influenced by bottom-up and top-down factors (Cave & Wolfe, 1990; Wolfe, 1994), where each perceived object is processed according to local salience-based features (e.g., brightness) and weighted by task relevance (Müller & Krummenacher, 2006; Zehetleitner, Proulx, & Müller, 2009). Accordingly, when salient objects are displayed along with a search target, they compete for attentional resources and have been shown to cause substantial interference (Bacon & Egeth, 1994; Becker, 2007; Fecteau & Munoz, 2006; Folk & Remington, 1998; Folk, Remington, & Johnston, 1992; Lamy, Tsal, & Egeth, 2003; Theeuwes, 1991, 1992; Yantis & Hillstrom, 1994). For example, it will be more difficult to look for a target triangle in a set of squares, when one of the squares is of an outstanding colour or brightness. In studies requiring a rapid eye movement to the search target, the eyes may even be inadvertently directed towards such a salient distracting object (oculomotor capture; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). But do distractors that attract the eyes also benefit from enhanced perceptual processing prior to the execution of the involuntary saccade?

### Shifts of attention before involuntary saccades

Pre-saccadic shifts of attention found specifically at locations where the targets of *intentional* saccades were displayed (Deubel & Schneider, 1996; Schneider & Deubel, 2002) demonstrate the tight coupling between attention and saccades. Just before a voluntary eye movement, attention is narrowly focussed (Zimba & Hughes, 1987), centred almost exclusively around the saccade target location (Kowler, Anderson, Dosher, & Blaser, 1995), and the corresponding perceptual facilitation effects continue to increase up until the moment the eye movement is initiated (Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). However, it is less clear where attention is directed when the eyes are captured by a salient distracting object in a purely bottom-up fashion.

Peterson, Kramer, & Irwin (2004) argued that attention briefly visits the capturing object before subsequently being directed to the target. They presented a probe (a C or mirror C) at the capture location that was either compatible or incompatible with the subsequent response to the target (likewise a C or mirror C; presented as a colour singleton). On capture trials, they found longer manual RTs to the target when a compatible probe was presented at the capture location, compared to incompatible trials. The authors argued that attention visited the distractor, thus explaining the counter-intuitive reverse compatibility effects. However, others (see for example Eimer & Schlaghecken, 2003) relate reverse compatibility effects to response processes and not to perceptual or attentional factors. Moreover, Zhao, Gersch, Schnitzer, Dosher, & Kowler (2012) explain how fixating a target offers no guarantee that it will be attended. Aspects of objects are more frequently missed when they are irrelevant to the task, proving that integrated object representations are not an inevitable consequence of an eye movement fixation (Droll, Hayhoe, Triesch, & Sullivan, 2005). In fact, particular visual routines dependent on the immediate behavioural context may allow only information required at a given moment to be extracted (Hayhoe, 2000). This could be the case in oculomotor capture, where despite an (involuntary) saccade being made, the perceptual representation of the object at the saccade endpoint, i.e., the salient distractor, may remain poor. Our first question thus concerned pre-saccadic perceptual facilitation effects at distractor locations.

## Predictive remapping of targets and non-targets

A second question concerns pre-saccadic enhancement at other non-target locations. Mechanisms that can cause a shift of attention to non-target locations in preparation of upcoming saccades have been documented in recent years. Predictive remapping relates to the change in spatial profile of the receptive fields of neurons at the time immediately preceding the saccade (Hall & Colby, 2011; Wurtz, Joiner, & Berman, 2011; Burr & Morrone, 2011). Remapping was first documented by

Duhamel, Colby, & Goldberg (1992) and is thought to allow us to keep track of interesting parts of a scene, while compensating for eye movements (Cavanagh, Hunt, Afraz, & Rolfs, 2010; for overview see Mathôt & Theeuwes, 2011). Remapping, as a theoretical stance, would posit that just before we make an eye movement to an intended location an interesting stimulus in our visual display, that draws attention to it, will be remapped. The neuronal activation associated with the stimulus' position on the retina would find itself at a completely irrelevant position, once the eye movement is completed, if it weren't remapped. For that reason, just before the movement is initiated, the neural activation is partly shifted in the direction opposite to the upcoming movement. The direction and amplitude of the upcoming saccade is used to shift the activation (associated with attention found at the interesting stimulus) in the opposite direction from it. This allows the activation to once again coincide with the stimulus' location when the eyes land on their destination (Cavanagh et al., 2010). Moreover, Jonikaitis, Szinte, Rolfs, & Cavanagh (2013) found that a salient non-target object can be predictively remapped, so as to keep track of it  after the saccade.

A particular case for remapping of relevant objects can be seen in the remapping of eye movement targets in saccade sequences: Before a sequence of saccades is initiated, attention is not only allocated to all future saccade targets (Baldauf & Deubel, 2008; Godijn & Theeuwes, 2003), but their locations are predictively remapped, such that perceptual enhancement has been found at non-target locations (Rolfs et al., 2010).

The two specific remapping situations mentioned above will be examined in the current study. The first experiment will examine the remapping of a non-target object, similarly to that in Jonikaitis et al. (2013), with the difference that here the object being remapped is a distractor competing for resources with the target. It is unclear whether a rejected distractor (one that does not capture gaze) is remapped, as it may not serve a particular purpose for it to be treated differentially after the eye movement is completed. Much will depend on whether the rejected distractor location is enhanced or suppressed. The second experiment will examine remapping when a sequence of two saccades is made, much like in Rolfs et al. (2010), but rather than two intended saccades, the sequence will be made up of one involuntary saccade to the distractor, followed by one intended saccade to the target. It is unclear what happens to the perceptual enhancement effects related to predictive remapping in the context of oculomotor capture. That is, whether attention is allocated almost exclusively to the saccade target (the intended landing point) with visual attention largely ignoring the capturing location and not accounting for the retinal displacement caused by this first, involuntary, saccade. In this case, facilitation at the remapped location of the saccade target would not be found at a location relative to the initial capturing saccade. Alternatively, attentional resources would be allocated to both saccade landing points (distractor and saccade target) and in sufficient measure to allow for the remapping of the saccade target to lead to perceptual benefits. Mirpour and Bisely (2012) conducted a single cell study using memory-guided saccades. They found that the remapping-related activation was stronger when there was a reward associated with fixating a particular stimulus (i.e. the object being remapped). This highlighted the fact that the remapping process is sensitive to the amount of activation found at the area of interest. There may well be quantitative differences in remapping activation depending on the status of the object being remapped (target or not, suppressed or not). Furthermore, involuntary saccades may be associated to less attentional enhancement, thus having an impact on perceptual effects related to remapping.

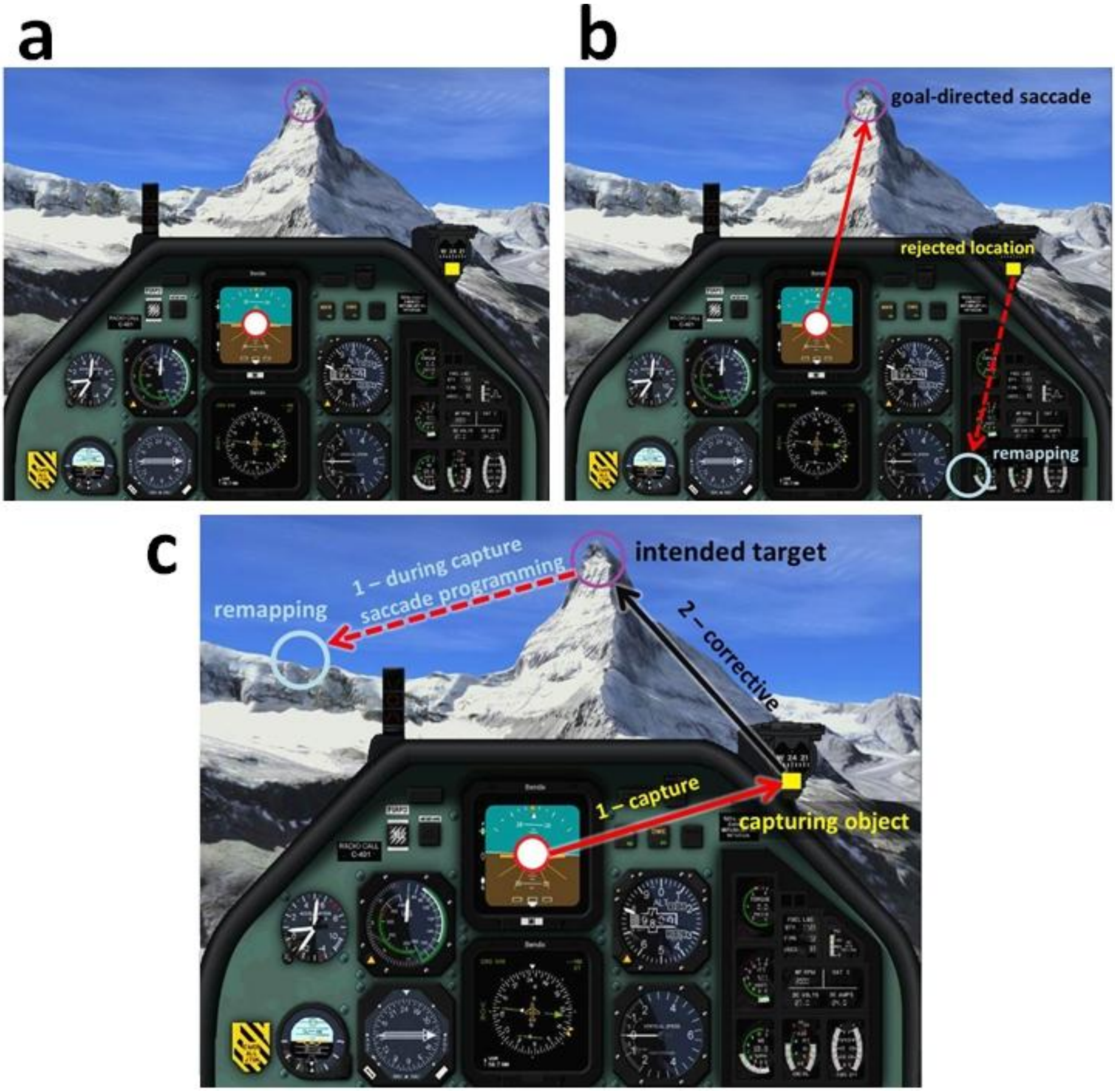

Figure 2.1 Predictive remapping. (a) While fixating the central indicator on the cockpit (white circle) the pilot proceeds to shift gaze to the nearest mountain summit (purple circle), to assess possible danger. Just before moving the eyes a flash appears (yellow square) beneath the magnetic compass in the upper right corner. (b) The pilot manages to move his eyes to the summit (goal-directed saccade), and ignore temporarily less useful information (flash). Before saccade initiation the flash is registered by a population of neurons with receptive fields at this location. In order to keep track of the flash, activity at this location is remapped to a novel location (white circle) corresponding to a population of neurons with receptive fields at the retinal location the flash will have after the saccade. This way, attention is maintained on points of interest across saccades. (c) The flash

captures the pilot's gaze, inducing an involuntary eye movement towards it. The eyes briefly visit this location (1-capture) before being diverted to their intended location (2-corrective). If attention also briefly visits this location, the intended target (the summit) may be remapped to a novel location (white circle) relative to the first saccade so attention is placed on the summit once the eyes land on the flash.

## Purpose of Study

We explicitly tested the allocation of attention at target and non-target locations by probing critical locations with briefly flashed stimuli requiring a discrimination choice. We compared involuntary to voluntary saccades and also compared the time course of the two. Secondly, we explored remapping effects expecting (1) facilitation at the remapped location of a salient object when a straight-to target saccade is performed (seen in Jonikaitis et al., 2013), see Figure 1 b), (2) the remapping mechanism to account for the retinal displacement caused by involuntary saccades as it does for voluntary saccades (seen in Rolfs et al., 2010), see Figure 1 c), (3) greater facilitation for the remapping of a saccade target than for a salient object, as the remapping mechanism has shown greater enhancement associated with highly attended, meaningful locations (seen in Mirpour et al., 2012).

## Experiment 1

Experiment 1 was designed to assess the pre-saccadic allocation of attention at target and non-target locations in straight-to target saccades and in capture saccades. Although we employed a modified version of a widely-used oculomotor capture paradigm (e.g. Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Theeuwes, Kramer, Hahn, & Irwin, 1998; Born, Kerzel, & Theeuwes, 2011), the amount of capture trials per participant (less than 5% of total trials) was not sufficient to allow adequate testing of our hypotheses for capture sequences. Still, we could explore how the presence of an onset distractor affects performance in target-directed saccades, both at the distractor location and all other locations, including the remapped location of the distractor.

## Methods

### *Participants*

Fourteen participants, all female, aged between 19 and 26, took part in Experiment 1. All were psychology students from the University of Geneva. All participants received course credits for their efforts.

### *Apparatus*

The experiment was written in Matlab 2011b (The MathWorks Inc., Natick, MA) using the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al, 2007) and run on a Dell Optiplex 755 system. The stimuli were displayed on a 21’’ CRT monitor (NEC MultiSync FE2111SB), which ran on 85 Hz and was set to 1280 x 1024 pixels. Viewing distance was 50 cm, allowing approximately 30 pixels per degree of visual angle. The EyeLink1000 desk-mounted eye tracker was used to record eye movements (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 1000 Hz. Participants were seated in a dimly lit room and placed their head within a fixed chin and forehead rest. Only movements from the right eye were recorded.

### *Stimuli*

We employed a fixation cross consisting of two grey lines 4subtending approximately 0.3° × 0.3°. Stimuli were presented at 5° from the centre of the screen. Circles were drawn with a radius of 1.5° and pen width of 0.33° (10 pixels). Crosses and masking squares were made up of bars of 1.4° × 0.17°. The stimuli in the display were grey, green or red, respectively 36.4, 29.9 and 16.3 cd/m$^2$, displayed on a grey background of 25.8 cd/m$^2$.

### *Design and Procedure*

The sequence of events in the main experimental blocks is illustrated in Figure 2. Participants had to carry out a dual-task: directing a saccade towards a colour singleton circle while simultaneously performing a perceptual discrimination task. Initially the fixation cross and three coloured circles were presented (green or red; counterbalanced across participants). After a variable delay of 400-700 ms the fixation cross disappeared leaving all other stimuli unaltered. This was done to facilitate low reaction times by bypassing the ocular fixation reflex (gap paradigm; Saslow, 1967). Following this gap interval lasting 200 ms, only one circle remained coloured and served as the saccade target, while the other two circles turned grey. A distractor circle appeared on screen on 75 % of the trials and was presented at a previously empty location when the colour change in the other circles occurred. In the "green" group the saccade target was green, while the distractor was red, and in the "red" group these colours were inverted. Light grey crosses subsequently appeared within the circles at a variable delay (0, 24, 47, 71, 94, 118, or 141 ms). One of these crosses was asymmetric and served as the discrimination target: its vertical bar was slightly shifted to the left or right. It was initially offset at 0.3° from the center and a 2-down 1-up staircase rule was employed throughout the experiment, with a step size of 0.1°and a minimum offset fixed at 0.05° if the staircase ran down to 0°. This procedure ensured discrimination across all trials at approximately 71% correct for each participant. The asymmetric cross could appear in any of the stimulus locations (saccade target, distractor, or a placeholder circle). All crosses were presented for 100 ms then masked. When the saccade had been executed within the afforded time window (<600 ms) and the masking squares displayed for one second, the participant was required to identify the correct perceptual target (left or right shift) flashed during the trial by tapping one of two buttons on a PC keyboard. Auditory feedback (tone) was received whenever the response was not correct. On-screen feedback was also received at the end of each trial, whenever eye movement errors were made (see below for criteria).

Participants initially carried out four single-task blocks. The initial two were saccade-only blocks where the goal was to perform a rapid saccade to the circle that did not change colour, training saccade target identification and speed of execution. These were followed by two discrimination-only blocks where gaze was kept locked on the central fixation cross while covertly attending to the stimuli. The task objective was to detect the briefly flashed asymmetric cross present at one of the locations, with the aim of getting participants used to perceiving the discrimination target without having to make eye movements. Once the training was completed, the dual-task, combining both single tasks, was carried out. Participants were instructed to move their eyes as fast and accurately as possible to the saccade target, and that correct ocular movements were the primary task.

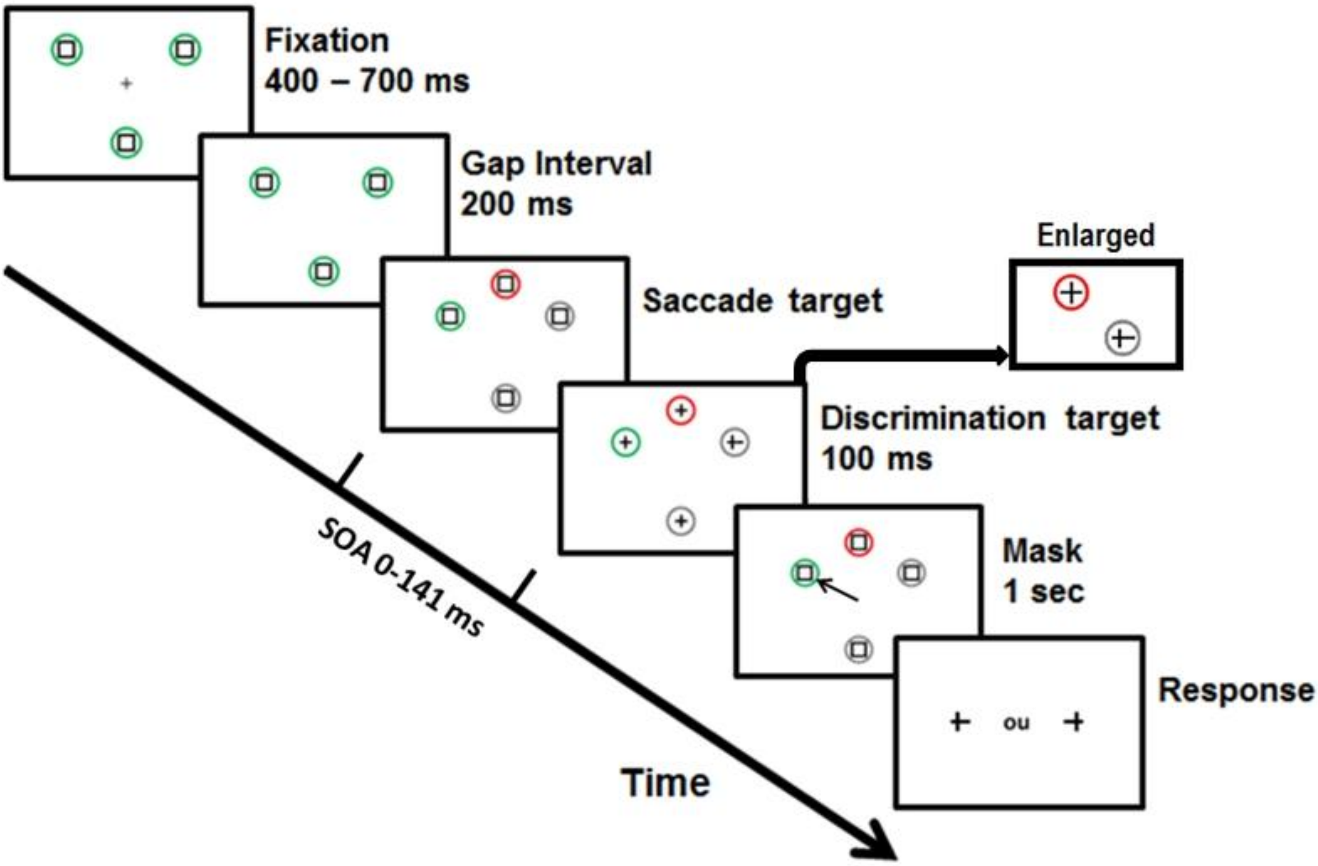

Figure 2.2 Sequence of events in Experiment 1. All stimuli were initially presented on screen in the assigned saccade target colour (green in the example). Gaze had to remain within 1.5° of the fixation cross, which disappeared after a random delay of 400-700 ms. After 200 ms of its disappearance, the display colour change occurred leaving only 1 object of the assigned colour (saccade target). On 75% of trials a distractor (red in this example) appeared at a previously unoccupied location (in between two of the presented objects). The discrimination target was an asymmetric cross (in the example shown at the grey placeholder position to the right of the distractor, where the remapping of the distractor in retinotopic coordinates is thought to take place; see enlargement) flashed for 100 ms in one of the objects

and was displayed after one of 7 possible SOAs (0-141). After eye movements participants stated whether the vertical bar of the asymmetric cross was displaced to the left or right (left in the illustration).

The experiment lasted four hours, including the training session mentioned above, and was distributed over four sessions on separate days. Each block was made up of 105 trials and participants ultimately carried out a differing number of blocks (ranging from nine to 15 blocks) depending on the speed of response and ease of calibration of the eye tracking system. All experiments were approved by the ethics committee of the Faculty of Psychology and Educational Sciences of the University of Geneva.

### Eye movement data analyses and feedback

Preliminary analysis of eye movement data was carried out after each trial. Saccade onsets and offsets were detected using the default algorithm of the EyeLink1000 parser (velocity criterion of 30°/s, acceleration criterion of 8,000°/$s^2$). Trials were followed by a written feedback message on the screen if (1) saccadic latencies were shorter than 50 ms (anticipation), (2) saccade latencies were longer than 350 ms, (3) gaze deviated by more than 1.5° from the display center at the time of saccade onset (failure to fixate), (4) no saccade was directed to the saccade target or (5) a blink was detected. In discrimination-only trials, a fixation control was performed and an error message was shown if (1) a failure to fixate or (2) a blink was detected. After the experiment, saccade onset and offset criteria were manually checked with the help of a graphical visualization for at least some trials for each participant and median saccade reaction times in the various conditions were computed.

## Results

### Data Exclusion

Data from two participants who had more than 50% of their trials excluded were omitted from analyses. One other participant was excluded for calibration failures. For the remaining participants, trials were removed if gaze deviated by more than 1.5° from the initial fixation cross (3.3%) and if the saccade landed on an object prior to masking (17.3%). Furthermore, trials in which the discrimination target was presented for longer than 120 ms due to technical issues were discarded (0.4% of trials). All other errors combined, accumulated to 6.3% (e.g. anticipatory saccades before colour change 0.9%, no valid saccade detected, 0.7%., blinks, 0.5% and the combination of all possible errors, 4.2%). Valid trials were therefore 72.7% of the total. Finally, of the valid trials those where the saccade was directed at a placeholder (5%) or at the distractor (1.5%) were also excluded. Our initial purpose was to examine capture saccades towards the distractor, as well as target-directed saccade. However, as the percentage of capture saccades was too small to allow for analysis, we only chose to analyze those saccades directed straight-to the target.

### Perceptual Discrimination

The primary goal of the experiment was to investigate how visual attention was distributed across objects in the display. To measure this, we obtained the percentage of correct discrimination responses at each probed location-: control, saccade target, distractor and remapped location of the distractor. The distractor in our study could appear at any of three possible locations, in between the presented stimuli. However, only trials where the distractor was present ($3/4^{ths}$) and appeared adjacent to the saccade target ($2/3^{rds}$) were included in this first analysis. Trials in which the distractor appeared opposite the saccade target do not have an equivalent location for the remapped distractor location. The control and remapped locations coincided with the two grey placeholder locations, the former at a neutral location while the latter at the distractor's remapped location. A one-way ANOVA with four levels, one per location, was carried out on the arcsine-transformed percent correct values gathered at each location. The main effect of location was significant, $F(3,39) = 32.966$, $p < .001$, partial $\eta^2 = .72$. We next performed paired t-tests (Figure 3) which showed that there was a significant difference in performance at all locations, except between the control and the remapped locations (mean difference 0.2 %), $t(13) = .19$, $p = .85$. Performance at the saccade target differed significantly from that at the control (mean difference 13.4%), $t(13) = 5.6$, $p < .001$, distractor (mean difference

23.7%), *t*(13) = 7.11, *p* < .001) and remapped locations (mean difference 13.1%), *t*(13) = 6.1, *p* < .001). This confirmed the occurrence of a pre-saccadic attention shift to the saccade target, leading to substantial facilitation at this location. Surprisingly, performance at the distractor was worse than at the control location (mean difference 10.3%), *t*(13) = 4.65, *p* < .001). How perceptual discrimination at the locations changed over time, leading up to the saccade, is reported in the Supplementary material (time course analysis section). In short, the gradual build-up of attentional facilitation at the saccade target already found in numerous previous studies was confirmed (e.g., Deubel, 2008). No differences across time were found at any of the non-target locations.

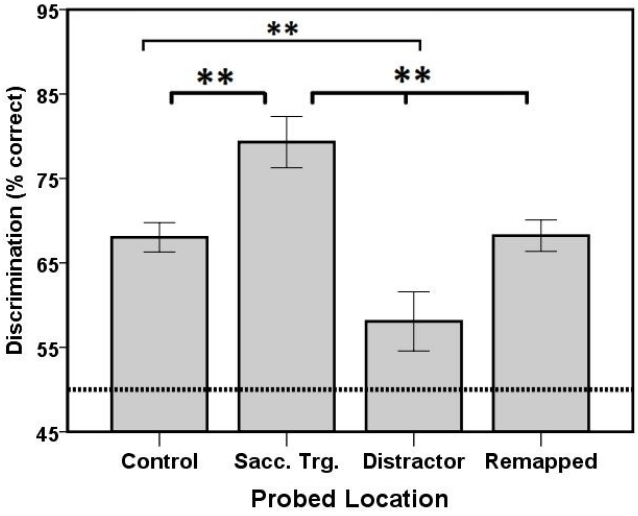

Figure 2.3 Discrimination performance at the three locations probed in Experiment 1. Error bars represent the standard error, with scores adjusted for between-subjects variability for within-subjects effects (Bakeman & Mcarthur, 1996) following method by Cusineau (2005).

While the target was a colour singleton with respect to the initial placeholder display, the distractor was an onset singleton with a colour different from the target. To test whether the observed differences were due to the oculomotor task or may have been influenced by the target and the distractor being singletons, we compared our results to performance in the discrimination-only control blocks, where participants were required to maintain central fixation while attending to the objects. Note that from here onwards we grouped both grey placeholders together (control and remapped), due to there being no performance differences, and treat them as control. Three participants were omitted from this analysis due to lack of trials. A 3 x 2 mixed ANOVA was employed, where the first factor was the probed locations (control, saccade target and distractor) and the second was task type (discrimination only versus dual-task). This highlighted a main effect of probed location (*F*(2,40) = 6.81, *p* = .003, partial $\eta^2 < .25$) and a significant interaction between probed location and task *F*(2,40) = 12.55, *p* < .001, partial $\eta^2 < .38$). The main effect of task type was not significant: *F*(1,20) = .63, *p* = .438, partial $\eta^2 < .03$. Post hoc paired t-tests confirmed there were no differences between locations in the discrimination only task (differences smaller 4%), *t*s(10) < .82, *p*s > .433) while we saw that all locations differed significantly from each other in the dual-task (Figure 4). This confirmed that the differences that emerged in the dual-task at the saccade target and distractor locations were both due to their role as target and distractor, respectively and not due to their being colour singletons or abrupt onsets.

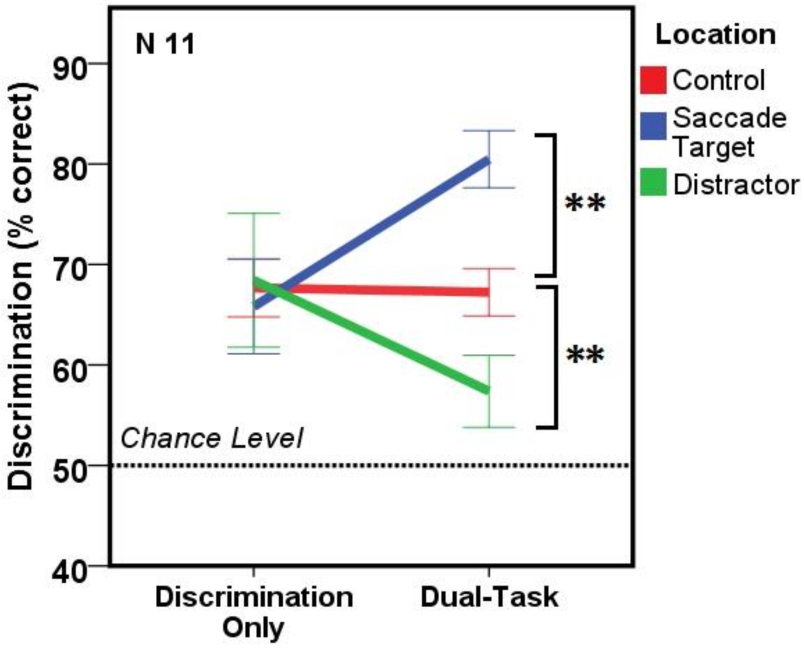

Figure 2.4 Discrimination performance at the three probed locations with (dual task) and without (discrimination only) eye movements in Experiment 1.

In the preceding section, we observed that perceptual performance at the distractor location was worse than at the other locations. We argue that this effect reflects distractor suppression mechanisms. However, an alternative explanation would be that the distractors fell into an attentional inhibitory surround of the target. It has been shown that performance can be poorer at an object positioned closely to a target, compared to further away (Bahcall & Kowler, 1999) suggesting that attentional selection of one object results in inhibition of perceptual processing for neighbouring objects (Mounts, 2000). When we analysed the 2/3 of trials with the distractor closer to the target, comparing these to the 1/3 of trials where the distractor was opposite the target, we saw that performance did not differ between conditions. A 3 (locations) x 2 (distractor distance: near versus far) ANOVA was carried out which yielded no effect for distractor distance ($F(1,13) = 2.07$, $p = .66$, partial $\eta^2 = .02$) and no significant interaction ($F(2,26) = 2.36$, $p = .11$, partial $\eta^2 = .15$), while the effect of location was significant $F(2,26) = 34.09$, $p < .001$, partial $\eta^2 = .72$). This points to an active suppression of the distractor colour singleton occurring in equal measure at all locations, regardless of target proximity. Further, the facilitation at the saccade target is not affected by the distance of the distractor.

Last, we inspected whether the presence of a distractor was affecting the allocation of visual attention at the control and saccade target locations. A 2 (distractor presence) x 2 (location) within-subjects ANOVA found a small, but significant performance decrease of 3.6% when a distractor was present, $F(1,13) = 8.37$, $p = .013$, partial $\eta^2 = .39$ (see Figure 5), showing that the distractor reduced attentional allocation at the control and target locations. Paradoxically, attention diverted from these locations did not benefit distractor processing, as made evident in the first analysis, where we observed worse performance at the distractor location. Further, the effect of location reported in the previous section was confirmed, $F(1,13) = 73.42$, $p < .001$, partial $\eta^2 = .85$. There was no significant interaction, $F(1,13) = 1.22$, $p = .289$, partial $\eta^2 = .09$.

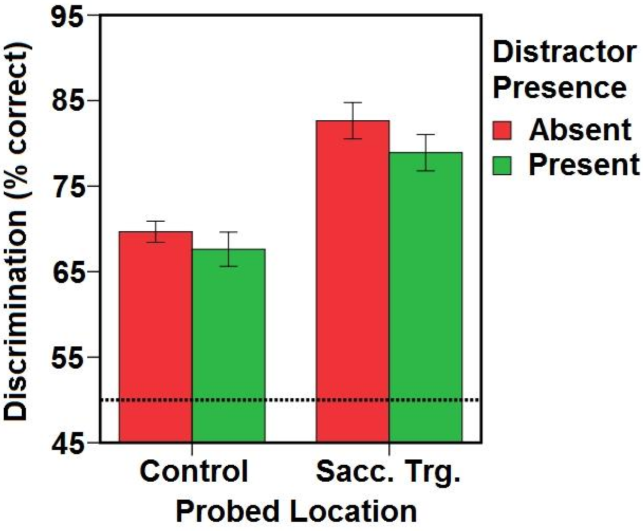

Figure 2.5 Discrimination performance as a function of distractor presence and probed location in Experiment 1. Sacc. Trg. = Saccade Target.

### Saccadic Reaction Times

In order to assess whether the location of the discrimination target (control, distractor, saccade target) or the colour of the objects (green-red) influenced saccadic reaction times of saccades directed to the saccade target, a one-way ANOVA was carried out on distractor present trials. No significant difference on SRTs was observed for probed location, $F(2,24) = 1.53$, $p = .237$, partial $\eta^2 = .11$. Thus, the observed differences in discrimination performance across locations cannot be explained by a speed-accuracy trade-off. Recall that the distractor had a detrimental effect on discrimination performance overall, that was not specific to any one location (see present vs. absent analysis above; Figure 5), and not due to the distractor drawing attention to itself, as performance at this location was very low (see Figure 3). Comparing saccadic reaction times in distractor present (277 ms) vs. absent (298 ms) trials showed that the presence of the distractor lead to swifter saccade initiation (mean difference 21ms), $t(13) = 6.07$, $p < .001$.

## Discussion

In Experiment 1, we originally set out to test for pre-saccadic attention shifts in capture saccades. While the number of capture trials turned out to not be sufficient to adequately investigate the hypothesis we could still effectively investigate the influence the distractor's presence had on pre-saccadic attentional enhancement in target-directed saccades. Unsurprisingly, the saccade target received the most enhancement. The distractor location was seen to receive less enhancement than all other locations, despite it being a visual onset. Presenting the distractor at an inhibited region, in between the potential saccade targets, appears to have led to its processing being compromised. This appeared to be dependent upon the movement preparation towards the possible targets, as performance at the distractor was not worse than at other locations in the discrimination-only task (i.e. in the absence of eye movements). Performance at the distractor was found to be equally low regardless of its closeness to the saccade target, therefore excluding biased competition induced suppression (e.g. Hickey et al., 2011; Mounts, 2000) as the principle cause. With the distractor being presented in the large majority of trials (75%) it is likely participants acquired a suppression strategy (Müller, Geyer, Zehetleitner, & Krummenacher, 2009) in order to effectively carry out the task. Lastly, it is clear the distractor was treated differently than the placeholders but this did not lead to any remapping effect, in terms of transfer of suppression to its remapping location. Performance at the rejected distractor's remapped location was in fact no different to that found at the control location. We can therefore conclude that while a saccade target receives location specific enhancement in the time leading up to the saccade (which steadily builds up, also see Supplementary material) a distractor onset appearing in between potential targets is suppressed, and this suppression does not influence performance at its remapped location. In the absence of a target, when no eye movements are required, pre-saccadic perceptual facilitation effects at the distractor locations return to baseline.

## Experiment 2

We now turn to Experiment 2 where the main purpose was to increase target selection difficulty in order to induce involuntary saccades towards a competing salient distractor. The well-known additional-singleton paradigm (e.g., Theeuwes, De Vries, & Godijn, 2003) allowed us to achieve an adequate number of capture sequences per participant (roughly 1/4th) and to test for facilitation at the end point of an involuntary saccade and the time course of the enhancement. The stimulus display also allowed predictive remapping effects to be studied; facilitation was tested at the distractor's remapped location, in straight-to target saccades (as in Jonikaitis et al., 2013), and at a future saccade destination's remapped location (as in Rolfs et al., 2010), when a capture sequence was performed. The goals were therefore (1) to test whether a distractor location that induces a capture sequence is enhanced prior to the saccade, (2) if there is enhancement, study the time-course of the enhancement compared to goal-directed saccades, (3) verify whether a salient distractor is remapped when the eyes go straight to the target and (4) whether there is evidence of the remapping of a saccade target prior to an involuntary eye movement when capture happens.

### Methods

#### *Participants*

A total of 13 participants (nine male, four female, with one having participated also in Experiment 1) were tested in Experiment 2, with age ranging from 19 to 32. They were run in a minimum of eight non-consecutive one-hour sessions, and a maximum of ten. Data from another eight participants were excluded midway through the study, with five participants reporting they could not see the perceptual stimulus being flashed (discrimination performance at chance level) while two attained perceptual discrimination scores below the 60% mark even in the most favorable conditions. One participant chose to not return for the continuation of the study once the course credits were obtained. All were paid or received course credits for their participation.

### *Apparatus*

Apparatus were the same as in Experiment 1.

### *Stimuli*

The fixation cross, perceptual stimuli (flashed discrimination crosses) and masking squares did not differ from those employed in Experiment 1. Surrounding stimuli were diamonds and circles, presented at 5° from the center of the screen. The diamonds were 3.2 deg diagonal, whereas the circles were 3 deg in diameter.

### *Design and Procedure*

While the nature of the dual-task remained identical to that in Experiment 1 (i.e., directing a saccade towards an eye movement target and discriminating a perceptual stimulus), the visual display and experimental sequence underwent a number of changes (see Figure 6). A fixation cross was initially displayed, varying randomly between 1 and 1.3 seconds, after which it disappeared for 200 ms, followed by the stimuli. These consisted of six objects in each trial, four identical, one shape singleton acting as the saccade target, and one colour singleton acting as the distractor.

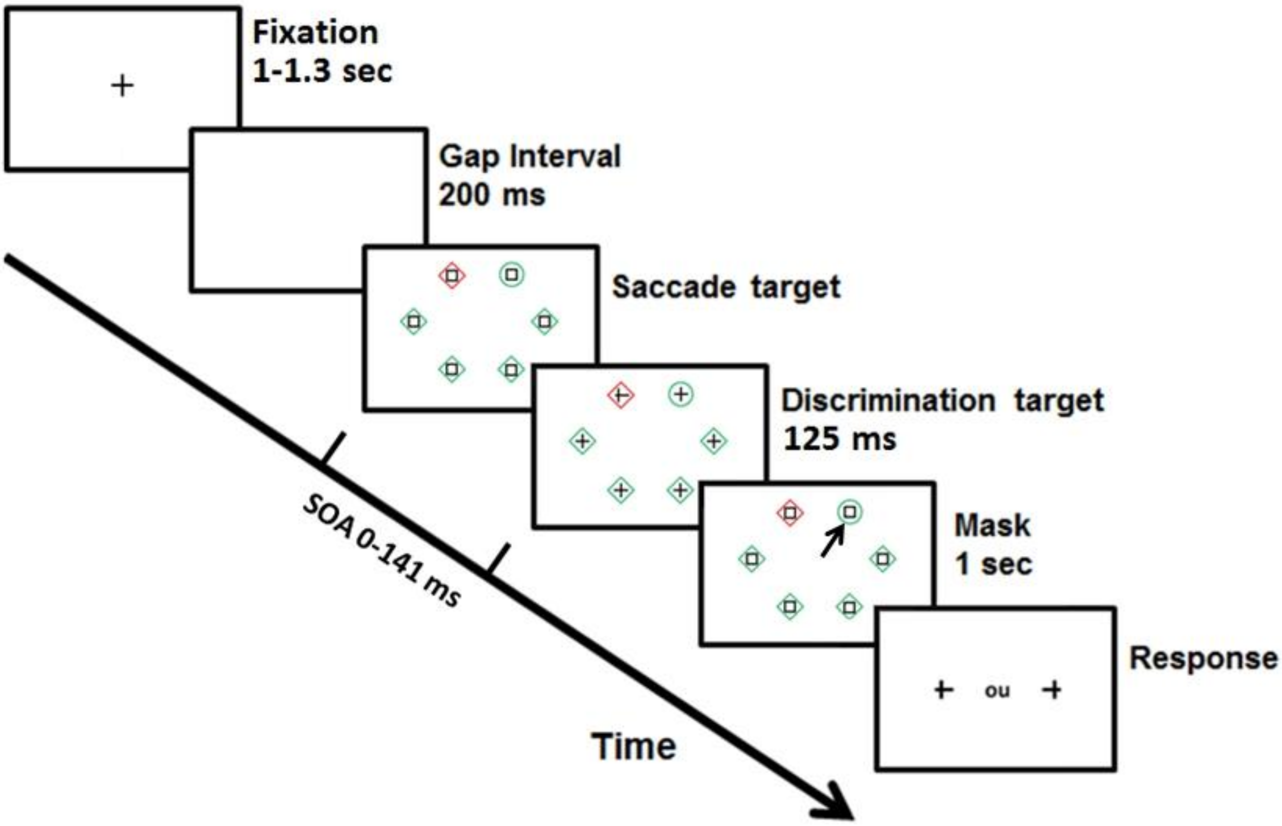

Figure 2.6 Sequence of events in Experiment 2. Participants were told to move their eyes to the shape singleton as soon as the objects appeared on screen. During the saccade latency period, perceptual stimuli (crosses) were displayed within the objects and masked before the eye movement (symbolized by an arrow in the mask display; arrow was not shown in the actual experiment) was initiated. One flashed cross was asymmetric (in the example depicted within the colour singleton distractor) and the shift of its vertical bar required forced-choice discrimination at the end of the trial.

Participants were instructed to fixate the cross and to move their eyes as fast as possible to the shape singleton once the objects came on screen. The saccade target shared the same colour (either green or red) as the rest of the objects on screen, except for the distractor, which was of the opposite colour. The distractor shared the same shape as the other non-target stimuli. The distractor was present on 75% of trials, while it was substituted by a placeholder of the same appearance as all other non-target objects in 25% of trials. The distractor was always presented adjacent to the saccade target. Shapes and colours of saccade targets and distractor varied randomly from trial to trial. The objects were presented initially containing a masking square. After one of five randomly selected SOAs ranging from 0 to 140 ms (where 0 means simultaneous to the appearance of the objects) the perceptual stimuli briefly replaced the masks. The crosses were identical to those employed in Experiment 1, but this time displayed slightly longer, for 125 ms before being masked once again.

Even though each object contained a flashed cross, the asymmetric target cross could only appear within one of four locations: the saccade target, the distractor, the control and the remapped location. The latter two were defined as follows: When a straight-to target saccade was performed the remapped location was a location in retinotopic coordinates corresponding to the predictive remapping of the colour singleton distractor (see right panel in Figure 7). In capture sequences instead the remapped location corresponded to the retinotopic remapping of the saccade target (see right panel in Figure 8). Each block was made up of 160 trials and a minimum of 24 blocks were carried out.

## Results

### Data Exclusion

Trials where the discrimination target was presented for longer than 135 ms or no eye tracking recording was obtained, due to technical issues were immediately discarded (2.5 % of trials). Of all remaining data, trials were removed if the saccade landed on an object prior to masking (7.3%), if gaze deviated by more than 1.5° from the initial fixation cross (3.8%), if the eyes never landed on the saccade target (4.6%) or if the saccade was initiated prior to the saccade target being presented for 50 ms (3.1%). Blinks, late saccadic responses taking longer than 600 ms to initiate and trials where multiple errors occurred accumulated to <3%. The percentage of valid trials left for analysis was 78.3%. Of these valid trials we examined those where the first saccade was directed straight to the eye movement target (48.1%) and saccades where an oculomotor capture sequence occurred, with an initial saccade directed to the distractor followed by a corrective saccade to the intended saccade target (27.3%).

### Perceptual Discrimination

*Straight-To Target Saccades.*

*Overall performance and distractor absent vs. present trials*

First of all, we examined the allocation of attention prior to saccade initiation, for those eye movements directed straight to the target. Note that the distractor and control locations were always on either sides of the saccade target. A 4 × 2 within-subjects ANOVA on the arcsine-transformed percent correct values for the four probed locations (saccade target, rejected distractor, remapping of a salient object and control), and the two distractor conditions (absent – present) was performed. A statistically significant main effect for probe location was observed, $F(3,36) = 52.76$, $p < .001$, partial $\eta^2 = .81$, highlighting that attention was not allocated evenly across the displayed objects. The main effect of distractor presence was found to also be significant, $F(1,12) = 10.71$, $p = .007$, partial $\eta^2 = .47$, confirming the slightly detrimental effect of distractor presence on performance overall already found in Experiment 1 (66.4% with vs. 69.3% without distractor). No significant interaction was found between probed location and distractor presence, $F(3,36) = 1.42$, $p = .253$, partial $\eta^2 = .11$, emphasizing that the presence of a distractor did not have a location-specific effect on performance (not even at the distractor location itself; that is, the colour singleton distractor did not benefit from perceptual facilitation when compared to the distractor absent trials, when another non-salient placeholder was presented in its stead; see Figure 7).

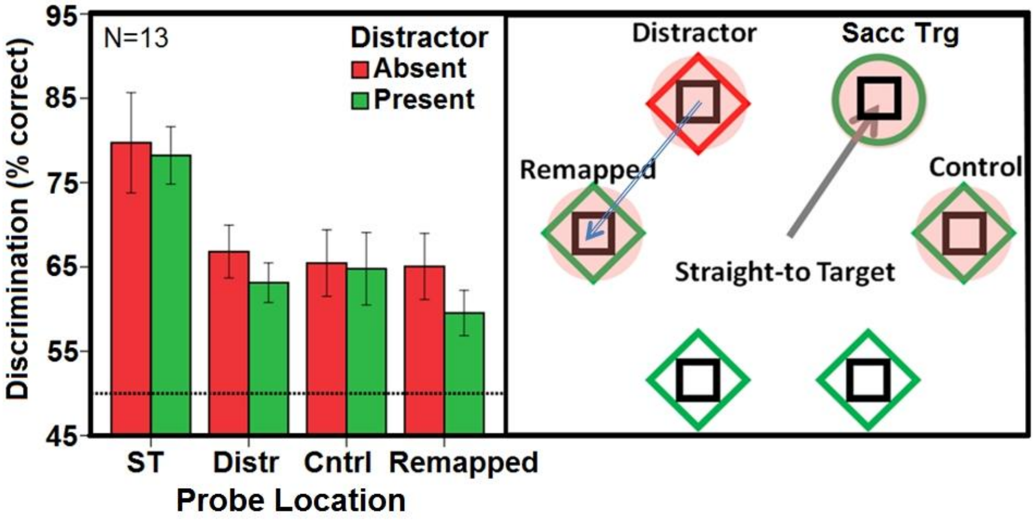

Figure 2.7 Discrimination performance in Experiment 2 for straight-to target saccades. The scores from the four probed locations (saccade target, rejected distractor, predictive remapping of a salient object and control) when the distractor was present or absent (replaced by a placeholder; i.e. another green diamond in the illustration). The probed locations are illustrated and highlighted on the right. The grey arrow indicates the saccade while the blue arrow indicates remapping of the salient colour singleton object.

We conducted a series of post hoc tests to better assess the distribution of attention across the different locations. Performance was better at the saccade target than the distractor (mean difference 16.2%), *t*(12) = 8.3, *p* < .001, the control (15.5%), *t*(12) = 13.4, *p* < .001, and the remapped locations (19.1%), *t*(12) = 9.43, *p* < .001, confirming the large perceptual benefits at the saccade target already found in Experiment 1. Performance at the remapped location was marginally worse than at the control (mean difference 3.6%), *t*(12) = 2.13, *p* = .055, and distractor location (2.87%), *t*(12) = 3.61, *p* = .004, respectively.  Given the layout of our stimuli, one may be tempted to assume that this small difference between the remapped location and the other two may indicate an attentional spread around the saccade target, as control and distractor locations were on either side of it, whereas the remapped location of the distractor was further away. However, in a supplementary analysis, we found some modulations in performance at the distractor location based on its salience (less luminant red vs. more luminant green distractors; see Supplementary, Figure 11). The difference was not strong enough to drive the critical three-way interaction (distractor presence × probe location × distractor colour), p = .463. Still, we think the observation warns against concluding that there was an even spread of attention around the saccade target and that the distractor was treated similarly to its non-singleton counterpart on the other side of the target. Our technique might not have been sensitive enough to detect the differences.

*Saccadic Reaction Times*

It took participants on average 284 ms to initiate the goal-directed saccade to the saccade target. We tested whether the location of the perceptual target or the presence of the distractor affected SRTs. To that end, a 4 x 2 repeated-measures ANOVA was run, with 4 levels for the location of the probe and 2 levels for distractor presence. No main effect was found for probed location, $F(3,36) = .58$, $p = .632$, partial $\eta^2 = .05$, or for distractor presence, $F(1,12) = 2.67$, $p = .128$, partial $\eta^2 = .18$, proving the perceptual task or the distractor's presence did not affect the motor task. The interaction was also not significant, $F(3,36) = .15$, $p = .93$, partial $\eta^2 = .01$.

*Oculomotor Capture Trials*

*Overall performance*

We define oculomotor capture trials as those where the eyes went initially to the distractor (1st saccade) and then to the eye movement target (2nd saccade). This sequence of saccades is therefore made up of an erroneous saccade which is then corrected successfully. The remapped location now corresponds to the remapped future saccade destination (see right panel in Figure 8). A one-way within subjects ANOVA was run on the arcsine-transformed percent correct values for the four probed locations, highlighting a significant main effect of location, $F(3,36) = 15.95$, $p < .001$, partial $\eta^2 = .57$.

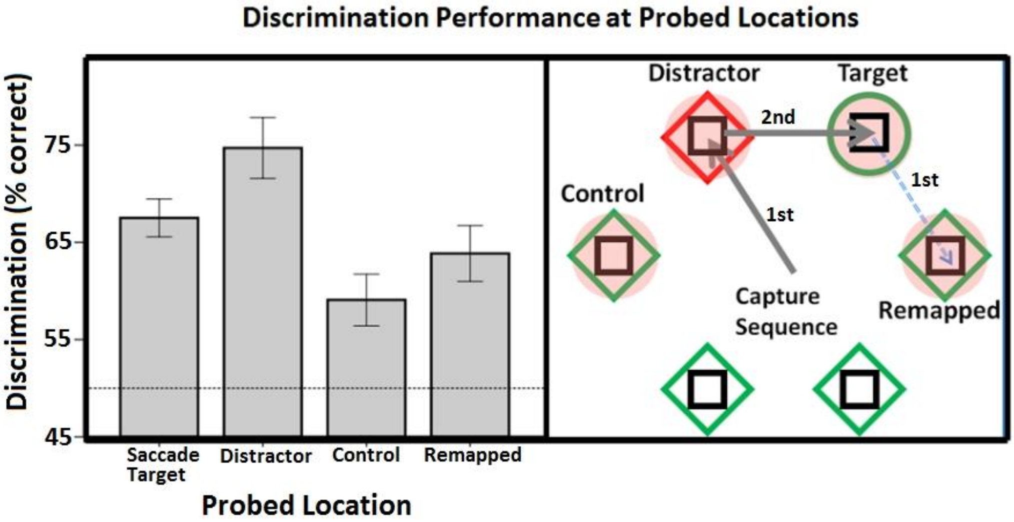

Figure 2.8 Perceptual discrimination scores for oculomotor capture trials, at the four probed locations, highlighted in red in the right diagram. The grey arrows indicate the saccades (first capture then corrective) while the dashed blue arrow indicates remapping of the saccade target triggered by the first capture saccade.

Focussing on the four locations, the largest amount of visual attention was now allocated to the distractor, surpassing even the saccade target. Paired t-tests highlighted a significant difference between the distractor location and all remaining locations (differences larger 8.3%), *t*(12)s > 3.95, *p*s < .002. Even involuntary saccades were therefore seen to be preceded by a shift of covert attention towards their endpoint, leading to perceptual enhancement at the distractor location prior to the distractor-directed saccade being initiated. The pre-saccadic time-course of this activation is illustrated in the Supplementary section. Still, participants were also significantly better at discriminating at the saccade target than at the control (mean difference 8.9%), *t*(12) = 5.0, *p* < .001. This indicated that a portion of attentional resources were being allocated to the saccade target, the eyes' second landing point. Significantly better discrimination performance was also recorded at the location corresponding to the remapping of the saccade target than at the control location (mean difference 4.9%), *t*(12) = 2.36, *p* = .036, emphasizing that a sequence of saccades where the first is involuntary leads to the remapping of a future saccade destination, much the same way as a sequence of voluntary saccades (see Rolfs et al., 2010). Furthermore, no difference in facilitation was observed between the saccade target and its remapped location (mean difference 4%), $t(12) = 1.71$, $p = .113$,

### *The influence of the inter-saccadic interval*

We sought to further examine the possibility that the distractor was temporarily mistaken for the saccade target and that the initial saccade was intended rather than erroneous. By focusing on the time spent fixating the distractor (inter-saccadic interval), before initiating the corrective saccade to the saccade target, it was possible to distinguish between types of capture sequences. Those sequences where the participant spent very little time on the distractor before moving the eyes onto the saccade target can be taken as an indication that the second saccade may have been programmed before the first saccade was completed (see Becker & Jürgens, 1979). We believe this pre-programming of the second saccade reflects a sequence where the first movement is realized to be erroneous, and starts to be corrected, presumably mid-flight or even before the first saccade has been initiated. Longer time spent fixating the distractor, on the other hand, before initiating the corrective saccade, is indicative of saccades being relatively separate one from the other, without parallel programming having taken place. Trials were divided into two groups with short and long inter-saccadic intervals, respectively. We wanted a cut-off value that would allow us to observe performance in saccades that were closely programmed in time but also keep most participants in the analysis. This was set at 190 ms. A 4 × 2 within subjects ANOVA was carried out for the four probed locations and two inter-saccadic time durations (see Figure 9). A significant difference was found for the main effect of location probed, $F(3,30) = 16.55$, $p < .001$, partial $\eta^2 = .62$, and for the main effect of inter-saccadic duration, $F(1,10) = 12.44$, $p = .005$, partial $\eta^2 = .55$. Importantly, there was also a significant interaction, $F(3,30) = 5.58$, $p = .011$, partial $\eta^2 = .36$.

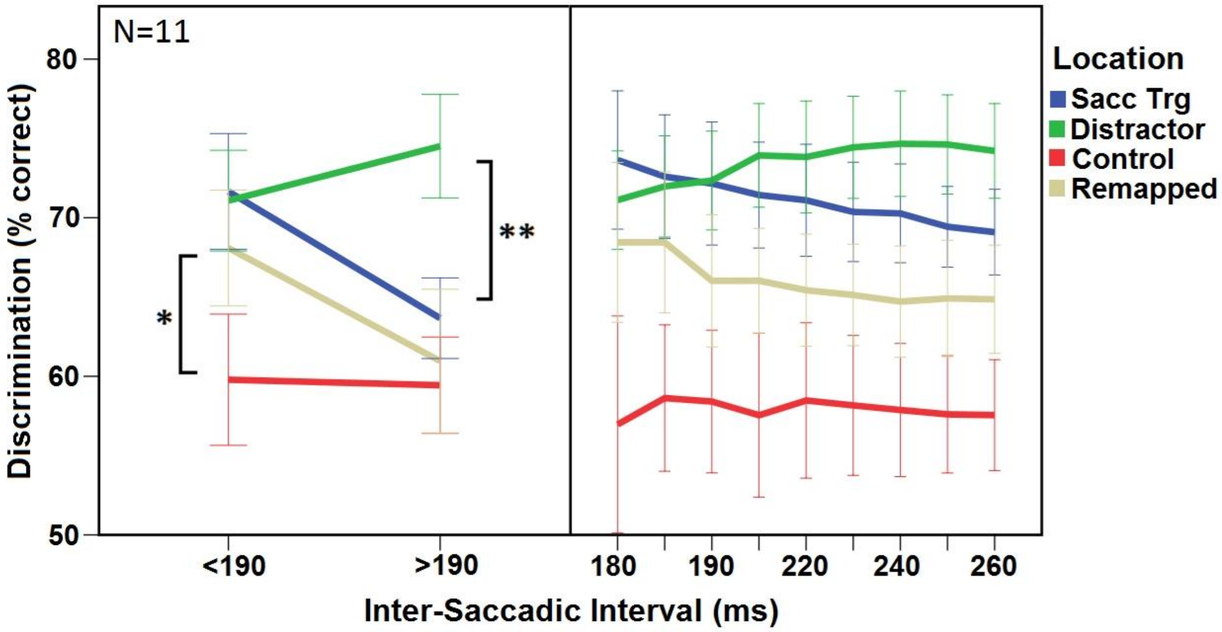

Figure 2.9 Performance in Experiment 2 as a function of how close in time the two saccades were, where the x-axis indicates the cut-off point, up to which trials were included. The left panel shows discrimination performance as a function of the temporal gap between the saccades being smaller or larger than 190 ms. The right panel shows discrimination performance as a function of increasing inter-saccadic intervals, going from 180 to 260 ms. The shorter the inter-saccadic interval the more attention is allocated to the saccade target and, in turn, to its remapped location. Sacc Trg = Saccade Target.

Parallel programming with short inter-saccadic time intervals (< 190 ms) led to an equal distribution of attentional resources to distractor and target locations (mean difference 1%), *t*(10) = -0.34, *p* = .74, suggesting parallel programming with equal allocation of attention to the two locations. This led in turn to strong perceptual facilitation at the remapped location of a future saccade destination over the control location (mean difference 10.5%), *t*(10) = 2.55, *p* = .029. It is also noteworthy that even when the sequence of saccades was performed in very rapid succession, with the first saccade to the distractor clearly being involuntary, there was still pre-saccadic facilitation at the capturing distractor location. Instead, when participants fixated longer (> 190 ms) between one saccade and the other, attentional deployment considerably favoured the distractor over the saccade target, (mean difference 14.3%), *t*(10) = 5.98, *p* < .001, suggesting that the distractor was erroneously identified as the target and received most attentional resources. No difference in performance was seen between remapped and control locations when the time between the saccades was long (mean difference 1.9%), *t*(10) = .56, *p* = .584. Thus, for short and long inter-saccadic intervals, performance at the remapped location was seen to be highly related with that at the saccade target, apparently mirroring the enhancement.

## Discussion

In summary, Experiment 2 provided evidence of a location-specific shift of pre-saccadic covert attention at the endpoint of a goal-directed saccade, in straight-to target saccades, and at the endpoint of an involuntary saccade (capture saccades). In straight-to target saccades, enhancement was in fact only seen at the saccade target, with little facilitation or suppression seen at any of the rejected locations. In contrast to Experiment 1, detrimental performance at the rejected distractor location was not seen. In sequences of capture saccades, performance was strongly dependent on the inter-saccadic interval. When there was a lengthy delay between the capture and corrective saccades (i.e. long inter-saccadic interval) most attention was allocated to the salient capturing distractor. When there was very little delay between saccades (i.e. short inter-saccadic interval) attentional resources were distributed far more evenly between both saccade landing points (distractor and target); this, in turn, led to stark facilitation at the remapped location of the saccade target. No facilitation was instead observed at the remapped location of a salient (but not looked at) distractor object, in straight-to target saccades.

## General Discussion

The present study provided evidence that involuntary eye movements induced by a salient object in the environment are preceded by an obligatory and location-specific shift of attention. Enhanced perceptual performance was found at the endpoint of a saccade, prior to its execution, whether this was a goal-directed saccade towards a target (Experiment 1 and 2) or an involuntary saccade to a salient capturing object (Experiment 2). Thus, the mechanism that allows attention to focus in on a target location before a voluntary saccade is made (Deubel & Schneider, 1996; Deubel, 2008; Rolfs et al., 2010; Godijn & Theeuwes, 2003) is also called into play when an involuntary stimulus-driven saccade is made. The mechanism, often taken as evidence of the tight coupling between attention and eye movements, appears to be relatively unconcerned about task goals. Pre-saccadic shifts of attention, instead, seem to be a defining characteristic of all saccades (see also Born et al., 2014). It is likely that our visual system cannot afford visual processing delays where attention lags behind or is caught by surprise whenever something in the environment catches our gaze.

### Perceptual performance at the endpoint of voluntary and involuntary saccades

Two points of diversion between involuntary and goal-directed saccades did however emerge. Firstly, the enhancement observed exclusively at the saccade target location for intended saccades was distributed differently for capture sequences. We see evidence of spatial attention being allocated in parallel to two saccade destinations, similarly to what was reported by Godijn et al. (2003) and Rolfs et al., (2010). These authors however observed more attention being allocated to the first saccade target than to the second. In the current study we see that when there was very little delay between the capture and corrective saccades, attention was distributed relatively evenly at both saccade destinations. This  points to a more equal distribution of attentional resources when the first saccade is identified as erroneous, leading to a greater emphasis on the following saccade destination than what was seen in Godijn et al. (2003) and Rolfs et al. (2010) where both saccades were voluntary. Secondly, the time-course analysis (Supplementary, Time course analysis) suggests that activation at an involuntary saccade end-point appears to begin, closer in time to saccade initiation, compared to voluntary goal-directed saccades. We see evidence in Experiment 2 of enhancement at a salient object that captures the eyes starting in between 85-60 ms before the saccade, while their goal driven counterparts led to facilitation over 130 ms before saccade initiation, in Experiment 1, and over 100 ms, in Experiment 2 (with evidence in the literature of pre-saccadic enhancement as early as 250 ms, Deubel, 2008). Despite the timeline of the activation of involuntary saccades being shifted closer to saccade initiation, and enhancement not reaching the peak seen in straight-to target saccades, the occurrence of a location-specific shift of covert attention that increases in the time leading up to the saccade is beyond doubt.

### Perceptual facilitation at the saccade target’s remapped location

With regards to perceptual facilitation at non-target locations, evidence for the remapping of a future saccade destination was observed prior to involuntary eye movements. When there was little delay between involuntary eye movement and its corrective counterpart, before any saccade was initiated participants allocated attention at the landing point of the two saccades and predictively remapped the saccade target. Similarly to the remapping of a future saccade destination in a sequence of voluntary saccades (Rolfs et al., 2010), attention accounts for involuntary saccades and predictively remaps locations of interest, in anticipatory fashion. Performance at the remapped location of the saccade target, in fact, appeared to mirror the performance levels observed at the saccade target location (see Figure 9). This is in line with the views of Mirpour et al. (2012), where the remapping process is sensitive to enhancement levels observed at the object of interest. Lastly, Duhamel et al. (1992) define remapping as a process that depends upon the intention to move, and that neurons anticipate the retinal consequences of intended eye movements. The current findings show how the remapping mechanism extends beyond voluntary movements; attention can be maintained on objects of interested while accounting for the retinal displacement across eye movements, whether these are intended or involuntary.

### Alternative accounts: Saccadic momentum and Biased-competition

So far, we attribute our enhancement effects at the so-called remapped location exclusively to remapping. However, could there be alternative accounts? Saccadic momentum (T. J. Smith &

Henderson, 2009) refers to a tendency the saccadic system has to continue in the same direction as the last executed saccade (A. J. Anderson, Yadav, & Carpenter, 2008). Similarly, it has been shown that attention is biased towards the direction of the last attentional shift (Bennett & Pratt, 2001). Also, when an eye movement is performed in the presence of a non-target object, facilitation can be found not only at the attended object's pre and post saccadic locations, but also at various locations in-between (Harrison, Mattingley & Remington, 2012), suggesting attention spreads in direction of the upcoming eye movement (see also Mathôt & Theeuwes, 2010). However, no literature within this context is present, to the authors' knowledge, suggesting deviations of attention direction associated to momentum, which would be necessary in order for attention to envelop the remapped location in the current study after having visited the saccade target. Instead, much evidence points to attention selection as being relatively sharp and narrow at an attended location or locations (e.g. Müller, Malinowski, Gruber, & Hillyard, 2003). For the reasons stated, saccadic momentum seems inadequate to effectively explain the facilitation found at the remapped location without presupposing a diversion of attention direction unrelated to the direction of the saccade to the target. Furthermore, if the spread of pre-saccadic attention from the distractor to the saccade target was fuzzy enough to lead to facilitation also at the remapped location, we would expect that when most attentional resources are allocated to the distractor (when the delay between capture and corrective saccades is long) the control location would also benefit from increased facilitation. It is, after all, in the distractor's proximity and roughly in the same direction. Instead, performance at the control location remained unaffected. Biased-competition based explanations (Desimone et al., 1995; Hickey et al., 2011) were also explored, proving an unsatisfactory framework to explain the current finding, as changes in distractor luminance led to differences in performance at the distractor alone, and not the target (Supplementary, Figure 11). In other words, the distractor did not prove to bias the competition, with regards to the target. This held true also for target-distractor proximity (Experiment 1), where no biased-competition effects were found. These proved unfruitful frameworks at explaining the cause of the shift of attention to the so-called remapped location, which instead predictive remapping elegantly accounted for.

### Perceptual performance at the salient distractor’s remapped location

No evidence was found for the remapping of a salient non-target object (Experiment 1 & Experiment 2, straight-to target saccades). In contrast to the findings by Jonikaitis et al. (2013), who gave a clear account of the remapping of an attended, but not foveated object, participants in the current study did not display facilitation (or suppression, which may have been expected in Experiment 1) at the remapped distractor location. Furthermore, the changes in luminosity at the attended distractor object in Experiment 2, which led to changes in performance at the distractor itself, did not affect performance at its remapped location in any way (further details in Supplementary, Figure 11). One possible explanation is that activation was not sufficiently high to lead to it being remapped before the saccade. After all, despite its salience, performance at the distractor location was not different from the controls in Experiment 2. Another possible explanation for this is that the distractor location in our study could be considered a rejected target location, and most definitely interfered with target selection. In line with the salient-signal-suppression hypothesis (Caputo & Guerra, 1998; Kumada & Humphreys, 2002; Sawaki & Luck, 2010; Burra & Kerzel, 2013), participants may have successfully suppressed signals arising from the salient distractor when searching for the target. It was recently shown that salience-driven distraction is mitigated by a suppressive mechanism, reducing the salience of potentially distracting stimuli (Gaspar & McDonald, 2014). Such a mechanism, in trials where the distractor did not lead to oculomotor capture, may have led to a successful suppression of the salient distractor object, and, in turn, to no remapping.

### Perceptual performance at the salient distractor location

Perceptual performance at the location of an onset singleton distractor was worse than at control locations in Experiment 1. This effect could neither be explained by its status as a sudden onset singleton, which may have masked the perceptual target more strongly (see discrimination-only analysis, Figure 4); nor was it due to the distractor being presented closer to the saccade target than the control locations, thus potentially falling into an inhibitory surround of the attended target. In addition, the distractor's proximity to the target did not lead to a performance bias at the saccade target location. Instead, we think the distractor was actively suppressed. At the beginning of the trial, the placeholders were potential target locations, requiring attention be directed at these locations. Subsequent to this initial distribution of attention, the distractor and the target were revealed. The non-target regions in between potential targets could have been inhibited, such as suggested by McSorley, Haggard, & Walker (2009). With the distractor presented at an inhibited region, its processing could have been compromised.

Moreover, occurrence of the distractor in a large majority (75 %) of trials, as well as being presented in a salient non-target colour, could also have induced additional inhibition. Moher, Abrams, Egeth, Yantis & Stuphorn (2011) found that when participants expected a distractor, rapid suppression occurred. Furthermore, frequently displayed distractors that are defined in another dimension and physically more salient than the target provide a high incentive for suppression (Müller, Geyer, Zehetleitner, & Krummenacher, 2009; Zehetleitner, Proulx, & Müller, 2009). Thus, participants in our study could have acquired a suppression strategy (Müller et al., 2009), limiting distractor processing to initial stages. Hence, contrary to our expectations, the distractor was not drawing resources directly to itself. Even more surprisingly, distractor presence led to faster saccadic reaction times. However, it also had a detrimental effect on discrimination performance at all other locations. This indicates that, in spite of its location being inhibited, the distractor still had a disruptive impact on behaviour. This is in line with Tsal & Makovski's (2006) notion of a process-all mechanism, where attention is initially distributed to all presented items regardless of their relevance.

## Concluding remarks

In conclusion, the end point of an involuntary eye movement benefitted from a location-specific shift of covert attention, prior to the movement being initiated. The specificity and incremental nature of the enhancement bore no difference from that observed for saccades going straight to their intended target. The timeline of the enhancement, instead, might differ slightly between the saccade types, with involuntary saccades leading to pre-saccadic enhancement only 70-80 ms prior to saccade initiation. This led us to conclude that all eye movements undergo the same process of location-specific enhancement build-up. Distractors that did not induce an involuntary eye movement were not perceptually enhanced. When the same distractor that on occasion captured gaze, was instead correctly rejected, no enhancement was observed. When, on the other hand, the distractor was a visual onset appearing in-between possible saccade targets it appeared to be suppressed, as performance was below baseline. Furthermore, the attention allocating process tightly linked to eye movements appears to also be the guiding force behind the remapping mechanism. Predictive remapping of a saccade target, in fact, also brought about location-specific pre-saccadic enhancement, perfectly accounting for the retinal displacement caused by involuntary movements. These shifts of covert attention appeared to be entirely associated with the motor command. No evidence was instead seen for the remapping of enhancement or suppression of an attended distractor object that was not fixated. Overall, the current findings show how the remapping mechanism extends beyond voluntary movements alone, accounting also for the retinal displacement caused by involuntary movements.

## Supplementary Material

### *Time Course Analysis*

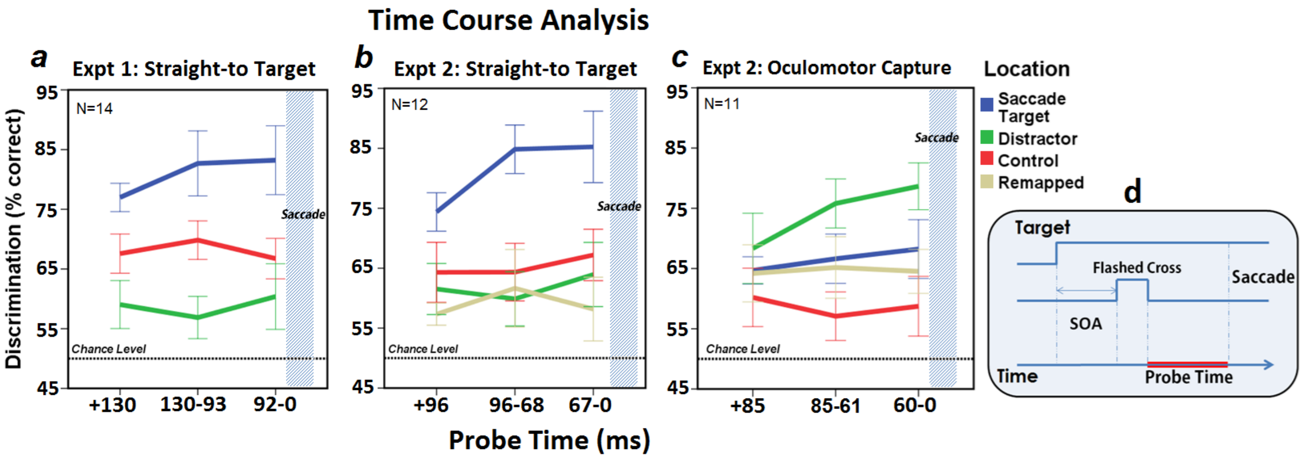

Figure 2.10 Results of the three time course analyses. (a & b) Perceptual discrimination scores in Experiment 1 and Experiment 2, as a function of the time the probe was flashed, prior to the saccade. Both graphs relate to goal-directed saccades going straight to the target. (c) Perceptual discrimination scores in Experiment 2 for involuntary saccades going to the distractor (then corrected by a second saccade to the target). (d) Illustration of the interval (Probe Time) considered for subdivision of the data into time bins. Probe Time = time of saccade onset to time of perceptual target offset (flashed crosses). Error bars represent the standard error, with scores adjusted for between-subjects variability for within-subjects effects.

In order to test whether attention allocated to the displayed objects differed over the time leading up to the saccade (similarly to Deubel, 2008; Rolfs et al., 2010; Jonikaitis et al., 2013), we split the data into three time bins. Note that the discrimination stimulus was flashed at varying SOAs in order to present the perceptual stimulus at various times before the onset of the saccade, which was unpredictable on a given trial. For each trial, we determined post hoc the time interval between offset of the perceptual stimulus (flashed crosses) and the onset of the saccade. Binning according to this interval, we could study the amount of attention allocated to the objects depending on the stage of saccade preparation. Or, in other words, we determine discrimination performance, time-locked to the beginning of the imminent movement (see Figure 9d).

We chose to split the data using fixed time bins (not percentiles). In **Experiment 1** concerning **straight-to target saccades** these were: 0 - 92, 93 – 130 and 130 +, where 0 indicated the time of saccade initiation. We did not test for post-saccadic visual attention. The choice of these specific bins allowed a fairly equal distribution of trials, but of course with some variability across participants (minimum: 12 trials, maximum: 613 trials per time bin and participant). A 3 x 3 within-subjects ANOVA was carried out, testing performance differences in the discrimination task across three time bins and three locations. A significant main effect was found for probed location, $F(2,26) = 38.9$, $p <.001$, partial $\eta^2 = .75$, but not for time bin, $F(2,26) = 1.98$, $p = .158$, partial $\eta^2 = .13$. There was a significant interaction between location and time, $F(4,52) = 2.93$, $p = .029$, partial $\eta^2 = .18$, highlighting how the length of the time interval between the flashed cross and the movement affected attentional deployment (displayed in Figure 9 a,b,& c).

Post-hoc analysis was carried out by means of three one-way ANOVAs to examine specific performance differences at each location for each of the time intervals. Temporal differences were seen to be specific to the saccade target, with a significant difference in performance depending on time of saccade initiation in relation to the perceptual stimulus, $F(2,26) = 3.41$, $p < .048$, partial $\eta^2 = .21$. Instead performance at the remaining locations did not change in the time leading up to the saccade, $Fs(2,26) < .95$, $ps > .399$, partial $\eta^2 < .07$. Paired *t*-tests emphasized that discrimination performance was significantly better when the cross was flashed 93 to 130 ms before the saccade, rather than +130 ms (mean difference 8.6%), $t(13) = 2.65$, $p = .02$. Performance was also significantly better in those trials when the cross was flashed directly before the saccade, 0-92 ms, rather than +130 ms (mean difference 13%), $t(13) = 2.45$, $p = .029$. Furthermore, a substantial activation at the saccade target location was already observable in the +130 time bin, with performance here found to be significantly better than at the control (mean difference 24.6%), $t(13) = 4.47$, $p = .001$.

**In Experiment 2** data relating to the **straight-to target saccades** were again split up into 3 time bins: 0-68, 69-96 and +96 ms. However, as a consequence of the fixed bins, one participant had to be excluded from the analysis, due to a lack of short-interval trials. We ran a 4 × 3 within-subjects ANOVA on the arcsine-transformed percent correct values, with four locations where attention was measured and three different time intervals. We found a statistically significant main effect for location, $F(3,33) = 38.39$, $p < .001$, partial $\eta^2 = .78$, and for the main effect of time bin, $F(2,22) = 5.13$, $p = .015$, partial $\eta^2 = .32$. Importantly, the interaction between location and time was also significant, $F(6,66) = 2.77$, $p = .018$, partial $\eta^2 = .2$. In order to better explore the temporal differences at the locations, four separate one way within-subject ANOVAs were carried out, one for each location. A significant difference in performance over time was seen only at the saccade target, $F(2,22) = 8.03$, $p = .002$, partial $\eta^2 = .42$, demonstrating increasing performance the shorter before the saccade the perceptual target was presented, while at all remaining (non-target) locations no significant effect across time was observed, $Fs(2,22) < .868$, $ps < .434$, partial $\eta^2 < .07$. From the first bin chosen, + 96 ms, performance at the saccade target already differed significantly from that at the control (mean difference 11.1%), $t(11) = 3.85$, $p = .003$. This emphasized that the enhancement at the saccade target location occurred earlier in time, as suggested by other accounts (see Deubel et al., 2008).

In **Experiment 2,** relative to **capture sequences,** 3 cut-off points were chosen: 0-60, 61-85, +86 ms. Two participants were excluded due to a lack of data in certain conditions. A 4 × 3 within subjects ANOVA was conducted for the four locations and the three time bins. A significant main effect was observed for location, $F(3,30) = 15.21$, $p < .001$, partial $\eta^2 = .6$, and the interaction was also significant, $F(6,60) = 2.5$, $p = .033$, partial $\eta^2 = .2$. The main effect for time was not significant, $F(2,20) = 1.8$, $p = .191$, partial $\eta^2 = .15$. A series of post-hoc one-way within subjects ANOVAs were carried out. A significant difference in discrimination performance was observed at the distractor location across time, $F(2,20) = 6.9$, $p = .005$, partial $\eta^2 = .41$, while no difference over time was reported at the remaining locations, $F(2,20)< .81$, $p > .46$, partial $\eta^2 < .07$. Performance at the distractor began to differ from that at the control from 61-85 ms (difference of 20.7%), *t*(10) = 5.59, *p* < .001, while it did not reach significance in the +85 ms bin (9.0%), *t*(10) = 1.88, *p* = .09. By comparing performance directly, at the saccade target in straight-to target saccades and at the distractor in capture saccades, for the time bin furthest away from saccade execution a significant difference emerged between conditions (mean difference 7.5%), *t*(10) = 3.09, *p* = .011. This highlighted that strong location-specific enhancement very probably occurs earlier for voluntary straight-to target saccades than for capture saccades.

This highlighted how enhancement over time, leading up to the saccade, happens at the end point of an involuntary saccade as it happens for voluntary goal-directed intended saccades. The only noticeable difference between these two types of saccades may be the timing of the activation, with enhancement at a location visited by an involuntary saccade occurring closer in time to saccade initiation. In straight-to target saccades, discrimination performance at the saccade target was already at 75 % and significantly different than that at the control approximately 100 ms before the saccade, while at approximately 90 ms before the involuntary saccade performance at the capturing object is still in the high 60s and does not differ significantly from that at the control. Performance at the saccade target and remapped location instead remained relatively constant in the time leading up to the saccade. We suspect this may be due to a great number of trials where the saccade target was either not yet identified or had indeed been identified but not sufficiently attended to, before the saccade to the distractor took place. Without stark improvement over time at the saccade target no improvement over time would be expected at its remapped location.

### **Experiment 2 (Straight-to Target): Saccade Target and Remapped location unaffected by changes in saliency at distractor**.

We found performance at the saccade target to be better than that at the distractor, control and remapped locations, whether the target was green (mean differences larger 13.1%), *t*s(12) > 5.56, *p*s < .001, or whether it was red (mean differences larger 12.1%), *t*s(12) = 3.5, *p*s ≤ .004. This replicated results of Experiment 1, confirming that most attentional resources are concentrated at the saccade target regardless of low-level features. Differences in colour at this location in fact left performance unaffected (difference of 0.1%), *t*(12) = 0.02, *p* = .985. In order to tease apart differences in attention allocated to non-target locations we compared performance at the distractor, control and remapped locations to expand on the probe location × colour ANOVA interaction reported in Results.

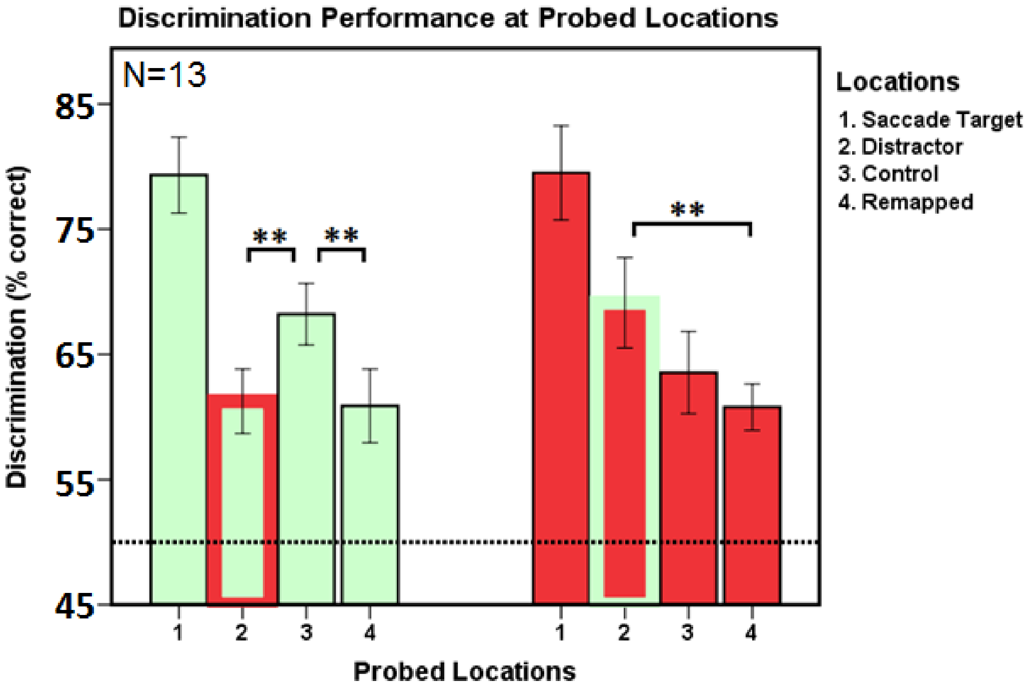

**Figure 2.11.** Graph illustrating discrimination performance affected by colour differences across the four locations for straight-to target saccades in Experiment 2. The distractor was always of the opposite colour from the rest of the stimuli for each colour condition: Green condition with Red distractor (left) and Red condition with Green distractor (right). Note that the colours were of different luminance (green > red).

A series of paired t-tests, comparing performance at the non-target locations per colour, highlighted that, when the stimuli were green participants were significantly better at discriminating at the control location than at the distractor (mean difference 7.4%), *t*(12) = 3.87, *p* = .002, and remapped location (7.7%), *t*(12)= 3.42, *p* = .005. Given that that the distractor and control locations are on either side of the saccade target, it seems that a less luminous colour singleton on one side receives less attention than a more luminous control object on the other side. In the red stimuli condition, performance was no longer better at the control than at the distractor, but a marginally significant difference favouring the distractor was observed (5.9%), *t*(12) = 1.88, *p* = .084. Discrimination capability was also significantly better at the distractor than at the remapped location (8.9%), *t*(12) = 3.89, *p* = .002. A more luminous green distractor was therefore seen to receive more allocated attention than its less luminous red counterpart (8.4%), *t*(12) = 3.08, *p* = .01. Furthermore, we did not see any evidence of the changes in distractor salience impacting upon performance at its remapped location (difference between the remapping of a red and green distractor (0.1%), *t*(12)= .07, *p* = .943. The differences in performance seen at the distractor, when this was either red or green, did not translate into any difference in facilitation at its respective remapped location (see Figure 11).

# Chapter 3

# Study 2: Race to accumulate evidence for saccade decision: an exception to speed-accuracy trade-off

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The increase in number of alternatives is directly proportional to the increase in time required to respond (Hick's law). Lawrence and colleagues report an exception to this law, whereby increased alternatives lead to shorter saccadic reaction times (SRTs), and an important accumulator model by (Usher & McClelland, 2001) predicts specific instances where this is expected. In the current study we aim to replicate the original controversial findings and compare them to the model's predictions by observing error rates and saccade distribution. Two experiments were conducted where humans made rapid eye movements to one of few or many alternatives. In Experiment 1 the saccade target was an onset that appeared at one of few or many possible locations. Participants started either with few or many targets and then alternated between conditions. An anti-Hick's effect emerged only when participants had started with a small set size block. In Experiment 2 placeholders were displayed at the possible target locations and independent groups were used. In addition to location uncertainty we added a time jitter to also have temporal uncertainty of saccade target appearance. A reliable anti-Hick's effect in SRTs was observed. However, results did not meet the model's predictions: anticipations and false direction errors were never more frequent when the set size was larger and SRT differences between the two set size conditions were not more pronounced at the slower end of the distributions. With the simple speed-accuracy trade-off proposed by the model not sufficing, we discuss inhibition-based alternative explanations.

Puntiroli, M., Tandonnet, C., Kerzel, D., & Born, S. (minor revisions). Race to accumulate evidence for saccade decision: an exception to speed-accuracy trade-off, *Journal of Exp Brain Res*.

## Introduction

In simple choice reaction time tasks, a predominant finding is that reaction times increase linearly with the logarithm of the number of response alternatives, a regularity known as Hick's law (Hick, 1952; Hyman, 1953). From early on, Hick's law has been modelled with different computational approaches. A more recent example comes from Usher and colleagues (Usher & McClelland, 2001; Usher, Olami, & Mcclelland, 2002) who developed an accumulator model, simulating the time it takes to reach a decision by assuming several competing units, each accumulating sensory evidence for one of the different response alternatives. A decision is ultimately made when activity in one of the units "wins the race" by reaching a threshold, leading to the execution of the corresponding motor response. Because accumulation is also driven by sensory noise and its rate is variable, sometimes the wrong accumulator unit reaches threshold first, leading to a premature, incorrect response. With a larger set size, that is, a larger number of incorrect response alternatives in the competition, the likelihood that one of those beats the correct response alternative to threshold is higher than with fewer response alternatives. Usher and colleagues (2001; 2002) suggested that Hick's law may be explained by a strategic raise in threshold with more response alternatives to counter this higher risk for error. If the response threshold is raised, the likelihood that the correct accumulator unit wins the race increases, as on a longer time scale, the accumulation of target evidence should eventually exceed any accumulation of noise. This increase in threshold comes at the expense of reaction time, though. In other words, Usher et al. (2001; 2002) postulate that Hick's law is the result of a simple speed-accuracy trade-off and participants' effort to maintain error rates at a constantly low level across set size conditions.

Although generally a robust finding, violations of Hick's law have also been reported in the literature. For instance, in a series of studies, Lawrence and colleagues (Lawrence, St John, Abrams, & Snyder, 2008; Lawrence, 2010; Lawrence & Weaver, 2011) measured eye movement reaction times in both monkeys and humans in a simple target selection task. Gaze was initially maintained on a central fixation stimulus that was surrounded by placeholders, one of which became the saccade target. Across blocks, they varied set size, that is, the number of saccadic response alternatives by varying the number of initial placeholders. Contrary to Hick's law, they found *faster* saccadic reaction times (SRT) with larger set sizes, an observation they termed an anti-Hick's effect. Experiments without placeholders were also conducted, where only the number of possible locations for the saccade target was varied across blocks, giving the same results. The authors tentatively framed their findings in terms of inhibition acting on initial motor preparation. When there are only few response alternatives, all of them are strongly pre-activated. However, while waiting for the saccade target to be revealed, inhibitory mechanisms are engaged to preclude premature execution of a saccade. Overcoming this inhibition comes at the cost of longer SRTs. Instead, when there are many possible target locations, there is less or no motor preparation of the different response alternatives in the first place, leading to weaker or no inhibition, and in turn to faster SRTs.

Interestingly, Usher and McClelland (2001; pp 582) describe an alternative, purely stochastic explanation of how anti-Hick's effects may occur. They note that in one of their tested computational models, faster reaction times with more response alternatives are to be expected when the same threshold criterion is used across set size conditions. As indicated above, similar thresholds should lead to more errors with larger set sizes as the likelihood that one of the incorrect response alternatives wins the race to threshold increases. However, it also follows that there should be fewer trials at the slow end of the RT distribution for correct trials: If target evidence accumulates slowly on a given trial (potentially leading to a slow, but correct response when only few response alternatives are present), the likelihood that one of the incorrect response alternatives reaches threshold prematurely is higher than when target evidence accumulates fast. Those trials, instead of becoming correct trials with long RTs, will thus more often end up as error trials, in particular, false direction and/or anticipation trials. Consequently, mean RTs on correct trials will be overall *faster* with increasing set size. In sum, Usher and McClelland's (2001) simple race model explanation makes very specific predictions for anti-Hick's effects: higher error rates with larger set sizes, along with a decreasing proportion of slower responses in the RT distribution for correct responses.

Our goal in the current study was two-fold: Our first aim was to replicate Lawrence and colleagues' (Lawrence et al., 2008; Lawrence, 2010; Lawrence & Weaver, 2011) anti-Hick's effect which, so far and to our knowledge, hasn't been confirmed in the literature by other labs. Second, we further explore error rates, specifically anticipation and false direction errors (Experiments 1 and 2) and reaction time distributions (Experiment 2) across set size conditions to see whether the predictions of Usher and McClelland's (2001) simple stochastic explanation could explain the anti-Hick's effect, or whether a more complex explanation, for instance in terms of inhibition, may be needed.

## Experiment 1

Following the design of Lawrence and colleagues (2008), we compared blocks with two vs. six saccadic response alternatives in a within subjects design in Experiment 1.

### Methods

#### *Participants*

Eighteen students from the University of Geneva, ranging between 18-33 years of age, were tested in the experiment. All were naïve as to the motives of the study.

#### *Apparatus*

The experiment was written in Matlab 2011b (The MathWorks Inc., Natick, MA) using the Psychophysics and Eyelink Toolbox extensions (Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007) and run on a Dell Optiplex 755 system. The stimuli were displayed on a 21'' CRT monitor (NEC MultiSync FE2111SB), which ran on 85 Hz and was set to 1280 x 1024 pixels and viewing distance was 70 cm. The EyeLink1000 desk-mounted eye tracker was used to record eye movements (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 1000 Hz. Participants were seated in a dimly lit room and placed their head within a fixed chin and forehead rest. Movements from the right eye were recorded for all participants bar one.

***Stimuli***

Displayed on a dark grey background (5 cd/m$^2$), the fixation stimulus was an open grey circle (14 cd/m$^2$) of 1.5° radius (pen width 0.33°) while the saccade target was a red circle (8 cd/m$^2$) of the same size at an eccentricity of 10° eccentricity from the center of the screen.

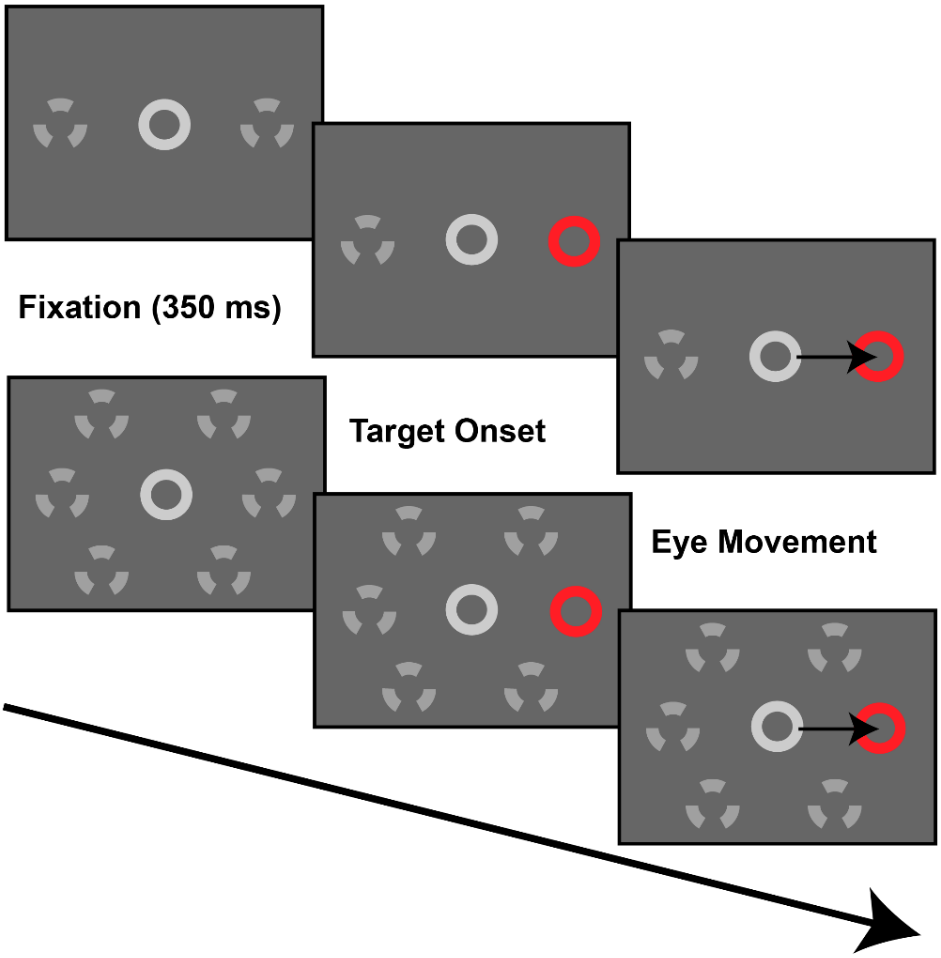

**Figure 1. Procedure in Experiment 1.** The central light gray circle is the fixation stimulus and the dashed grey circles denote locations where the saccade target could appear (not visible during the experiment). In red is depicted the saccade target, which appeared unpredictably in any of the two or six locations within a block of trials.

### *Design and Procedure*

Figure 1 illustrates the sequence of events in Experiment 1. Participants were instructed to maintain gaze on the central grey circle for 350 ms. After this fixation period, the red saccade target circle appeared abruptly at one of either two or six possible locations (blocked), requiring participants to move their gaze as fast and accurately as possible towards it. Preliminary analysis of eye movement data was carried out after each trial and a feedback screen indicated if anticipations, breaks of fixation, saccades in the wrong direction or if no saccade was detected (see below for criteria). At the end of a trial, the participant pressed the spacebar to commence a new trial. All participants took part in both set size conditions, performing three blocks of 60 trials in each (360 trials total). One group of participants started with a block with two possible target locations, another started with a block with six possible target locations. Both groups proceeded by alternating between set size conditions across blocks.

## Results

### *Trial exclusion*

To ensure that any differences we observed were due to set size effects and not affected by different saccade directions, we first excluded all trials from the larger set size condition where the saccade target was presented at another than the two locations also used in the small set size conditions. That is, only trials were analyzed in which the target was presented on the horizontal meridian, either left or right from fixation (180 trials in the small set-size and 60 trials in the large set-size). From those, another 8.7% of trials were excluded either because the saccade starting point deviated more than 1.5° from the center of the screen (break of fixation), the saccade landed more than 5° from the center of the saccade target, the SRT was above 500 ms, or because of technical issues.

Trials were marked as anticipations if latency was below 80 ms. False direction errors were defined as trials in which the saccade’s direction deviated more than 30° away from the direction of the target.

Anticipations and false direction trials were excluded from the SRT comparisons, but analyzed separately (see section 2.2.3).

### ***Saccadic Reaction Times***

Median SRTs for correct trials are illustrated in Figure 2A. A 2*3*2 Mixed ANOVA was performed, with two levels for set size (two vs. six possible target locations; within subjects), three levels for block (first, second or third block within a given condition; within subjects), and two levels for order, to see whether performance was affected by beginning the task with a block of two vs. six response alternatives (between subjects). Neither the main effect of set size, $F(1,16) = 0.63$, $p = .441$, partial $\eta^2 = .038$, nor the main effect of order was significant, $F(1,16) = 0.05$, $p = .820$, partial $\eta^2 = .003$. There was a marginally significant main effect of block number, $F(2,32) = 3.22$, $p = .057$, partial $\eta^2 = .168$, and a marginally significant interaction between set size and order, $F(1,16) = 3.89$, $p = .066$, partial $\eta^2 = .196$. None of the other two-way interactions was significant, F*s* < 1.65, *p*s > .208. But there was a significant three-way interaction, $F(2,32) = 3.97$, $p = .029$, partial $\eta^2 = .199$.

Following up on this interaction, separate ANOVAs for the two participant groups revealed that for participants starting with two response alternatives (left graph in Figure 2), there were no significant main effects, *F*s < 0.80, *p*s > .396, but a significant two-way interaction between set size and block, $F(2,16) = 3.65$, $p = .049$, partial $\eta^2 = .313$. Post-hoc tests indicated there was no statistical difference between set size conditions in the first or second block, *t*s(8) < 0.50, *p*s > .634. However, the third time a subject was presented with blocks of two or six possible target locations a significant difference in SRTs favouring the six possible target condition was observed, $t(8) = 2.43$, $p = .041$. This comparison was the only occurrence of an anti-Hick's effect in the data of Experiment 1 and it suggests that the anti-Hick's effects built up slowly across trials, at least in one group of observers. In contrast, Lawrence et al. (2008; 2010; 2011) never observed an effect of learning. Experiment 3 performed by Lawrence et al. (2008) bears the strongest resemblance to the current experiment, and was carried out on six participants, which were a mix of students and university employees, one of whom was the author.

Perhaps a likely familiarity with the task and previous training would have counteracted any effect of learning.

In contrast, for the participant group starting with six response alternatives, no significant interaction was observed, *F*(2,16) = 2.26, *p* = .136, and there was also no significant main effect of set size, *F*(1,8) = 3.37, *p* = .103, but only a significant main effect of block, *F*(2,16) = 5.97, *p* = .012, partial $\eta^2$ = .427, indicating a general speed-up of responses across blocks.

In sum, we could only partially replicate Lawrence and colleagues' (Lawrence et al., 2008; Lawrence & Weaver, 2011; Lawrence, 2010) anti-Hick's effect: we observed faster reaction times with a larger set size only when participants had started with a small set size block, and even then the difference only developed at the end of the experiment, that is, when comparing the last pair of blocks. Note also, however, that we did not observe any reliable Hick's-like pattern, which is, increasing SRTs with a larger number of response alternatives in any of our comparisons. Although Figure 2 shows slightly faster SRTs with two vs. six response alternatives in the first and third block for the group starting with set size six, these differences were not sufficiently reliable to result in any significant effects or interactions.

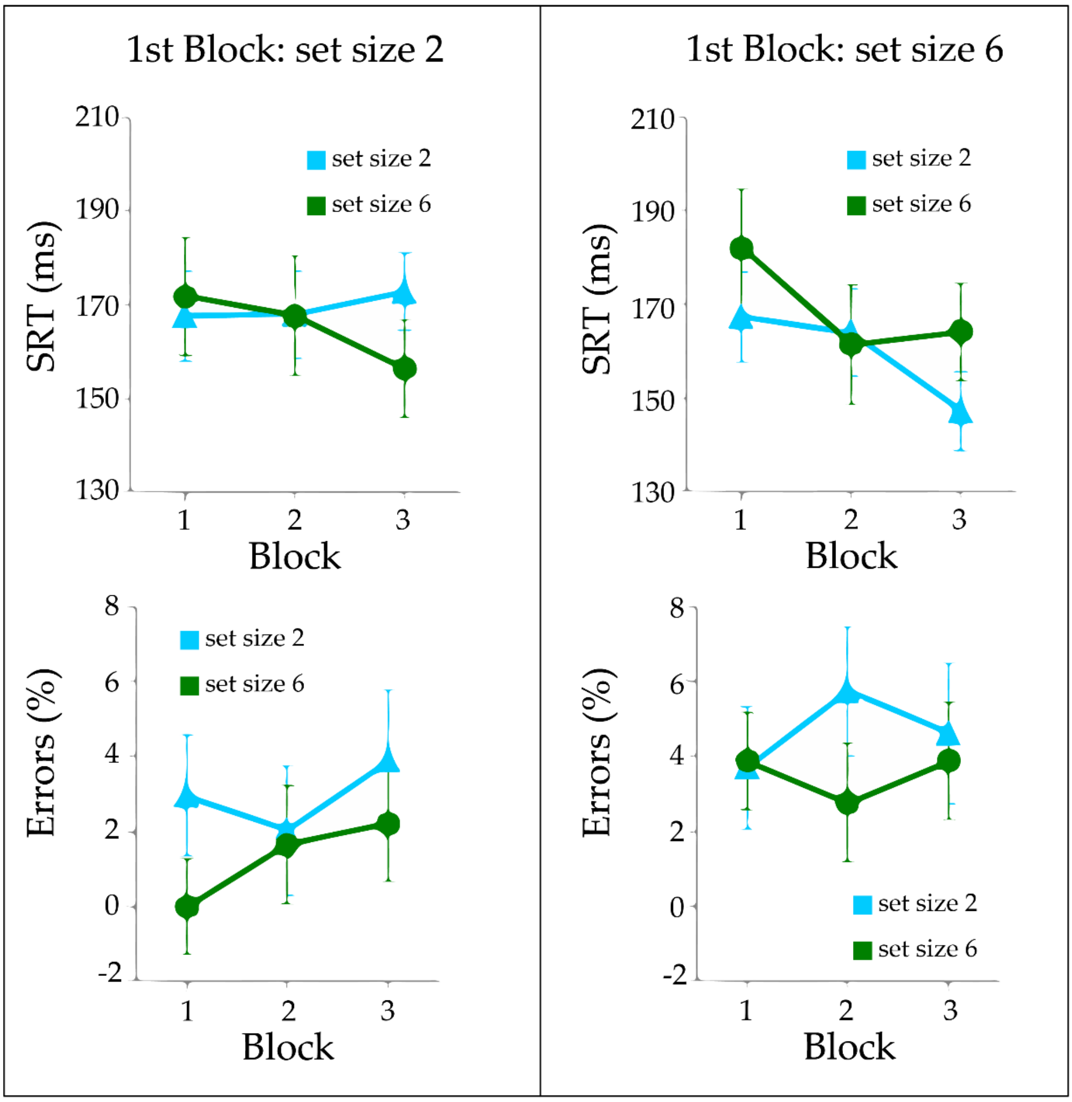

**Figure 2. Results of Experiment 1.** The different columns compare the data (saccadic reaction times on correct trials and percentage of errors: anticipations and false direction) across the two participant groups starting with two (left column) or six (right column) response alternatives. Set size conditions (blue: two, green: six) are compared for each of these groups across the duration of the experiment (first, second or third block within each set size condition).  Error bars: standard error of the means.

### *Anticipations and false direction trials*

Figure 2 (lower panels) illustrates the percentage of anticipations and false direction trials across conditions. Equivalent to the SRT analysis, we conducted a 2*3*2 Mixed ANOVA, including the factors set size, block and order. Only a marginally signficant main effect of set size was observed, *F*(1,16) =

3.53, *p* = .079, hinting at a slightly higher rate of anticipations and direction errors with the smaller set size. No further effect or interaction approached significance, *F*s < 1.45, *p*s > .242. Thus, error rates did not mirror the SRT results as Usher & McClelland's race model account predicted.

## Experiment 2

In Experiment 1, we observed an anti-Hick's effect only when participants had started with a small set size block. It has been shown that the way a motor task is initially approached may affect subsequent conditions (e.g. see Tandonnet, Burle, Vidal, & Hasbroucq, 2014). Therefore, using a within subjects design and alternating set size blocks may not have been ideal to obtain a strong effect, despite Lawrence and colleagues reporting the anti-Hick's effect even in a within-subjects design. In Experiment 2, we therefore employed a between subjects design with two set size groups.

### Methods

In total, 30 participants were tested in Experiment 2 with age ranging from 18-35 years. Apparatus and stimuli remained as in Experiment 1 with the following exceptions: Placeholders of the same size, colour and luminance as the fixation stimulus were displayed from the beginning of a trial at each of the possible saccade target locations. This would make the eye movement locations immediately obvious and drive saccade planning from the experiment onset, thus bypassing the learning period observed in Experiment 1. A between subjects design was employed, where each participant carried out only three blocks with either two or six response alternatives. Gaze was to be initially maintained on the central fixation stimulus for 800-1200 ms, after which one of the placeholders turned red to mark the saccade target.

## Results

### *Trial exclusion*

Again, only trials with targets presented on the horizontal meridian were kept for analysis. From those, another 12.6% of trials were excluded due to breaks of fixation, saccade amplitude errors, late or missed saccades, or technical issues (see section 2.2.1. for criteria).

### *Saccadic reaction times*

Figure 3 illustrates the results of Experiment 2. A 3*2 mixed ANOVA was carried out, where block was the within-subjects factor with three levels, and set size the between-subjects factor with two levels. There was a significant main effect of block, *F*(2,56) = 3.63, *p* = .033, partial $\eta^2$ = .115, reflecting an overall speeding up of responses across blocks, and a significant main effect of set size, *F*(1,28) = 4.89, *p* = .035, partial $\eta^2$ = .149. Figure 3A illustrates that this effect was due to an anti-Hick's pattern: SRTs were faster with the larger set size. The interaction was not significant, *F*(2,56) = 0.59, *p* = .559.

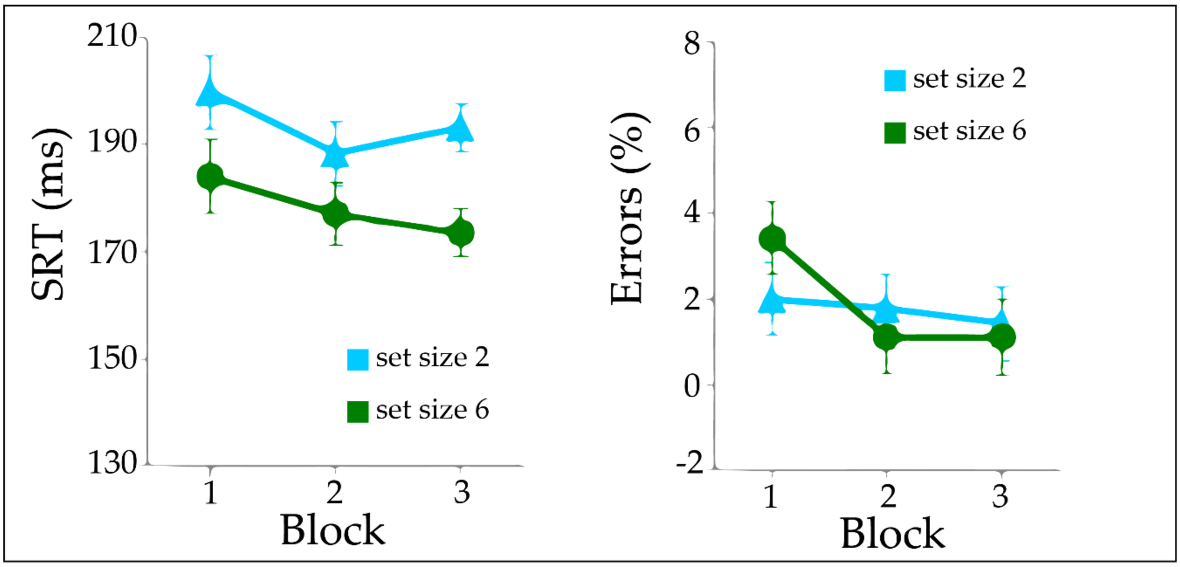

**Figure 3. Results of Experiment 2.** Saccadic reaction times on correct trials and error percentages (anticipations and false direction trials) in the grouped set size conditions (blue: two, green: six) are compared across the three blocks of the experiment. Error bars: standard error of the means.

### *Error trials*

An ANOVA equivalent to the SRT analysis on the percentage of anticipations and false direction trials only revealed a marginally significant main effect of block, *F*(2,56) = 2.48, *p* = .093, partial $\eta^2$ = .081, reflecting a slightly decreasing error rate across blocks. The main effect of set size, *F*(1,28) = 0.03, *p* = .871, and the interaction, *F*(2,56) = 1.27, *p* = .288, did not approach significance. Thus, similar to Experiment 1, the error rates did not mirror the SRT results. More specifically, the anti-Hick's effect in SRTs was not accompanied by a higher error rate for the larger compared to the smaller set size.

### *SRT distributions*

As we obtained a stable anti-Hick's effect in all three blocks of Experiment 2, we were able to also explore SRT distributions for correct trials. For each participant, SRTs of all blocks were collapsed and we calculated percentiles, comparing the 10%, 30%, 50%, 70%, and 90% cut-off of the individual distributions. Figure 4 illustrates the mean cut-off points across participants in the two groups. For all percentiles, the cut-offs in the smaller set size group were reached at faster SRTs. A 2*5 mixed ANOVA including the factors set size (between subjects) and percentile (within subjects) revealed an unsurprising main effect of percentile, *F*(4,112) = 268.40, *p* < .001, partial $\eta^2$ = .906, but also a significant main effect of set size, *F*(1,28) = 4.74, *p* = .038, partial $\eta^2$ = .145. The interaction was not significant, *F*(4,112) = 0.36, *p* = .834, indicating that faster SRTs in the larger set size condition were not restricted to the slow end of the distributions, as might have been expected from the predictions of a simple race model account. This was further confirmed in an additional analysis for which we fitted normal cumulative distribution functions to the data of each participant, and then compared the mean and variance parameters across the two groups. The mean parameters $\mu$ of the fitted distributions differed significantly in the two groups, (set size 2: mean $\mu$ = 205 ms, set size 6: mean $\mu$ = 188 ms), *t*(28) = 2.52, *p* = .018, confirming that the distributions in the larger set size condition were shifted towards faster SRTs. In contrast, the variance parameters $\sigma$ did not differ significantly (set size

2: mean σ = 49.55, set size 6: mean σ = 44.19), *t*(28) = 1.34, *p* = .193, confirming a similar shape of the distributions across groups, that is, a largely parallel shift of the two distributions.

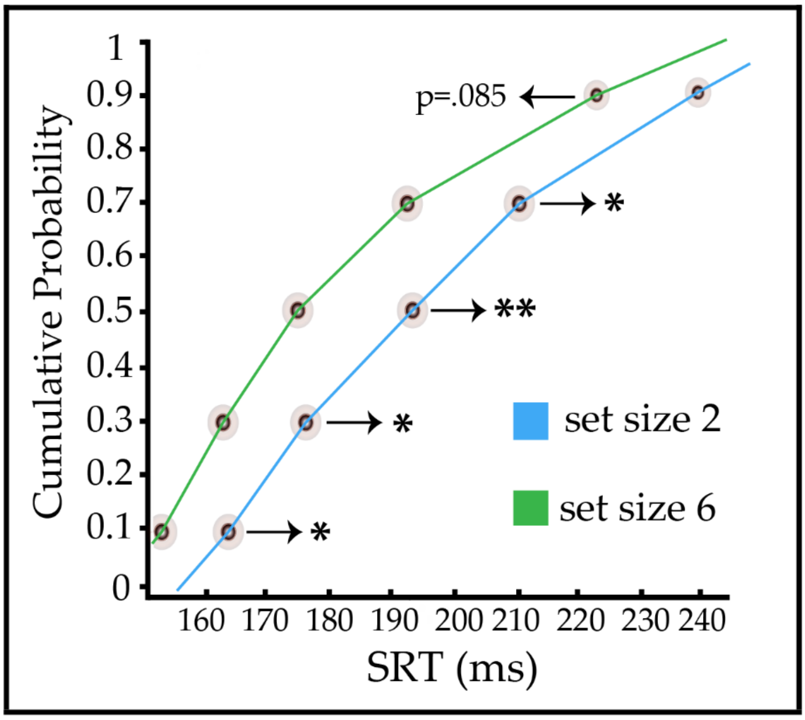

**Figure 4. SRT distributions in Experiment2.** Cut-off points at the 10%, 30%, 50% 70% and 90% percentile compared across the grouped set size conditions (blue: two, green: six). Significance star is for *p*<.05, two stars is for *p*<.01.

## General Discussion

In two experiments, we aimed at replicating the anti-Hick's effects, that is to say, a speeding up of saccadic reaction times when faced with a larger number of response alternatives, as reported by Lawrence and colleagues (Lawrence et al., 2008; Lawrence, 2010; Lawrence & Weaver, 2011). We further explored whether the effect could be explained by a simple speed-accuracy trade-off as proposed in an accumulator race model (Usher & McClelland, 2001). Employing a within subject-design without placeholder (Experiment 1), we only found an anti-Hick's effect in the last block of the participant group starting with a small set size block. In contrast, with a between-subject design with placeholders (Experiment 2), we found a reliable anti-Hick's effect in SRTs. However, anticipations and false direction errors were never more frequent in the larger set size condition and a distribution analysis for correct trials showed that the SRT differences in the two set size conditions were not restricted to, or more pronounced at, the slower end of the distributions. Thus, although Usher and McClelland's (2001) accumulator race model offers an appealing and simple explanation for the potential occurrence of anti-Hick's effects, our results were not in line with its prediction and we conclude that a more complex explanation might be needed to explain the effect under the present conditions.

We see that the anti-Hick's observation is a reproducible effect, despite it being in stark contrast with entire bodies of literature (visual search, heuristics and visual attention are all but a few). In fact, having to act upon, or decide between, fewer stimuli almost ubiquitously leads to shorter reaction times and Lawrence (2010) reports conditions where the effect does not emerge (i.e. endogenous saccades). Churchland & Ditterich (2012) report that when the number of response alternatives is increased, the level of uncertainty is also increased, requiring the brain to accumulate more evidence before the decision is reached. The current findings, coupled with those of Lawrence and colleagues, suggest that exceptions do exist. It has been suggested that when the alternatives are many then the cost to decision time can be mitigated by temporal pressure (Churchland et al., 2008), thus rendering SRTs in this condition equal, or even faster, than its few alternative counterparts. However, there was no added time pressure for the larger set-size in the current study, and any such pressure would likely come at the expense of accuracy, in terms of errors (see Brown, Steyvers, & Wagenmakers, 2009, for speed-accuracy trade-offs). We saw that the speeding up of responses for a larger set-size did not lead to an increase in error rate.

The distribution analysis highlighted that the difference between large and small set sizes was present from the fastest trials to the slowest trials. This means that all saccades fast and slow reached threshold quicker when the set size was larger. Numerous studies have investigated movement initiation times in relation to states of motor readiness and distance to threshold. Reddi & Carpenter (2000) applied the accumulator model framework to eye movements and showed that the entire distribution is shifted towards faster responses when a sense of urgency is placed on movements. This highlighted that changes in the movement preparation phase can lead to distribution shifts. Neuronal firing rates in the lateral intraparietal area (LIP) for eye movements made to few or many alternatives were directly compared  by Churchland et al. (2008). The authors observed higher firing rates for the few-alternatives task, particularly at the initial preparatory stage before the actual target had been revealed. Very similar results have been obtained through measuring neuronal activity in the superior colliculus (M. a Basso & Wurtz, 1998), suggesting higher preparatory activity in both brain structures is associated with fewer alternatives. Thus, there is consensus in the literature that when the possible motor alternatives are few, movements are planned and the accumulation of activation begins closer to threshold; when instead the alternatives are many, it is potentially too costly to compute all of them, therefore little or no planning takes place.

Given these observations, it seems reasonable to assume that an explanation of the current effects should be centred on the small set-size condition, as few response alternatives have been seen to increased brain activity and that their well-documented advantage did not take place in our study. In different studies, it has been shown that when movements are being prepared the corticospinal pathway is highly involved in activating inhibitory components which assure execution is not triggered prematurely (for a review see Cohen, Sherman, Zinger, Perlmutter & Prut, 2010). This mechanisms has been named global inhibition, and the key notion here is that the movement must be temporarily inhibited while our senses continue to process and accumulate external information. Perhaps this was the inhibitory process Lawrence et al. (2010) were alluding to; a process that is linked to the planning of movements when the set size is small and that has a detrimental effect on movement initiation.  It was recently shown by Wessel, Reynoso, & Aron (2013) that suppressing saccades reduced corticospinal excitability of hand movements. This constituted strong evidence that eye movement activity can produce global motor effects (see also Cai, Oldenkamp, & Aron, 2012; Majid, Cai, George, Verbruggen, & Aron, 2012). In line with Cohen et al.'s (2010) notion of global inhibition emerging at the planning phase, perhaps planning eye movements while in settings requiring high levels of motor control, is sufficient to activate global inhibition, which could be related to anti-Hick’s effects. A study found increased activity in the sub thalamic nucleus of the basal ganglia, an area with direct connections to the corticospinal pathway, in saccade-countermanding and NoGo tasks (Isoda & Hikosaka, 2008). There is therefore support for the view that a high-levels of control during eye movement preparation is achieved thanks to activity in the corticospinal pathway, which is common to other limb movements. This activity temporarily inhibits movements and may be the process that is added to the otherwise beneficial preparation seen for small set sizes.

In conclusion, the current study provides evidence for the controversial finding that a larger number of alternatives can reliably lead to reduced SRTs. By comparing error rates and saccadic distributions it became clear that the predictions made by the Usher and McClelland (2001) accumulator model, based on speed-accuracy trade-off, could not account for our findings. We believe that a process such as global inhibition that can become activated during the movement planning phase could be a candidate to account for the findings, particularly in conditions requiring high control and a strong stimulus-response pairing. Future investigations will be needed to determine whether other limb movements or cognitive activity are temporarily suppressed in instances when the anti-Hick’s effect emerges and to map out its neurophysiological underpinnings.

# Chapter 4

# Study 3: Objects and their arrangement affect Visual Attention before Eye Movements

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Visual elements at the location where the eyes will land undergo preferential processing. It is widely believed that a copy of the saccadic motor command (efference copy) is sent to the structures of the brain adept at processing perceptual information before an eye movement is initiated. We ask whether saccade metrics alone determine the locations selected for preferential processing or whether visual objects presented at, and around, the eye movement landing-point also affect the distribution of attentional resources. In a series of experiments the location of visual objects and their time of presentation was manipulated. A dual-task was employed requiring humans to perform eye movements either to a target or an empty location, and to discriminate a briefly flashed probe presented at one of three locations. Preferential processing of the saccade target only occurred when visual objects (placeholders) were displayed at the tested locations simultaneous to the presentation of the perception target, while the absence of visual objects led to a fairly even distribution of attention across probed locations. This was due to the objects having a masking effect that hindered perception of peripheral locations which was overcome by the pre-saccadic shift of attention. When objects were displayed at non-tested locations their arrangement also affected the distribution of visual attention. Overall the findings suggest that the shift of attention before eye movements does not rely only on saccade metrics, but objects and their arrangement also play a crucial role. The observed effects revolved around noise exclusion and not signal enhancement.

*This chapter presents unpublished material currently in preparation*

## Introduction

To explain how we, as humans, perceive the world, it is vital to understand how our visual system attributes importance to certain aspects of the visual scene over others. When a location is selected over another it undergoes in-depth processing, allowing its fine visual details to be acquired. The allocation of processing resources is accomplished by visual selective attention and often occurs automatically, against the observer's top-down intentions (e.g. Awh, Belopolsky, & Theeuwes, 2012; Gayet, Paffen, Belopolsky, Theeuwes, & Van der Stigchel, 2016; Hickey, McDonald, & Theeuwes, 2006; Hickey, van Zoest, & Theeuwes, 2010; Burra & Kerzel, 2013). Moreover, attentional selection has been shown to be intrinsically tied to the planning and execution of eye movements, which has led to the postulation of prominent theories such as the premotor theory (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). Just before an eye movement is made attention is necessarily shifted to the location where the eyes will land (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Hoffman & Subramaniam, 1995) regardless of the observer's goals (Puntiroli, Kerzel, & Born, 2015). This pre-saccadic shift of attention, has been linked to the mechanisms that ensure we see the world as a stable and coherent whole around us, and not a as a series of snapshots constantly moving and changing on our retina (as discussed in Deubel, Bridgeman, & Schneider, 1998; McConkie & Currie, 1995; Zirnsak, Steinmetz, Noudoost, Xu & Moore, 2014). It has been shown that at the time immediately preceding the eye movement cognitive abilities are suppressed or impaired, such as mental imagery (Jonikaitis, Deubel, & de'Sperati, 2009), estimation of time duration (Morrone, Ross, & Burr, 2005), mental rotation (Irwin & Brockmole, 2000) and non-saccade-related visual processes (Brockmole, Carlson, & Irwin, 2002). While the reasons for these impairments are far from clear it is possible they occur in order to put full priority on the perception for action. In the time preceding the eye movement, attentional effects build-up and peak in the last tens of milliseconds just before the saccade (see Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011) highlighting the sheer influence the upcoming movement has on perception and cognition. von Holst and Mittelstaedt (1950) were the first to propose that for each eye movement, an efference copy is created (i.e., a copy of the motor command), with Hermann von Helmholtz (1867) planting the initial conceptual seeds. It has been suggested the efference copy allows us to anticipate the sensory changes of the movement and thus distinguish between self-induced retinal motion and motion in the external world (e.g., Deubel, Schneider, & Paprotta, 1998; Currie, McConkie, Carlson-Radvansky & Irwin, 2000; Melcher, 2009). While the exact mechanisms that allow the visual system to resolve this ambiguity are not yet understood, a neural pathway from a subcortical saccade-related area (the superior colliculus) to the frontal cortex (frontal eye field) has been identified whose neurons show a discharge pattern fulfilling the criteria for an efference copy signal (e.g. the signal originates in a motor structure, is time-locked to the eye movement and does not trigger the saccade; see Sommer & Wurtz, 2008a, 2008b). It is however unclear whether the pre-saccadic attentional shift simply reflects preferential processing at the end-point of the saccade vector, therefore purely driven by the motor command, or whether it is also shaped by the visual landscape. Visual landscape is defined here as the objects present in the visual field and their arrangement (i.e. the spatial relations they share). Since it has been argued that pre-saccadic shifts of attention may facilitate the maintenance of perceptual stability and continuity across saccades one would imagine attention to be highly concerned with, and therefore shaped by, the visual elements present in and around the end-point of the saccade vector. On the other hand, the pre-saccadic shift of attention may be a fixed process rigidly dictated by saccade metrics. We address the issue by asking whether the attentional shift simply anticipates the saccade in order to begin processing at the saccade landing point or whether the visual landscape also plays a major role in determining what gets processed and how much. If the pre-saccadic shift of attention is modulated by the visual landscape is that in order to enhance processing at a given location or to exclude noise from peripheral locations? Furthermore, the use of placeholders is ubiquitous when studying the distribution of attention and it was recently argued by Taylor, Chan, Bennett, & Pratt (2015) that their presence is oddly taken for granted in endogenous and exogenous cuing paradigms. This is particularly true for visual attention in relation to eye movements, where every single experiment to date (to the best of the author's knowledge) has made use of placeholders. To this purpose a series of experiments was conducted where we investigate discrimination performance (measured as % correct) before eye movements, in conditions where placeholders are either present at varying locations in and around the saccade target or not present at all.

# Experiment 1

We employed a dual-task paradigm very similar to those employed in previous pre-saccadic attention studies (e.g. Deubel & Schneider, 1996; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Rolfs et al., 2011) with the aim of determining whether attention is anchored to the saccade landing point only in the presence of a stable object to which it can bind, or whether the shift of attention is common to all saccades regardless of the visual landscape. We therefore presented participants with two conditions: one where eye movements were made towards a central placeholder and one where eye movements were made towards the empty screen center (see also Zimmermann, Morrone, & Burr, 2014), with no placeholders presented in or around it.

## Methods

### *Participants*

Data was gathered from 13 participants, eight of whom were female, who performed the task for a minimum of three to a maximum of five hours. This discrepancy in experiment duration depended on the error rate (explained in the "saccade rejection criteria" below), on the distribution of saccade latency, in order to obtain sufficient trials with a probe-saccade interval below 80 ms (described in the "Perceptual performance with short times between Probe and Saccade" section below) and on the saccade landing points, in order to bin trials based on the distance from the center of the target location. We aimed to achieve a minimum of 25 trials per experimental condition. The age of the participants ranged from 18-31 years of age and all were paid or given course credits for their efforts. Ethical consent for the project was awarded by the ethics committee of the University of Geneva and all participants gave their signed consent for participation. All reported normal or corrected-to-normal vision.

### *Apparatus*

The experiment was written in Matlab 2011b (The MathWorks Inc., Natick, MA) using the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Pelli, 1997; Kleiner et al., 2007) and run on a Dell Optiplex 755 system. The stimuli were displayed on a 21'' CRT monitor (NEC MultiSync FE2111SB, 40.5 x 30.3 cm), which ran on 85 Hz and was set to 1280 x 1024 pixels and viewing distance was 70 cm. The EyeLink1000 desk-mounted eye tracker was used to record eye movements (SR Research Ltd., Mississauga, Ontario, Canada) at a sampling rate of 1000 Hz. Participants were seated in a dimly lit room and placed their head within a fixed chin and forehead rest. Movements from the right eye were recorded for all participants bar one.

### *Design and Procedure*

The procedure of Experiment 1 is illustrated in Figure 1. On every trial, the fixation cross appeared 5 dva (degrees of visual angle) left from the center of the screen for 600 ms. Next, three dark grey placeholders (10.1 cd/m$^2$) of 0.8 dva radius appeared on a grey background (16.4 cd/m$^2$) in the placeholder Present condition: one at the center of the screen, one slightly above and one slightly below (both lateral placeholders at an angle of 30 deg of rotation from the central placeholder and at 5 dva from fixation). The empty placeholders remained on screen for 60 – 95 ms (59 – 94 ms given screen refresh rate), after which perceptual stimuli were flashed inside the three placeholders. Two of the perceptual stimuli were symmetrical crosses (0.8 dva per horizontal and vertical bar), while one was asymmetrical and could appear randomly at any of the three locations. This asymmetric cross served as the discrimination target (i.e. perceptual probe), with its vertical bar slightly shifted to the left or right. The initial shift offset was at 0.175 dva from the center and the maximal allowed shift was 0.4 dva. A 2-down 1-up staircase rule was employed throughout the experiment, with a step size of 0.025 dva and a minimum offset fixed at 0.025 dva if the staircase ran down to 0 dva. This procedure ensured discrimination across all trials at approximately 71 % correct for each participant. The perceptual stimuli were displayed for 50 ms (47 ms given screen refresh rate), followed by the empty placeholders which remained on screen for another 500 ms (494 ms given screen refresh rate). Once the eye movement was completed the observer stated with a key press (left or right directional keys) whether the flashed asymmetric cross had a leftwards or rightwards shift in the vertical bar. In the placeholder Absent condition, the procedure was identical, but no placeholders were displayed throughout the trial and participants were asked to move their eyes towards the screen center as soon as possible after the fixation crossed disappeared. The order of the blocks was counterbalanced across conditions and each block was made up of 90 trials. The participants were instructed that carrying out efficient eye movements (at the desired time and to the desired location) had priority over the perceptual discrimination task.

# Results

*Saccade Rejection Criteria*

Very conservative saccade rejection criteria were employed resulting in the exclusion of 34.4 % of trials collected. In particular, saccades whose landing point deviated more than 0.8 dva from the center of the screen, that is, the targeted saccade landing point in both object present and object absent conditions were excluded (6.7%). Trials were also excluded due to the saccade landing on a yet to be extinguished perceptual stimulus (12.7 %), anticipatory saccades with latencies less than 100 ms (9%), late saccades with latencies longer than 350 ms (2.4%), blinks and undetected saccades (1.9%), failure to maintain gaze on the fixation cross (usually attributable to poor calibration, 1.1%), and erroneous button presses (0.6%).

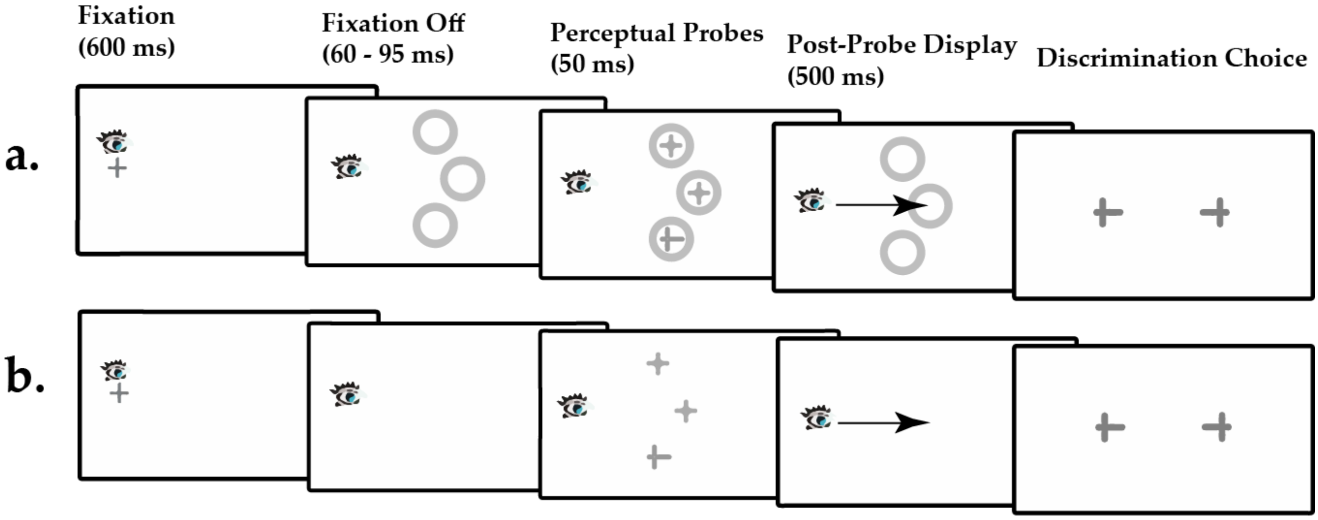

Fig 1. Flowcharts for the Present (a) and Absent (b) placeholder conditions with a description of each display and the duration in milliseconds. The fixation offset represented the trigger to initiate the eye movement. The perceptual probes were flashed for 50 milliseconds shortly before the eye movement, at a variable interval after the fixation offset (SOA 60 – 95 ms). The asymmetric cross functioning as the perceptual probe (i.e. the measure of attention) could appear at any of the three locations (lower location in the example).

*Perceptual performance*

We first sought to determine whether performance differed between the three Probe Locations (Saccade target, upper control and lower control) and between Object conditions (target objects displayed and target objects *not* displayed). A within-subjects ANOVA was performed and a significant main effect for Probe location, $F = (2, 24) = 6.01$, $p = .007$, partial $\eta^2 = .34$, and for Object condition, $F = (1, 12) = 20.20$, $p = .001$, partial $\eta^2 = .52$, emerged. The interaction between the factors was also found to be significant, $F = (2, 24) = 10.86$, $p < .001$, partial $\eta^2 = .49$, see Figure 2.

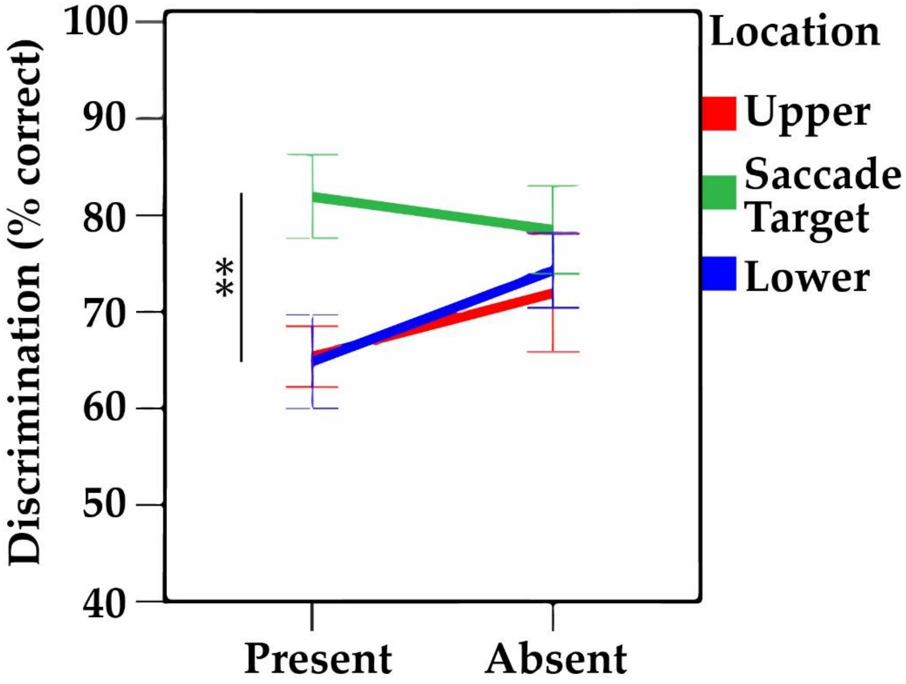

Figure 2. Discrimination performance at the three probed locations when the placeholders were Present and when they were Absent. Error bars represent the standard error, with scores adjusted for between-subjects variability for within-subjects effects (Bakeman & Mcarthur, 1996) following the method by (Cousineau, 2005). Asterisk indicates significance, where p-value is less than .001.

Separate one-way ANOVAs for the Present vs. Absent condition revealed no significant main effect of Location in the Absent condition, $F(2, 24) = 1.15$, $p = .334$, partial $\eta^2 = .09$. This suggests rather equal perceptual processing at the three locations when attention has no objects to bind to in the absence of a target. In contrast, there was a significant main effect of Probe Location in the present condition, $F(2, 24) = 14.3$, $p < .001$, partial $\eta^2 = .54$, highlighting the typical (e.g. Deubel & Schneider, 1996) spatially selective pre-saccadic shift of attention toward the saccade landing point when a target object is present. Follow-up paired t-tests highlighted a significant difference in performance between the saccade target and the lateral locations for the Present condition (mean difference with upper 16.8%, $t(12) = 4.79$, $p < .001$, $d = 2.76$; mean difference with lower 17.8%, $t(12) = 4.05$, $p = .002$, $d = 2.34$).

*Saccadic Reaction Time*

We examine median *saccade reaction time* (SRT) between the placeholders Present (155 ms) and Absent (183 ms) conditions. A paired-samples *t*-test highlighted a significant difference between latencies, $t(12) = 5.48$, $p < .001$. It is not surprising that it takes longer to initiate a saccade to an empty location. This, however, highlights the necessity to control for the time interval separating the perceptual probe from the saccade, since longer intervals associated with longer latencies may explain the lower performance at the saccade target in the "absent" condition.

*Perceptual performance with short times between Probe and Saccade*

To control for the different latencies, we repeated the analysis on perceptual performance looking at only the saccades initiated a short time after probe presentation. Deubel (2008) and Rolfs et al (2010) show that attentional benefits at the saccade target can begin as early as 250 ms and 170 ms respectively, and build up gradually till saccade onset. We therefore only looked at trials where the saccade was initiated within 80 ms after the perceptual probe's disappearance, so the attentional build-up at the saccade target should have been close-to maximal. A 3*2 within-subjects ANOVA confirmed the previous analysis: there was a significant main effect for Probe Location ($p = .008$) and for Object condition ($p < .001$), and importantly also a significant interaction between these factors ($p = .010$). Post-hoc t-test analysis confirmed significant differences in performance when the placeholders were present between the saccade target and the lateral locations (upper: $p < .001$; lower: $p = .003$), and no differences between the saccade target and the lateral locations when placeholders were not present (upper: $p = .304$; lower: $p = .260$).

*Saccadic Landing Points*

We examined the landing points along the X and Y axes for the object Present condition and the object Absent condition (see Figure 3, Left). Negative x-values indicate that the saccade amplitude was shorter than expected and negative y-values indicate that saccades deviated downwards. Performing a 2*2 within-subjects ANOVA highlighted a main effect for Object condition, $F(1, 12) = 116.79$, $p < .001$, partial

$\eta^2$ = .91, and for Measured dimension (X or Y), *F*(1, 12) = 48.76, *p* < .001, partial $\eta^2$ = .80, with the interaction also proving to be significant, *F*(1, 12) = 108.23, *p* < .001, partial $\eta^2$ = .90.

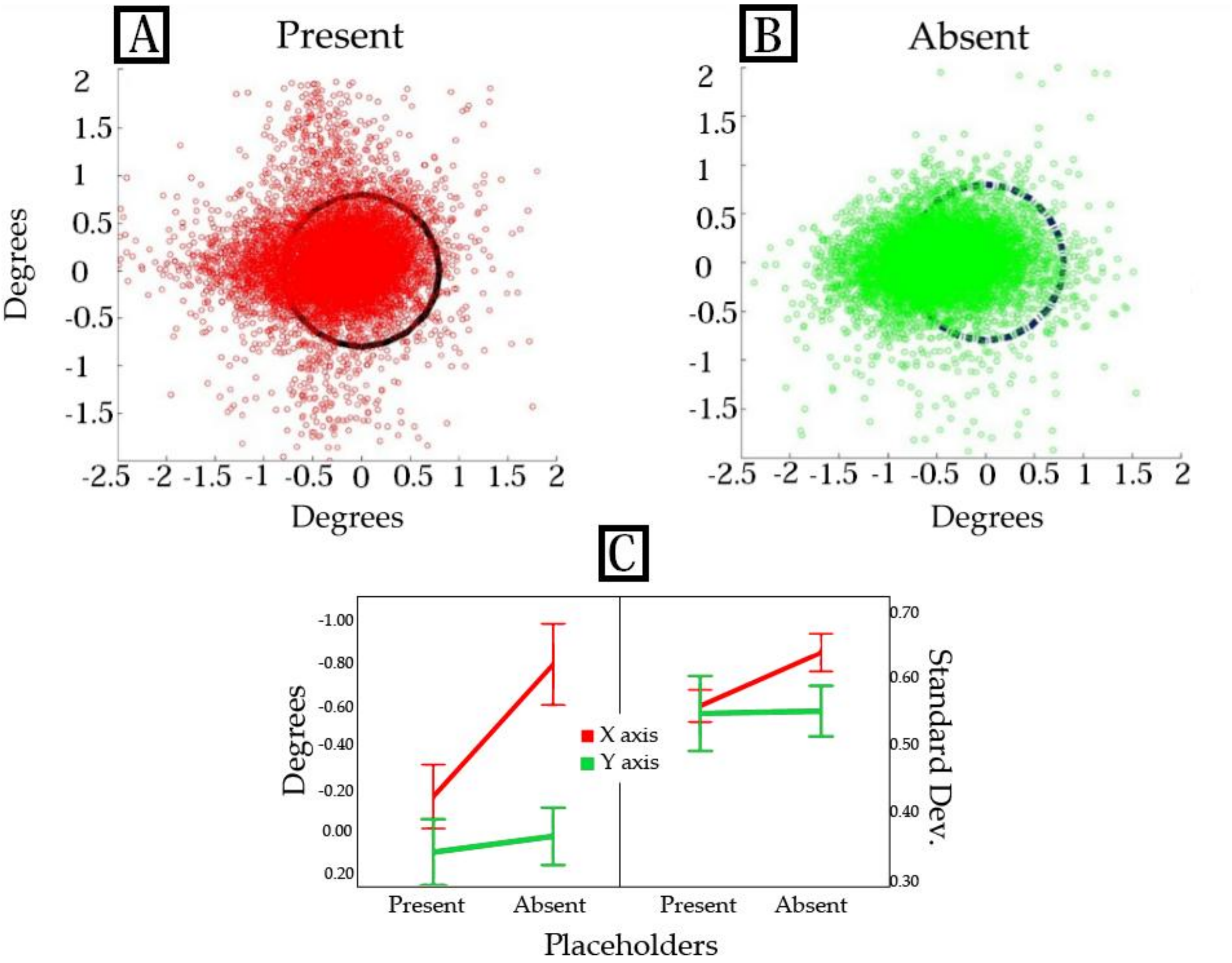

Figure 3. The graphs illustrate saccade landing points for both Present (A) and Absent (B) placeholder conditions. C, Left) Mean deviation of saccadic landing points in degrees between object presentation conditions for X and Y axis are figured in graph C. Value of 0 degrees indicates the center of the screen and therefore the center of the target in both conditions. C, Right) Mean standard deviation compared across conditions.

Post hoc analysis revealed a non-significant difference across conditions for mean landing points along the Y axis, *t*(12) = 1.6, *p* = .129, *d* = 0.92, while differences among conditions along the X axis were instead significant, *t*(12) = 16.8, *p* < .001, *d* = 9.7. This highlighted a larger systematic undershoot along the X axis in the object Absent condition. Analysis of the standard deviations revealed the same pattern of results (see Figure 3, Right), with a 2*2 within subjects ANOVA highlighting a significant main effect for Object condition, $F(1, 12) = 7.77$, $p = .016$, partial $\eta^2 = .39$, and for Measured dimension, $F(1, 12) = 5.3$, $p = .040$, partial $\eta^2 = .31$, and a significant interaction, $F(1, 12) = 13.95$, $p = .003$, partial $\eta^2 = .54$. Paired post hoc t-tests showed no significant difference in standard deviation between object presentation conditions along the Y axis, $t(12) = .18$, $p = .861$, $d = 0.1$, but a significantly larger spread of landing positions along the X axis (mean difference .14 degrees), $t(12) = 4.74$, $p < .001$, $d = 2.74$.

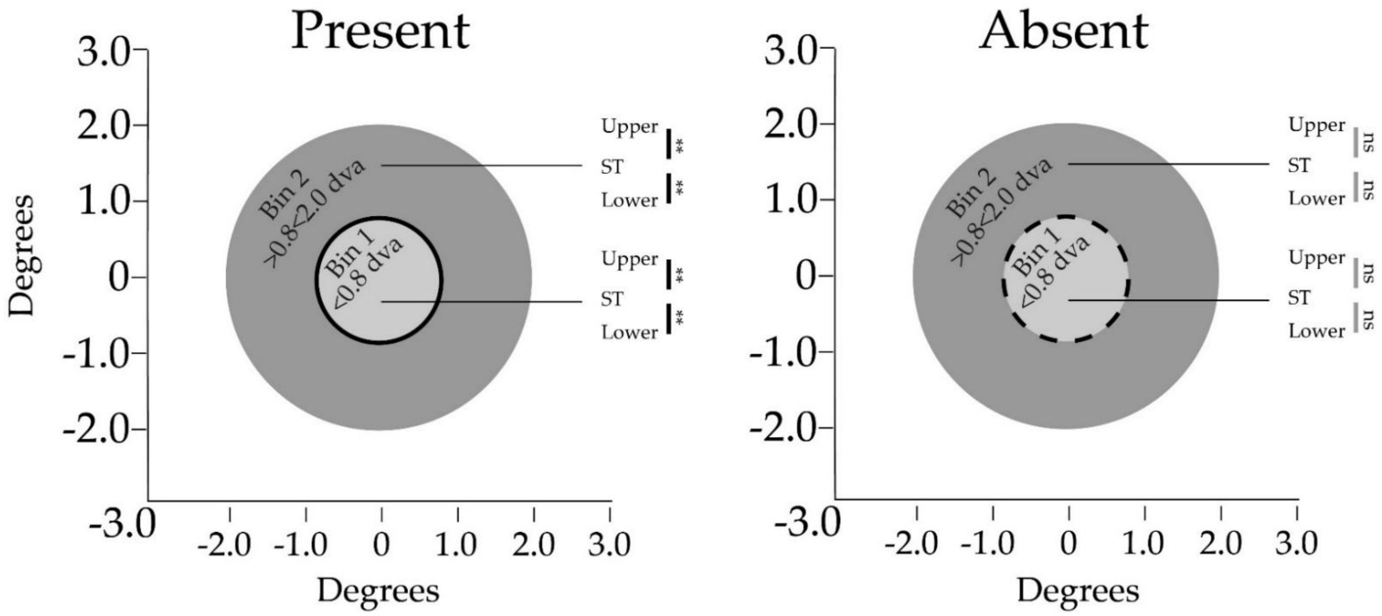

Figure 4. The graphs illustrate the relationship between perceptual performance and saccadic precision. Perceptual performance was compared between locations (upper placeholder, ST and lower placeholder), in both placeholder Present and Absent conditions, when saccades landed within 0.8 deg from the center (Bin 1) and when they landed within 0.8 to 2.0 deg from the center (Bin 2). Perceptual performance differences between ST and other placeholder locations were observed only in the Present condition, regardless of precision.

As stated, the saccade rejection criteria for landing-point precision was 0.8 dva from the center of the screen (corresponding to the center of the target circle in the Present condition and to the targeted saccade landing point in the Absent condition). The size of 0.8 dva also corresponded to the radius of the placeholders, with saccades that deviated from this generating an error message instructing participants to be more precise. We sought to examine perceptual performance in relation to the saccadic landing points, to determine whether differences in saccade precision were driving the effect. Trials were split into two bins based on saccade precision, based on the distance of the saccade landing point from the center of the screen (coinciding with the center of ST when this was present). Bin 1 grouped precise saccades that landed 0.8 deg or less from the center, while Bin 2 grouped less precise saccades landing in between 0.8 and 2 deg from the center (see Figure 4). Saccades included in these bins accounted for 96 % of trials. A 2*2*3 within-subjects ANOVA where the factors were Saccadic Landing point (2 levels, Bin 1 and 2), Placeholder condition (2 levels, Present and Absent) and tested Location (3 levels, Upper, ST and Lower) showed a significant main effect of Placeholder condition, $F(1, 12) = 24.92$, $p < .001$, partial $\eta^2 = .67$, and of Location, $F(2, 24) = 5.67$, $p = .010$, partial $\eta^2 = .32$, but no effect of Saccadic Landing Point, $F(1, 12) = 0.89$, $p = .364$, partial $\eta^2 = .07$. Once again a significant interaction between Placeholder condition and tested Location emerged, $F(2, 24) = 8.21$, $p = .002$, partial $\eta^2 = .41$, but no other interaction containing the Saccadic Landing point factor was statistically significant: 2-way interaction with Placeholder condition, $F(1, 12) = 0.44$, $p = .520$, partial $\eta^2 = .035$, 2-way interaction with tested Location, $F(2, 24) = 1.40$, $p = .266$, partial $\eta^2 = .10$, and 3-way interaction with Placeholder condition and tested Location, $F(2, 24) = 1.70$, $p = .204$, partial $\eta^2 = .12$.

### *Perceptual Difficulty*

The staircase procedure regulated the difficulty of the discriminability of the asymmetric cross by shifting the vertical bar, rendering the probe more or less discriminable as a function of participants' responses. We sought to assess possible differences across conditions in the extent to which the vertical bar shifted to see whether the visual landscape affected perceptual difficulty. The range of the shift was of 0.025 dva (minimal) and 0.400 dva (maximal). When the placeholders were present the mean shift was 0.123 dva while when no placeholders were displayed the mean shift was of 0.100 dva. A 2*3 repeated-measures ANOVA on the shift values per Object condition and Location (upper, saccade target, lower) highlighted a significant main effect for Object condition, $F(1, 12) = 14.29$, $p = .003$, partial $\eta^2 = .54$, no main effect of Location, $F(2, 24) = .60$, $p = .557$, partial $\eta^2 = .05$, and non-significant two-way interaction, $F = (2, 24) = 1.71$, $p = .203$, partial $\eta^2 = .12$.

## Discussion

Pre-saccadic attention was measured by means of a discrimination probe in conditions where placeholders were or were not present. While the presence of placeholders was seen to have a positive effect on saccade precision (see saccadic landing points) they were overall detrimental to the perceptual task: the shift in the vertical bar that defined the critical target asymmetry to be judged had to be much larger with than without placeholders to achieve an overall percentage of correct responses of 71%. The placeholders also changed how these 71% correct were distributed across placeholders: when no placeholders were presented, performance was equal at all locations. This strongly suggests that pre-saccadic attentional shifts are not dictated by the efference copy alone, rigidly allocating attention to the saccade landing-point. When instead placeholders were present, the typical pre-saccadic enhancement at the saccade target was found, with discrimination performance higher there than at the other two placeholder conditions. This means that the presence of the placeholders made it more difficult to discriminate the perceptual target at all locations and only the pre-saccadic shift of attention found at the saccade target gave this location an advantage over the others.  Overall, the results can be interpreted in two ways: 1) the presence of visual objects during the saccade preparation phase is necessary for the pre-saccadic attention shift to occur, signifying that a visual object is required to focus on, or 2) the placeholders have a detrimental effect on perceptual performance, producing either masking or crowding effects. In the latter case the placeholders could be acting as masks that reduce the visibility of the target stimuli without actually overlapping with them (known as lateral masking; Polat & Sagi, 1993) or they could be causing crowding, that is, the inability to recognize the target in the clutter produced by the surrounding stimuli (overview in Levi, 2008, and Whitney & Levi, 2011). A test between masking and crowding is presented in Experiment 4. To foreshadow, masking was found to more adequately explaining the results which is why we mention the crowding hypothesis less frequently. Instead, Experiments 2a and 2b aim to disentangle the two alternative interpretations, between the necessity to have an object to be focused on or placeholders being detrimental for in-depth processing at their location. We therefore examined whether the initial presence of placeholders during the saccade preparation phase triggers the difference in perceptual performance at the saccade target and the other locations (object selection hypothesis). Alternatively, the presence of placeholders at the tested locations at the time of the presentation of the perceptual stimulus, or thereafter, might have been crucial (detrimental object hypothesis). Common to both Experiments 2a and 2b, the placeholders were visible before target presentation in one condition, but not in another condition where they only appeared at target onset. Experiments 2a and 2b differed with respect to time after target offset. In Experiment 2a, the placeholders disappeared at target offset, whereas they remained on the screen in Experiment 2b. Thus, Experiments 2a and 2b disentangle forward and backward masking.

The following experiments employed the same apparatus, feedback and saccade rejection criteria to that used in Experiment 1. All analysis were carried out on data where the eye movement fell within 0.8 dva from the center of the screen (Bin 1 in Figure 4) and with a probe-saccade interval of < 80 ms (see "*Perceptual performance with short times between Probe and Saccade"* section in experiment 1). The analysis of the saccade landing-point bins was skipped, which greatly reduced the duration of the experiments to approximated 1.5 hours each.

# Experiment 2

### Method

Experiment 2 is subdivided into part A and B. Both experiments will present a comparison between two conditions (Stable vs. Transient, Stable vs. Late onset) and participants alternated between blocks of each condition, where the order of the blocks was counterbalanced between participants.

Experiment 2a: Twelve students from the University of Geneva participated, of which 7 were female. Years of age ranged from 21-32.The procedure is illustrated in Figure 5. Participants were instructed to prepare an eye movement to the central placeholder (Stable condition), or to prepare an eye movement to the middle of the screen (Transient condition), and to trigger the movement once the fixation cross disappeared. As before, they were also instructed to state at the end of the trial whether the asymmetric cross had the vertical bar displaced to the left or right.

Experiment 2b: In this experiment eight students from the University of Geneva participated, four of which female. Instructions remained the same as in Experiment 2a and again we had a condition with placeholders present from the beginning (Stable) and a condition where placeholders were presented only upon appearance of the perceptual stimuli (Late onset). The sole difference was that the placeholders did not extinguish after presentation, instead they remained on screen till after eye movement completion (see Figure 5).

## Results

### *Perception*

Perceptual performance was analyzed with 2*3 repeated-measures ANOVAs, with Placeholder condition (Stable, Transient/Late Onset) and probe position (upper, target, lower) as within-subject factors. Results are illustrated in Figure 5.

Experiment 2a: The analysis highlighted a main effect of Placeholder condition, $F(1, 11) = 7.52$, $p = .019$, partial $\eta^2 = .41$, and of Probe location, $F(2, 22) = 27.30$, $p < .001$, partial $\eta^2 = .71$, and the two-way interaction was not significant, $F(2, 22) = .96$, $p = .398$, partial $\eta^2 = .08$. Follow-up analyses confirmed better performance at the saccade target compared to the lateral locations for the Stable condition (upper control: $t(11) = 5.33$, $p < .001$, $d = 3.21$; lower control: $t(11) = 4.98$, $p < .001$, $d = 3.0$), and for the Transient condition (upper control: $t(11) = 5.09$, $p < .001$, $d = 3.07$; lower control: $t(11) = 3.34$, $p = .007$, $d = 2.01$). No difference emerged between the lateral locations in both Stable ($t(11) = 1.08$, $p = .304$, $d = 0.65$) and Transient conditions ($t(11) = 0.27$, $p = .789$, $d = 0.16$). This highlighted that the presence of stable objects upon which to focus was not driving the differences observed in Experiment 1 (also see Appendix 1 for control analysis).

Experiment 2b: The analysis revealed no main effect of Placeholder condition, $F(1, 7) = 1.60$, $p = .246$, partial $\eta^2 = .19$, a main effect of Probe location, $F(2, 14) = 12.65$, $p = .001$, partial $\eta^2 = .64$, and no significant two-way interaction, *F*(2, 14) = 1.31, *p* = .300, partial $\eta^2$ = .16. Follow-up analyses confirmed again better performance at the saccade target compared to the lateral locations for the Stable condition (upper control: *t*(7) = 4.60, *p* = .002, *d* = 3.5; lower control: *t*(7) = 4.18, *p* = .004, *d* = 3.16), as well as the Late Onset condition (upper control: *t*(7) = 2.55, *p* = .038, *d* = 1.93; lower control: *t*(7) = 2.46, *p* = .044, *d* = 1.86). No difference emerged between the lateral locations in both Stable (*t*(7) = 0.23, *p* = .826, *d* = 0.17) and Late Onset conditions (*t*(7) = 1.66, *p* = .142, *d* = 1.25).

*Perceptual Difficulty*

Experiment 2a: Analysis of the shift of the vertical bar of the flashed asymmetric cross was carried out across Stable (mean shift: 0.084 dva) and Transient (mean shift: 0.097 dva) conditions. The same ANOVA as used for perceptual performance revealed no main effect of Placeholder condition, *F*(1, 12) = 2.81, *p* = .12, partial $\eta^2$ = .19, no main effect of Location, *F*(2, 24) = 1.71, *p* = .201, partial $\eta^2$ = .12, and no two-way interaction, *F*(2, 24) = .375, *p* = .691, partial $\eta^2$ = .030.

Experiment 2b: In this Experiment, a main effect emerged for Placeholder condition (mean shift Stable: 0.091 dva; mean shift Late Onset: 0.122 dva), *F*(1, 6) = 38.58, *p* = .001, partial $\eta^2$ = .86, but not for Location, *F*(2, 12) = 2.84, *p* = .098, partial $\eta^2$ = .32, or for the two-way interaction, *F*(2, 12) = .56, *p* = .586, partial $\eta^2$ = .085.

*Saccadic Reaction Time*

Experiment 2a:

Despite having controlled for possible perceptual differences that may have arisen from differences in SRT by conservatively analyzing only saccades initiated 80 ms, or less, after the saccade (probe-saccade interval), we sought to compare median SRTs when the placeholders were Stable (164 ms) and Transient (170 ms). A paired-samples *t*-test showed there was no significant difference between in latencies between conditions, *t*(11) = 1.2, *p* = .254, *d* = 0.72.

Experiment 2b: We repeated the SRT comparison for experiment 2b between Stable (171 ms) and Late Onset (199 ms) conditions. There was a significant difference in latencies between conditions, *t*(7) =

1.86, *p* = .044, *d* = 1.41, highlighting that the concurrent presentation of placeholders and perceptual stimuli in the Late Onset condition led to faster SRTs. This again emphasized the relevance of accepting only small probe-saccade intervals of less than 80 ms for both conditions.

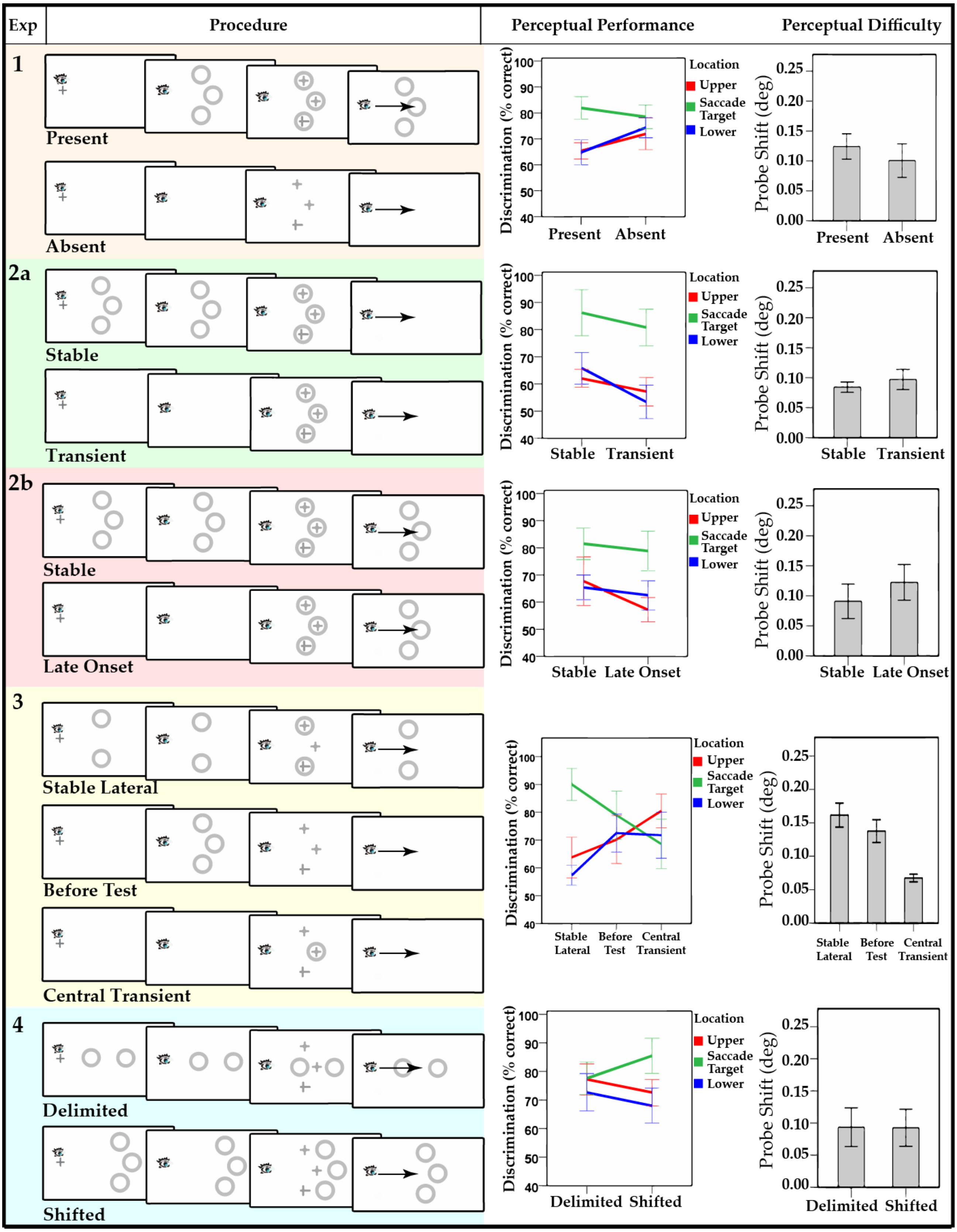

**Figure 5.** Each of the five experiments (1, 2a, 2b, 3, 4) are listed with procedures of each experimental condition, a graph of the perceptual discrimination performance measured at each location and a graph of the perceptual difficulty of the task based on the discriminability of the probe given the visual landscape.

**Discussion**

Regardless of the placeholders being presented from the beginning, giving the visual system an object to focus on, or appearing only at the same time as the probes, and therefore the final stages of saccade planning, a perceptual performance benefit was observed at the saccade target. Only at this location could attention overcome the detrimental effect of the placeholders. This was also the case when the placeholders were presented longer than the probes itself (Experiment 2b). Overall, these results speak for the detrimental object hypothesis. In particular, comparison between conditions point to simultaneous masking as the underlying mechanism. The transient condition in Experiment 2a demonstrates that it was not necessary to present the placeholders before target presentation or after target presentation to observe the difference between saccade target and remaining locations. Thus, simultaneous rather than forward or backward masking is at play. The results of Experiments 2a and 2b therefore suggest that perception was not altered by the differences in visual landscape during the saccade preparation phase but it was rather the presence of objects at the tested locations simultaneous to target presentation (i.e. simultaneous masking) that brought about the differences that emerged in Experiment 1. Furthermore, the placeholders remaining on screen after the perceptual targets (Experiment 2b) led to a more challenging perceptual task, as a larger probe shift was needed, than when they disappeared with the perceptual targets. A decrease in performance is usually found when the duration of masking stimuli is increased (Di Lollo, Enns, & Rensink, 2000; Vincent Di Lollo, von Mühlenen, Enns, & Bridgeman, 2004), which can explain the current findings.

In Experiment 3, we further tested predictions of the masking and the object selection hypotheses. Specifically, we tested: a) whether the perceptual benefit at the saccade target would be strongest when placeholders were presented only at the lateral stimuli, but not the saccade target itself (predicted by the masking hypothesis; not predicted by the object selection hypothesis); b) whether placeholders presented before but not simultaneous with the perceptual stimuli lead to benefits at the saccade target (predicted by the object selection hypothesis, not predicted by the masking hypothesis); and c) whether a simultaneous placeholder only around the saccade target affects performance (not predicted by lateral masking).

# Experiment 3

## Method

Participants were nine students of Geneva University, 6 of which female. They were tested across three conditions (see Figure 5): In Stable Lateral, placeholders were present at the lateral locations from the beginning of the trial, and no placeholder was displayed at the saccade target location. In Before Test, placeholders were displayed briefly before the perceptual stimuli (similar to the present condition of Experiment 1), followed by the perceptual stimuli without placeholders. In Transient Central, at the time of the perceptual test a single central placeholder appeared at the saccade target location that was extinguished along with the perceptual stimuli. In all three conditions participants were instructed to make an eye movement to the center of the screen when the fixation cross disappeared.

### *Results*

Perceptual performance (illustrated in Figure 5) was analyzed with a 3*3 repeated-measures ANOVA, with Placeholder condition (Stable Lateral, Before Test, Transient Central) and Probe location (upper, target, lower) as within-subject factors. This analysis revealed no main effect of Object condition, $F(2, 16) = 2.08$, $p = .703$, partial $\eta^2 = .04$, a main effect of Probe location, $F(2, 16) = 3.93$, $p = .041$, partial $\eta^2 = .32$, and a significant two-way interaction, $F(4, 32) = 12.83$, $p < .001$, partial $\eta^2 = .62$. Follow-up analyses confirmed significant differences between performance at the saccade target and the lateral locations for the Stable lateral condition (upper control: $t(8) = 4.38$, $p = .002$, $d = 3.1$; lower control: $t(8) = 6.57$, $p < .001$, $d = 4.64$), no differences between the saccade target and the lateral locations for the Before Test condition (upper control: $t(8) = 1.39$, $p = .200$, $d = 0.98$; lower control: $t(8) = 1.00$, $p = .346$, $d = 0.71$), and that performance at the saccade target in the Transient Central condition was even marginally worse than at the upper control location, $t(8) = 1.89$, $p = .095$, $d = 1.34$, but not worse than at the lower control, $t(8) = .32$, $p = .755$, $d = 0.23$.

### *Perceptual Difficulty*

To explore differences in task difficulty we examined the shift of the vertical bar of the asymmetric cross for Stable Lateral (.161 dva), Before Test (.138 dva) and Transient Central (.067 dva). A 3*3 repeated-measures ANOVA with 3 levels for Placeholder condition (Stable Lateral, Before Test, Transient Central), which highlighted a significant main effect, $F(2, 16) = 52.33$, $p < .001$, partial $\eta^2 = .87$, and 3 levels for Probed Location, where no main effect emerged, $F(2, 16) = 1.73$, $p = .209$, partial $\eta^2 = .18$. The interaction between factors was not significant, $F(4, 32) = 1.3$, $p = .292$, partial $\eta^2 = .09$. Follow-up analysis on the main effect between Placeholder conditions showed that there was no difference in shift between the Stable Lateral and the Before Test conditions, $t(8) = 2.25$, $p = .055$, highlighting no difference in difficulty. Statistical differences instead emerged between the Central Transient and the remaining two conditions (Stable Lateral: $t(8) = 9.11$, $p < .001$; Before Test: $t(8) = 9.71$, $p < .001$), highlighting that this condition required a smaller shift and was therefore easier to perform.

## *Saccadic Reaction Time*

As in the previous experiments, despite analyzing only trails where the probe-saccade interval was less than 80 ms, accounting for possible SRT differences, we nonetheless sought to compare SRT between Stable Lateral (156 ms), Before Test (150 ms) and Central Transient (147 ms) conditions. A One-way repeated measures ANOVA was run on the SRTs relative to the three placeholder conditions and highlighted a significant main effect, $F(2, 16) = 4.86$, $p = .022$, partial $\eta^2 = .38$. Post-hoc paired t-test comparisons showed that the SRTs for the Stable Lateral condition were significantly longer than for the remaining two conditions (Before Test: $t(8) = 2.43$, $p = .041$, $d = 1.72$; Central Transient: $t(8) = 2.87$, $p = .021$, $d = 2.03$). No significant difference emerged between Before Test and Central Transient conditions, $t(8) = 1.07$, $p = .316$, $d = 0.76$.

**Discussion**

The results largely confirmed the masking hypothesis: In the condition where the placeholders were present only at the lateral locations (Stable Lateral) performance at the saccade target was better than at the lateral locations. Despite no object being present (no object to focus on according to our object selection hypothesis), performance was best at the saccade target as it was the only location without masking from the placeholders. This suggests the anchoring of attention to a location does not necessarily require an object to be selected towards which attention can bind. On the other hand, presenting the placeholders briefly before the saccade, followed by the probes without the placeholders (Before Test), produced equal performance at all locations, just as in the Absent condition of Experiment 1, when no placeholders were displayed. In the last condition where a placeholder was presented only at the saccade target, Transient Central, the results revealed a small (marginally significant) hindering effect on perceptual processing at this location, compared to the upper but not the lower location. Because effects of pre-saccadic attention are present with two placeholders, but absent with just one, we conclude that there has to be a certain amount of lateral masking for pre-saccadic attention to take effect. Lateral masking appears to act not only on the crosses inside the placeholders, but also on the neighboring placeholders. If pre-saccadic attention eliminated masking from the placeholder on the cross contained inside, a single placeholder around the saccade target location should show the same or even stronger effects than placeholders around the upper and lower location. This is not what we observed. Rather, pre-saccadic shifts of attention only affected performance when two placeholders were present. While we favor an explanation in terms of lateral masking, it may be possible that the two placeholders result in stronger crowding than a single placeholder. The next experiment tries to decide between the crowding and lateral masking hypotheses. In sum, results indicate that pre-saccadic attention shifts towards the saccade target engage processes that diminish a form of simultaneous lateral masking that arises from placeholders around the potential locations of the perceptual target. So far we tested conditions where placeholders and the perceptual stimuli were always presented at the same locations, but not necessarily at the same time.

In Experiment 4, we explore two further conditions in which placeholders and perceptual targets did not overlap in space. In one condition, we positioned the placeholders at more eccentric locations than the target. In the other condition, two placeholders surrounded the saccade target location on a straight line through fixation. Importantly, placeholders in the Shifted condition have a tangential arrangement, whereas placeholders in the Delimited condition have a radial arrangement. Crowding is known to be twice as strong with radial compared to tangential arrangements (Toet & Levi, 1992). Thus, if it was crowding that was modulated by pre-saccadic shifts of attention, we should find strong effects in the Delimited condition.

# Experiment 4

### Method

Participants in the current experiment were 12 students of Geneva University, 5 of whom female. In the Delimited condition, placeholders were present at either side (2 dva left and 2 dva right) of the saccade target from the beginning of the trial. In the Shifted condition, placeholders were displayed by 2 dva rightwards from the tested locations (beyond the screen center). None of the placeholder displayed in the conditions were presented at the tested locations and participants were told so in advance. In both conditions participants were instructed to make an eye movement to the center of the screen, (i.e., between the two placeholders in the Delimited condition, slightly short of the central placeholder in the Shifted condition) when the fixation cross disappeared.

### Results

#### *Perception*

Perceptual performance was analyzed with a 2*3 repeated-measures ANOVA, with Placeholder condition (Delimited, Shifted) and probe position (upper, target, lower) as within-subject factors. This analysis revealed no main effect of Placeholder condition, *F*(1, 11) = .2, *p* = .666, partial $\eta^2$ = .02, a main effect of Probe location, *F*(2, 22) = 3.57, *p* = .045, partial $\eta^2$ = .24, and a significant two-way interaction, *F*(2, 22) = 3.87, *p* = .036, partial $\eta^2$ = .26. Follow-up analyses also confirmed that in the Delimited condition performance at the saccade target did not differ from that at the lateral locations (upper control: *t*(11) = .09, *p* = .932, *d* = 0.05; lower control: *t*(11) = .93, *p* = .372, *d* = 0.56) while performance at the saccade target was superior to that at both lateral locations in the Shifted condition (upper control: *t*(11) = 2.71, *p* = .020, *d* = 1.63; lower control: *t*(11) = 3.05, *p* = .011, *d* = 1.84).

### *Perceptual Difficulty*

We compared the shift of the perceptual stimulus across Delimited (.093 dva shift) and Shifted conditions (.092 dva shift). A 2*3 repeated-measures ANOVA was performed on Placeholder condition (Delimited, Shifted) and Placeholder locations (upper, saccade target, lower). This showed no main effect for Placeholder condition, *F*(1, 11) = .28, *p* = .61, partial $\eta^2$ = .02, no main effect for Location, *F*(2, 22) = .99, *p* = .389, partial $\eta^2$ = .08, and no two-way interaction, *F*(2, 22) = 1.48, *p* = .248, partial $\eta^2$ = .12.

### *Saccadic Reaction Time*

SRTs were compared between Delimited (155 ms) and Shifted (161 ms) conditions by means of a paired t-test. This confirmed a significant difference, *t*(11) = 3.52, *p* = .005, *d* = 2.76, whereby the Delimited condition was associated with shorter latencies.

## Discussion

The results showed that performance was distributed differently across the two conditions where no placeholders were shown at the tested locations. In one condition the placeholders were displayed on either side of the saccade target location and here performance was equal at all three locations. This replicated the findings of the previous experiments whereby performance at the saccade target did not differ from that observed at the lateral locations when no placeholders or only a single central placeholder were displayed. However, in the condition where the placeholders were shifted by 2 dva beyond the tested locations results were very similar to those obtained when the placeholders were displayed at the tested locations. A perceptual performance benefit was in fact observed at the saccade target location, compared to the lateral locations. The results of this experiment demonstrate that pre-saccadic shifts of attention modulate lateral inhibition and not crowding. The radial arrangement of placeholders, which is supposed to result in strong crowding, did not yield effects of pre-saccadic attention shifts, suggesting that lateral masking and not crowding is modulated by pre-saccadic shifts of attention. The results with radially arranged placeholders are similar to those observed with a single placeholder on the saccade target location (Central Transient condition in Experiment 3). Thus, we conclude that placeholders needed to flank the saccade target location at or close to the possible locations of the perceptual target. Presenting the placeholders at task-irrelevant locations did not result in pre-saccadic shifts of attention. Overall, the results further emphasize that the shift of attention that anticipates the eye movement is sensitive to changes in the visual landscape and does not follow solely the efference copy.

# General Discussion

With a series of experiments we show how the presence of objects and their arrangement influence the distribution of attention across locations prior to eye movements. Preferential processing was not dictated by saccade metrics alone, and the associated concept of efference copy, occurring rigidly at the end-point of the saccade vector. Rather, it was modulated by visual objects present at, and around, the end-point of the saccade. The presence of the objects rendered perception at the various tested locations more difficult, which only the pre-saccadic shift of attention was able to overcome at the saccade target location. Perceptual differences could not be attributed to differences in saccade precision, since only precise saccades were examined throughout the study (see Figure 4, Bin 1). For the classic pre-saccadic shift effect to emerge the stable presence of visual objects was not necessary. We saw that objects appearing along with the perceptual stimuli at the final stage of the planning phase led to a shift of attention to the saccade target comparable to when stable objects were present from the beginning of the trial. It became apparent that that the objects were having a detrimental effect on in-depth perception, and they were likely producing masking effects at the tested locations. These effects greatly impaired perception at the more peripheral locations and helped produce the traditional pre-saccadic shift of attention narrowly focused on the saccade target. Interestingly, even when the saccade target was the only location to be penalized by presenting an object only at its location, processing at its location did not drop below that found at the favored peripheral locations. Lastly, the arrangement of the objects produced changes in the distribution of the attentional resources, even when the objects were not presented directly at the tested locations. The arrangement which was aimed at producing crowding effects did not constrain visual attention around the target location, while a lateral masking arrangement did. This indicated changes in perceptual processing, based on the presence of visual objects before eye movements, were not limited exclusively to the areas within the boundaries of the presented objects. Also, taken together, the experiments suggests that the visual objects produced effects akin to masking on the perception before eye movements. The discussion will focus on these points in turn.

### *Visual Objects: Noise exclusion versus signal enhancement*

In the presence of visual objects at the saccade target and lateral locations pre-saccadic attention produced better performance at the target location compared to lateral locations. This is consistent with previous findings by e.g., Deubel & Schneider (1996), Deubel (2008), Kowler et al. (1995), Puntiroli et al. (2015), Rolfs et al. (2011) & Baldauf & Deubel (2008) who all show this pattern on focused perceptual processing at the saccade target location. The absence of objects at the tested locations instead led to a roughly equal allocation of attention at the saccade target and lateral locations. This difference between visual objects being displayed or not was striking, especially when considering that their presence in vision science experiments is both ubiquitous and largely taken for granted, as recently stated by Taylor et al. (2015). In order to pinpoint the reasons for these perceptual differences we proposed an object selection hypothesis, whereby narrow processing at the target location results from attention being focused on the selected object, and a detrimental object hypothesis, whereby the placeholders hinder in-depth perception of what is contained within the object's boundaries or nearby. Rather surprisingly, no support for the object selection hypothesis was found. The pre-saccadic shift of attention appeared to be relatively unconcerned with the presence of a stable object to focus on, towards which eye movements could be planned. On the other hand the findings corroborate the detrimental object hypothesis, with the placeholders acting as masks, mainly impeding the processing of peripheral locations where clarity is limited. In fact, visual objects not overlapping with the perceptual stimuli (lateral masking, e.g. Polat & Sagi, 1993) increased perceptual difficulty when placeholders were present. The hindering effect of the placeholders affected the redistribution of visual attention effects across the locations, as their presence at the time of the target presentation led to benefits being found only at the saccade target. Masking effects can be produced by visual objects that closely surround the perceptual targets (Bruchmann, Breitmeyer, & Pantev, 2010), and increase with the increase of the duration of the masking stimuli's presentation, following the perceptual test (Di Lollo, Enns, & Rensink, 2000; Vincent Di Lollo, von Mühlenen, Enns, & Bridgeman, 2004). In the current study stimuli that remained on screen after the perceptual stimuli were presented rendered the perceptual task more difficult than when perceptual stimuli and visual objects disappeared simultaneously, thus complimenting the existing literature. With the findings suggesting that the presence of visual objects produced a masking effect, this provides an interesting indication of what the pre-saccadic shift of attention is able to overcome, in terms of disambiguating noisy or cluttered visual landscapes, suggested also by Harrison, Mattingley, & Remington (2013) and Wolfe & Whitney (2014). In fact, while the placeholders mainly limited perception by rendering discrimination more difficult, a disadvantaged saccade target was nonetheless processed roughly equally to advantaged lateral locations (see Central Transient condition of Experiment 3). When instead the saccade target was advantaged (see Stable Lateral condition of Experiment 3), high performance was only observed at this location, with perceptual processing of the lateral locations dropping considerably. The pre-saccadic shift of attention can therefore lead to in-depth processing at an eye movement target in difficult perceptual conditions (e.g. visual noise) and can overcome visual hindrances rendering the processing of the target equal to that of easily discriminable lateral locations.

### *Masking and Noise Exclusion*

The previous observations suggest that the effects of pre-saccadic attention are achieved by excluding external noise (Lu & Dosher, 2008). That is, pre-saccadic attention filters out external noise and focuses on relevant characteristics of the stimulus. This mechanism can only operate when there is sufficient external noise in the stimulus to filter out. From this perspective, the effects of placeholder timing and spatial arrangement arise from the necessity to provide visual noise at the right time and right location for effects of pre-saccadic attention to be observable. Thus, visual noise has to occur simultaneously to the presentation of the perceptual target and it has to occur at the possible target locations. Displays without placeholders, with only one placeholder or placeholders occurring before the perceptual target do not result in effects of pre-saccadic enhancement because they do not produce sufficient noise at the moment of target perception. In contrast, pre-saccadic attention does not seem to operate through signal enhancement, whereby attention amplifies the signal (Carrasco, 2011). Signal enhancement should be visible in visual contexts of low noise. For instance, removing the placeholders is expected to reduce visual noise. Because effect of pre-saccadic attention were absent with low visual noise, we conclude that pre-saccadic attention does not act by signal enhancement. Finally, we admit that the relationship between noise suppression and lateral masking is far from clear. While we have framed the paper in terms of attention shifts tied to the efference copy on the one hand and lateral masking on the other hand, it may be equally correct to frame it in terms of signal enhancement versus noise exclusion. However, previous research on noise exclusion has preferentially used overlap masking to produce visual noise. Therefore, we await future studies to clarify the relationship between lateral masking and visual noise, but it seems reasonable to assume that lateral masking results in visual noise, too.

### *Alternative Explanations*

It is worth discussing alternative explanations, such as inhibition of unattended locations, in order to provide a clear picture. Despite inhibition typically being found around a region of enhanced visual processing (Cutzu & Tsotsos, 2003; Müller, Mollenhauer, Rösler, & Kleinschmidt, 2005; Serrano-pedraza, Gamonoso-cruz, & Derrington, 2013; with detailed models of the underlying cortical circuitry being proposed see Fester & Miller, 2000; Shapley, Hawken, & Ringach, 2003) the findings, especially those of Experiment 2a, proved that the lack of preferential processing at the lateral locations was not due to suppression surround effects, nor was it due to the active suppression of competing stimuli (see Seidl, Peelen, & Kastner, 2012; Sawaki & Luck, 2010). Displaying the placeholders at the time of the test meant that both placeholders and perceptual stimuli were presented on average less than 50 ms before the eye movement. This is simply too short for any kind of perceptual process of this kind, as suggested by studies investigating event-related potentials where spatial attention leads to evidence of sensory-evoked P1 component 100 ms after stimulus onset, with feature-related activity taking considerably longer (M Eimer, 1995; Zhang & Luck, 2009).

### *Objects at non-Tested Locations: Arrangement and Masking*

Altering the disposition of the placeholders by displaying these at various non-tested locations helped determine that crowding could not account for the findings. In fact, in conditions where perceptual difficulty was matched and no masking took place the structure of the visual field alone was able to produce dramatic effects on the allocation of attention (Experiment 4). When the saccade destination was clearly delimited by the placeholders attention was fairly distributed across saccade target and lateral locations. When instead the planning of an eye movement relied on a visual landmark, which was the central placeholder shifted to the right, in order to orient gaze, attention was focused almost entirely around the very center of the screen. This was supported by the verbal reports of the participants, who stated focusing intently on the displaced central placeholder in order to carry out the task. These findings strongly suggest that the pre-saccadic shift of attention is not entirely driven by the copy of the motor command sent to the perceptual areas of the brain (i.e. efference copy). Rather, the objects that make-up the visual landscape also play a role in defining how the attentional resources are distributed around the landing point of the saccade. It has been argued that the role of the pre-saccadic shift of attention is that of allowing a “perceptual preview” of the visual information that is about to fall on the fovea (Henderson, Pollatsek, & Rayner, 1989; Mathôt & Theeuwes, 2011). Here we see that there is a certain margin of flexibility the preview can take, based on the arrangement of the visual elements present at the end-point of the saccade vector. Pre-saccadic shifts of attention are known to be instrumental for the guidance and control of saccades. Zhao, Gersch, Schnitzer, Dosher, & Kowler (2012) explain how these shifts define the effective input to the saccadic system and suppress the influence of competing or irrelevant signals in order to avoid saccadic landing errors, particularly in cluttered visual environments. By allowing this minute preview window to have a degree of flexibility, in a similar vein to the expansion and shrinkage of the attentional window observed by Belopolsky, Zwaan, Theeuwes, & Kramer (2007) in the absence of eye movements, saccades might be better directed to their intended location and related errors better curtailed. In fact, if by efficiently allocating pre-saccadic attention in a flexible manner, the observer can better disambiguate the relationship between the visual elements present at the landing point of the eye movement, this may avoid the need to perform secondary corrective-saccades (for a psychophysical account see Hollingworth, Richard, & Luck, 2008; for a neurophysiological account see Murthy, Ray, Shorter, Priddy, Schall & Thompson, 2007). It has often been argued that saccades are physiologically cheap in terms of energy required (e.g. Bekkering, Adam Kingma, Huson, & Whiting, 1994; Belopolsky & Theeuwes, 2012), which leads to their relatively large number (3 per second) and their highly explorative nature, at least in naturalistic settings. One can presuppose that without a snap-preview of what is about to appear on the fovea and a degree of leeway in the production of that preview based on the visual input, the number of saccades per second may be larger, and the role of the saccade far more exploratory and less goal-oriented.

### *Concluding Remarks*

In a series of experiments it was made apparent that visual objects have a substantial role in shaping the distribution of visual attention effects when an eye movement is imminent. Presenting objects at tested locations simultaneously with the perceptual target produces a masking effect that the pre-saccadic shift of attention can only overcome at the landing point location. This masking effect vanishes when objects are not displayed, allowing a fairly even distribution of perceptual resources across saccade target and lateral locations. The way the visual objects are arranged influences how attentional resources are allocated during the planning of an eye movement, likely through an increase in masking effects requiring noise exclusion. Taken together, these findings suggest that the pre-saccadic shift of attention is not driven by the saccade metrics of the motor command alone. Rather, a degree of flexibility is at play, in order to best process the visual elements present at the landing-point of the eye movement and exclude noise. In conclusion, our results are compatible with the idea that pre-saccadic shifts of attention exert their beneficial effects by excluding noise from surrounding locations rather than by enhancing the signal at the target location.

# Chapter 5

# Study 4: Malleable pre-saccadic shifts of attention

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When preparing a saccade, attentional resources are deployed towards the saccade target, but do not spread towards surrounding locations. Here we show that such binding of pre-saccadic attention with the saccade target location only holds when eye movements are prepared towards an object still present, but not towards a recently extinguished one. In our study, participants made 10 degree saccades toward an object that could either remain present or get extinguished before the onset of the saccade. We obtained detailed maps of pre-saccadic shifts of attention to the saccade target and its surrounds. We observed that when saccades were prepared towards an object currently present, attention was concentrated within a ~2 degree-radius around the object. However, when saccades were prepared towards an object that extinguished shortly before the saccade, although eye movements remained highly precise, attention was reduced at the saccade target. Interestingly, when saccades were prepared towards an object that disappeared long before the eyes moved, attention spread to locations further away (within a ~5 degree-radius) from the memorized object. Our findings therefore suggest that 1) enhancement is narrow and focused specifically in and around the saccade landing point when there is a visual object to which attention can bind 2) when a visual object is no longer present attention spreads much further to the surrounds and 3) as the memory of the visual object decayed an increase in attentional resources was observed in more distal locations. In conclusion, the current study indicates that the pre-saccadic shift of attention is a highly malleable process, bound to the saccade target only when a present visual element can funnel it.

*This chapter presents unpublished material currently in preparation*

## 5.1 Introduction

Visual attention can be intended as the preferential processing of parts of the visual environment over others. Preferential processing can occur largely independently of one’s volition, driven by brightness and salience (J Theeuwes, 1993) or previous experiences (B. a Anderson et al., 2011), where visual attention is allocated to particular locations in apparent automatic fashion. One of the most reliable and investigated effects in vision science is the shift attention makes just before an eye movement is made. Eye movements are constantly made in order to bring objects into the fovea for detailed processing, as peripheral vision does not offer the same clarity. It has been shown that in the time immediately preceding an eye movement visual attention anticipates the eye movement consequences and shifts to the location where the eyes will land (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995). Preferential processing can be found at this location while the eye movement is being programmed and it continues to increase up to the moment the movement is initiated (Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Various accounts that are more or less complimentary have been put forward to explain how the shift of attention occurs. Studies have found that just before an eye movement cells in a number of brain areas transiently change the location and extension of their receptive fields (Duhamel, Colby, & Goldberg, 1992; Melcher & Colby, 2008; Wurtz, 2008), possibly in order to keep track of objects across eye movements by accounting for the retinal displacement that such movements cause (Cavanagh, Hunt, Afraz, & Rolfs, 2010; Duhamel et al., 1992; Wurtz, Joiner, & Berman, 2011; Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013; Szinte, Carrasco, Cavanagh, & Rolfs, 2015; Mirpour, & Bisley, 2013). In other studies it was observed that just before an eye movement the entire visual space converges towards the target location, which drives the shift of attention (Zirnsak, Lappe, & Hamker, 2010; Zirnsak & Moore, 2014; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014). Regardless of the specific school of thought adhered to it seems to be unanimously accepted that all saccades are preceded by a covert shift of attention that leads to preferential processing at the target location.

Saccades bring objects from the periphery into the fovea and visual attention begins preferential processing at the target location before the eye movement is made. A question naturally follows: is this mechanism that shifts attention before eye movements concerned about objects or solely by locations? That is to say, does the area of preferential processing remain fixed or is it determined by the presence of a saccade object that is about to be foveated? Research into visual attention as a means of selection has led to a distinction between two independent and complimentary modes of selection, one involving spatial locations and the other involving objects (Mozer & Vecera, 2004). This distinction arises almost entirely in the absence of eye movements. Space-based attention is the process that allocates attention to regions or locations of the visual environment (Posner, Snyder, & Davidson, 1980). Object-based attention on the other hand leads to attention being allocated to organized chunks of visual information corresponding to coherent patterns and shapes (Duncan, 1984; Scholl, Pylyshyn, & Feldman, 2001; Drummond, & Shomstein, 2010; for a review see Chen, 2012). Studies directly comparing the two have found that object-based effects tend to be much smaller and variable in size (Pilz, Roggeveen, Creighton, Bennett, & Sekuler, 2012), and that these distinct systems interact with one another in a way that prioritizes selection by location over object-based selection (Soto & Blanco, 2004). To Taylor, Chan, Bennett, & Pratt (2015) goes the merit of mapping a detailed spatiotemporal cartography of the distribution of attention when objects, i.e. placeholders, are and are not present. The authors employed a spatial cueing paradigm where one of four locations, located at each of the four quadrats of the screen, was cued while gaze was maintained centrally. A target would then appear at one of 121 possible locations covering the entire screen and a key press was required once it had been detected. Crucially, objects were either present or not at the possible cue locations. The results showed that the placeholders acted as a visual anchor, constraining attention, while their absence gave-way to a far greater spread of attention throughout the visual field. These findings paired with what is already known about objects limiting the spread of attention (e.g. Egly, Driver, & Rafal, 1994) raise the question of whether the pre-saccadic shift of attention is also affected by whether it is directed towards space or objects.

Advancement on the subject matter has already been made, and comes from various angles. Firstly, it has been shown that the oculomotor system is sensitive to representations of perceptual groups and objects. First, McCarley, Kramer, & Peterson (2002) then Theeuwes & Mathôt (2010) proved that observers prefer to make eye movements within the boundaries of the same object rather than to a different object even when the distances do not differ. McCarley et al. (2002) also showed that the dwell times were shorter between eye movements made to the same object. A detailed account of how object size influences eye movements to various parts of an object and the annexed within-object fixations was offered by Pajak & Nuthmann (2013). Taken together, these findings strongly suggests that object-based effects apply also to the programming and execution of eye movements. Second, pre-saccadic attention appears to be maintained differently at attended locations when objects are presented. An eye movement study that directly compared the deployment of attention in the presence or absence of objects was carried out by Lisi, Cavanagh, & Zorzi (2015). The authors found that when visual attention was allocated to objects, attention remapped and was successfully maintained at the desired location across eye movements. Instead when the objects were removed and attention was allocated to an empty location observers failed to maintain attention at the location of interest. Interestingly, preferential processing seemed to follow a different time course when no object were present. These results demonstrate that pre-saccadic attention at locations of interest can be influenced by the presence of objects.

In the present study we ask a basic question: is the pre-saccadic shift of attention influenced by whether an eye movement is directed towards an object or space? To what extent does attention spread in both conditions? We know the attentional window, as in the ensemble of visual objects attended to, can be expanded or shrunk (Belopolsky et al., 2007); does this flexibility extend to the shift of attention that precedes eye movements? There seems to be a mismatch between what is known about visual attention in the absence of eye movements and what is known about the visual attention that necessarily precedes eye movements. Perhaps this is not a genuine gap in the literature but it stems from an assumption that the pre-saccadic shift of attention is relatively fixed and that whether it involves space or objects is not relevant. Here we bridge the gap by directly testing whether making an eye movement towards a sustained visual object leads to a different spread of pre-saccadic attention to eye movements directed to a location previously occupied by an object. To these means we produced attentional maps for eye movements performed in both conditions demonstrating that: 1) preferential processing is narrow and focused specifically in and around the saccade landing point when there is a visual object to which attention can bind, 2) when an eye movement is made towards an object that is no longer present attention spreads away from the landing point and further to the surrounding locations.

## Methods

**This section presents a schematic explanation of the methods used. The procedure is explained briefly and the illustration of the results are largely descriptive.**

### *Participants*

Data was gathered from 13 participants, eight of which were female, who performed the task for a minimum of five hours, spread over different days. The age of the participants ranged from 18-31 years of age and all were paid or given course credits for their efforts. All participants except one of the authors were naive as to the purpose of the study and all had normal or corrected-to-normal vision. Ethical consent for the project was awarded by the ethics committee of the University of Geneva and all participants gave their signed consent for participation. The experiments were undertaken with the understanding and written consent of all participants and were carried out in accordance with the Declaration of Helsinki.

### *Apparatus*

Participants sat in a quiet and dimly illuminated room, with their head positioned on a chin and forehead rest. The experiment was controlled by an Apple iMac Intel Core i5 computer (Cupertino, CA, USA). Manual responses were recorded via a standard keyboard. The dominant eye's gaze position was recorded and available online using an EyeLink 1000 Desktop Mounted (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The experimental software controlling the display, the response collection as well as the eye tracking was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink toolboxes (Cornelissen et al., 2002). Stimuli were presented at a viewing distance of 60 cm, on a 21-in gamma-linearized SONY GDM-F500R CRT screen (Tokyo, Japan) with a spatial resolution of 1024 x 768 pixels and a vertical refresh rate of 120 Hz.

*Procedure*

The study comprised of a threshold procedure and the main saccade task. The main saccade task required participants to maintain fixation on a central stimulus for 500 ms and to move their eyes to the saccade target, which was either still present (Sustained) or had disappeared (Transient), only at fixation offset. The saccade target was a black circumference presented either 10 dva to the left or right of fixation. The saccade target was always presented for 500 ms before the saccade was triggered and in addition to this time a 0.2-1.1 second time jitter was added. In the transient condition the time jitter offered a variable time interval between saccade target presentation and fixation offset, which allowed for testing of perceptual discrimination at various times of saccade target disappearance. In the time leading up to the saccade perceptual probes were flashed (Gabor patches) for 25 ms. One patch was tilted to the left or to the right, while another 6 non-tilted patches were also flashed and acted as distractors. At the end of each trial the participant indicated by button press if the tilt of the perceptual test was to the left or right. Approximately 40 trials were obtained at each of the 25 tested locations (see Figure 2) at and around the saccade target location. The study was set up so as to have the same number of trials in each of the conditions (one sustained condition and three transient). Participants carried out approximately 2000 trials each. Before the main saccade task a threshold procedure was run. This was identical to the main saccade task, except for no saccades were performed (gaze was maintained on the fixation stimulus) and a cue which was identical to the saccade target appeared at one of the 25 locations, where the test would be presented. Participants stated the orientation of a tilted Gabor by button press. The extent of the tilt at the cued locations was constantly modified (ranging from 2 to 25 deg of angle). The threshold procedure made it possible to establish the tilt required at various locations in order to achieve a level of perceptual performance of 85% correct.

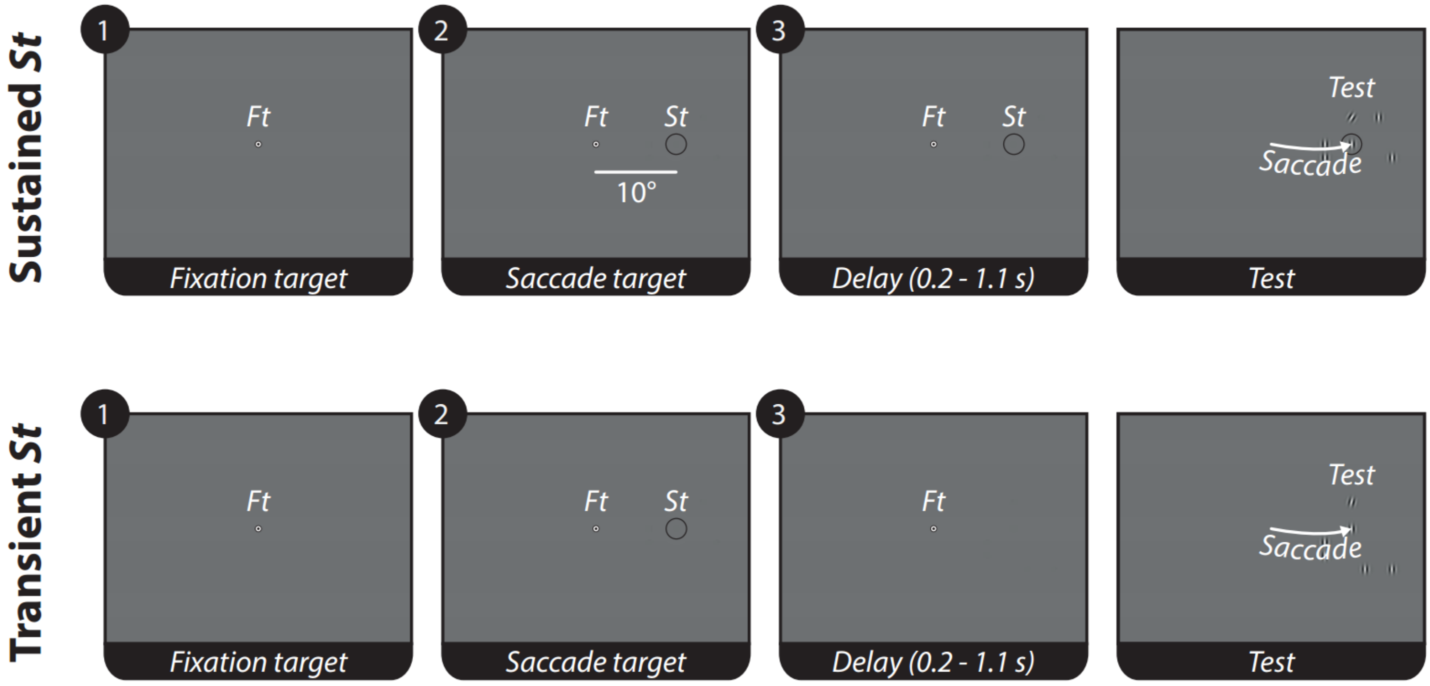

**Figure 1.** Flowchart illustrating both experimental conditions (Sustained and Transient saccade targets)

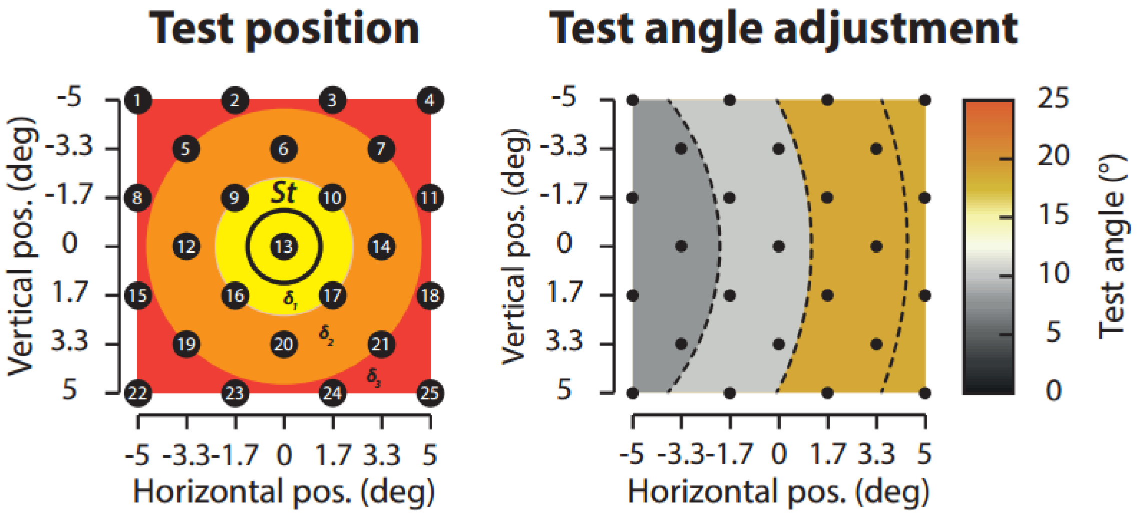

**Figure 2.** On the left are displayed the 25 tested locations. On a given trial one test was played (tilted Gabor), along with 6 distractor (non-tilted Gabors), approximately 50 ms before the saccade. In order to determine the allocation of attention in the presence of a sustained or disappeared visual target the percentage of correct responses was obtained from each of the 25 tested locations. These locations (black numbered circles) were divided into 3 groups, according to their eccentricity from the saccade target. Based on equidistant spacing of the tests, the most central eccentricity was tested at 5 locations (yellow area), the middle eccentricity at 8 (orange area), and the most external eccentricity at 12 (red area).
On the right are displayed the tilt angles obtained from the fixation threshold task. These tilt angles guaranteed discrimination performance at 85% correct at all tested locations, accounting for the test's distance from the Fixation target (e.g. a closer test requires a smaller tilt).

The adjusted estimate of saccade initiation was based on regression analysis of the fixation offset jitter. More time (longer random jitter selected) =shorter latency. Less time (shorter random jitter selected) = longer latency. This observation held true for all participants so by applying a linear regression model (obtaining slope and intercept values) to the saccadic reaction times we were able to almost perfectly estimate the saccade latency on a given trial for each participants.

*Eye Movements processing*

Before proceeding to the analysis of the behavioral results we scanned offline the recorded eye-position data. Saccades were detected based on their velocity distribution (Engbert and Mergenthaler,

2006) using a moving average over twenty subsequent eye position samples. Saccade onset was detected when the velocity exceeded the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within an 2.0° radius centered on *ft* (all tasks), if a correct saccade started at *ft* and landed within an 2.0° radius centered on *st* (saccade and saccade threshold tasks only) and if no blink occurred during the trial (all tasks).

*Illustrative Results*

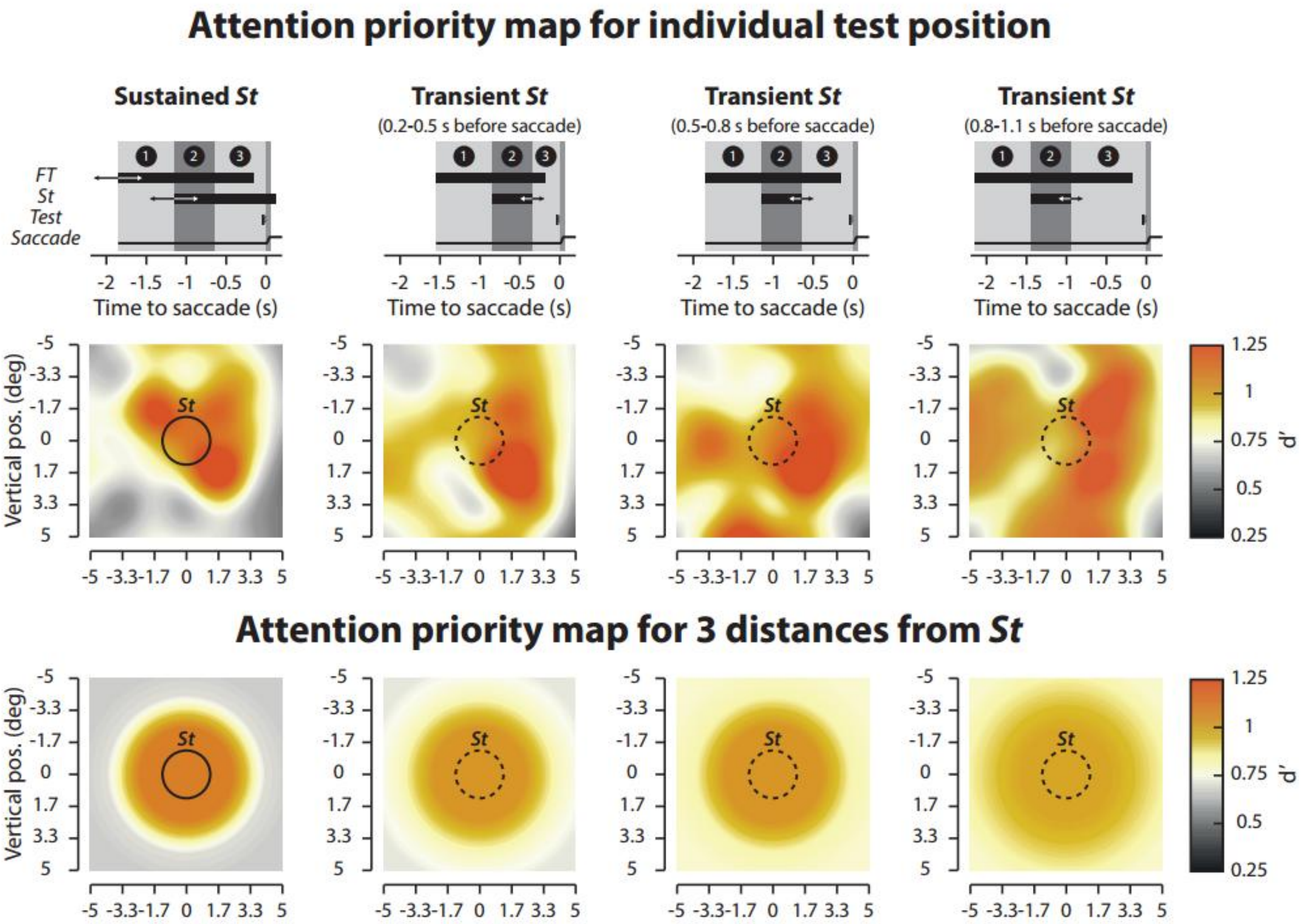

**Figure 3.** The figure illustrates in the first row the time-course for each experimental condition. The difference between the conditions was that in the Sustained eye movements were made to a present saccade target (st), in the 1st transient condition required a saccade to be performed approx. 300 ms after st disappearance, the 2nd transient condition approx. after 650 ms and the 3rd transient condition approx.

after 1 second. Perceptual test was always administered approx. 40 ms before the saccade. The second row shows raw plotting of d-prime sensitivity at for each of the 25 locations tested. The third row illustrates averages of the d-prime sensitivity scores based on the eccentricity of the test. This means that the results shown in row 2 were simply binned into 3 eccentricity groups, illustrated in yellow, orange and red in Figure 2.

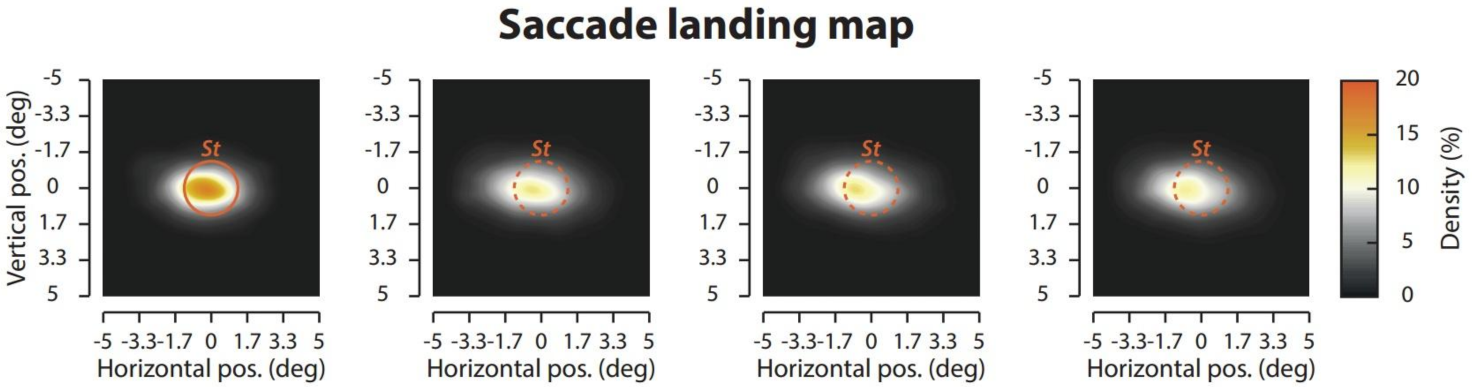

**Figure 4.** Illustrated are heat maps of saccade accuracy, with saccade precision highlighted by the solid and dashed circumferences. Accuracy was greater when st was sustained than when st was transient. However, accuracy did not differ across transient conditions.

*List of Findings*

- When saccades were prepared towards a sustained object (”Sustained St”), attention was concentrated within ~2° around the St.
- However, when saccades were prepared towards an object that disappeared earlier (”Transient St”), attention was dispersed to locations further away from the memorized object.
- This spread of attention increased over time, reaching a radius of 7 degrees a second after the disappearance of the St.
- Saccade accuracy and precision were also affected by the disappearance of the target. However, contrary to attention, saccade landing didn’t spread with time from object disappearance.
- Our findings show that the pre-saccadic shift of attention is a highly malleable process, exclusively bound to the saccade target only when a placeholder can funnel it.

# Chapter 6

# General Discussion

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**Summary of Study 1**

A brief summary of the motives driving the studies and findings is provided at the end of the introduction, along with a detailed explanation of the finding at the end of each published or submitted article. The discussion will now mainly treat the findings as a whole, and only seldom explicitly state the article the finding derives from.

### 6.1 Pre-Saccadic Shift of Attention to Non-Target Visual Objects

In a series of studies (1,3 & 4) we replicated the classic pre-saccadic shift of attention effect, whereby visual attention shifts to the saccade target location before the eye movement (behaviourally: Duebel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; neurophysiologically: Tolias et al 2001; Zirnsak et al., 2014), and continues to increase up to the moment the movement is initiated (Deubel, 2008b; Rolfs et al., 2011). Preferential processing was in fact found to be narrowly focused almost exclusively around the saccade target object, when goal-directed saccades were executed. These were saccades that went straight to their intended target, while in the presence of a salient distractor (Study 1), non-salient adjacent distractors (Study 3) or no distractors objects (Study 4). Interestingly, the same pattern of behaviour was observed also for oculomotor capture saccades (Study 1). That is to say, a pre-saccadic shift of attention, to the saccade landing point, took place even when gaze was captured by a salient distractor object. Just as for their goal-directed counterparts, visual elements at the landing location of a capture saccade underwent in-depth processing, and increased over time, up to the moment the saccade was initiated. In order to rule out the possibility the distractor had been mistaken for the saccade target, focus was placed on the inter-saccadic interval, between error and corrective saccade sequences (first to the distractor then to the saccade target). When the dwell times between saccades are short, it can be assumed that the saccades are programmed largely in parallel (see Becker & Jürgens, 1979), with the programming of the second saccade occurring during execution of the previous saccade, or even before the previous saccade was triggered (McPeek, Skavenski, & Nakayama, 2000; Theeuwes, Kramer, Hahn, & Irwin, 1998; Peterson, Kramer, & Irwin, 2004) . This was in contrast to trials where the dwell times were long, and an initial independent saccade to the distractor was later followed by a new saccade to the saccade target (possibly after the realization the initial saccade was erroneous). Selecting only sequences of saccades where the eyes spent little time fixating the distractor, before shifting gaze to the saccade target, highlighted the stability of the effect. That is to say, that even when the observer realized that their saccade to the distractor was erroneous, and concurrently began planning the second corrective saccade to the target, attention still shifted to the distractor location. Preferential processing was, in fact, observed at both the distractor and saccade target locations, mirroring the findings by Godijn & Theeuwes (2003), Baldauf & Deubel (2008) and Rolfs et al. (2011) who found that attention could shift towards two saccade targets, when a sequence of intended saccades was made. These three groups of authors all find that the planning of saccade sequences to two or even three locations leads to clear perceptual benefits at the saccade goal locations, compared to locations where eye movements do not land. This is seen also in our findings. There is strong reason to believe that pre-saccadic attention is allocated independently to these sequential saccade landing-points, such as the distractor and intended saccade target in Study 1. The assumption here is that attentional selection, rather than being a single entity that simply widens its window of interest in order to envelop both locations (as suggested by Pan & Eriksen, 1993; Posner, Snyder, & Davidson, 1980; McCormik, Klein, & Johnston, 1998; Eriksen & Yeh, 1985) can involve spatially non-contiguous locations. Baldauf & Deubel (2008) findings support this assumption. The authors required observers to execute sequences of two or three saccades and measured attentional performance at the saccade locations and also at the intermediary non-saccade locations. While perceptual performance at the saccade goals was enhanced, performance dropped barely above chance level at the intermediary locations. This occurrence clearly could not be predicted by a single widened focus of attention over multiple saccade goals. Very similar behavioural results were obtained by Klapetek, Jonikaitis, & Deubel (2016), who employed an antisaccade paradigm and observed attention being split to the cue location and to the antisaccade goal, when erroneous saccades were made to the cue. Müller, Malinowski, Gruber, & Hillyard (2003) have also provided undisputed evidence that attention could be efficiently split to non-contiguous locations, by looking at steady-state visual evoked potentials (SSVEP) in the absence of eye movements. The authors required observers to pay attention to symbol sequences presented at two out of four locations, and to push a button when the symbols matched at both attended locations. Important to note that SSVEP are larger for attended stimuli. The main findings were that the SSVEP amplitudes at intermediary locations (between two attended locations) were greatly reduced compared to when those same locations were attended, as part of an attended duo of separate locations. Also interestingly, there was no apparent cost of splitting attention, as attending to two adjacent locations or two separate ones proved not to differ. Furthermore, there is strong reason to believe that attention was allocated in parallel to both saccade landing points in our Study 1, as in Godijn & Theeuwes (2003), Baldauf & Deubel (2008), Rolfs et al., (2011) and Müller et al., (2003), therefore rejecting a serial model of pre-saccadic attention allocation. Even with the relatively long capture SRTs to the capturing distractor (in between 200 and 250 ms), identifying a visual object, then switching attention to another, depending on the task and ease of attentional disengagement, requires 200-500 ms (Duncan, Ward, & Shapiro, 1994; C. M. Moore, Egeth, Berglan, & Luck, 1996; Peterson & Juola, 2000; Reeves & Sperling, 1986), rendering this an unlikely occurrence. This spatially non-contiguous allocation of pre-saccadic attention, allocated in parallel to the capturing distractor and the intended saccade target, has important implications for other non-saccade locations, which will be discussed subsequently ("Residual Attention: Mechanical Allocation" section).

Taken together, the findings highlight that a substantial amount of attentional resources are obligatorily allocated to locations visited by eye movements, and preferential processing can be found at these locations, irrespective of the observer’s top-down set. The examination into attentional allocation prior to oculomotor capture saccades (Study 1), prior to goal-directed saccades (Study 1, Study 3, in conditions when noise was present and perception was not hindered exclusively at the saccade target, and Study 4) and prior to memory-guided saccades (Study 4) emphasized once again the strong coupling that exists between saccades and attention. These findings all support the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994), which states that activating the motor system, in order to carry out an eye movement, leads to an obligatory shift of attention. In other words, the theory regards attention as functionally equivalent to saccade preparation. The theory is based on four tenets, where the first two are the most relevant to the current discussion. Firstly, it is postulated that attention and movement planning rely upon the same neural substrates. Secondly, and highly related to the first point, it is postulated that planning a movement causes activation of spatial attention. Here we see evidence in support of the second tenet, as planning eye movements in the experiments mentioned, triggered a shift of attention, even in the absence of observer goals. A large number of studies have found goal-directed actions to be preceded by shifts of attention (e.g. Duebel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Rolfs et al., 2011, just to mention a few), so the tight link between attention and movement preparation is not in question. It is, however, worth noting that a growing body of literature has emerged, that not only questions these tenets, but show them to be largely false. The most compelling of findings came from Gregoriou, Gotts, & Desimone (2012), who provided simple and straightforward evidence that visual neurons in FEF were activated during a fixation only task, while movement neurons were not. Findings by McPeek and Keller (2002) and Sato and Schall (2003) also showed an anatomical difference between attention and eye movements, with visual neurons in FEF and in the SC responding to visual targets presented in the visual field, but not leading to the activation of any motor plan. These findings entirely refute the first tenet and also cast doubt on the second. The premotor theory can, however, still be useful as a theoretical framework and proves to still be a popular theory, in a greatly amended form (see Smith & Schenk, 2012).

Minor differences between shifts of attention preceding goal-directed saccades, and those that preceded capture saccades, did however emerge. One difference regarded the start of the attentional build-up and the second difference regarded the distribution of attentional resources. The beginning of the enhancement build-up took place later in time (i.e. closer to the saccade) for capture saccades. Perhaps the late attentional build-up was due to a reduction in intentionality at the saccade planning phase (endogenous signal), since the saccade was driven by the capturing distractor (exogenous signal). This may have limited a lengthier attentional build-up phase. Support for this derives from Peterson et al., (2004), who also examined the relationship between visual attention and oculomotor capture, but examined only compatibility effects by measuring SRTs. They report that "the exogenous system either generates a fast signal that is always capable of winning the race for control or generates no signal at all". It is precisely this fast exogenous signal that can win the race for eye movement control, leading to a capture saccade, that might cause the bypassing of the standard attentional build-up and induce clear facilitation only just before the saccade is initiated.

With regard to the second difference, Godijn & Theeuwes (2003), Baldauf & Deubel (2008) and Rolfs et al. (2011) all found that preferential processing within the saccade sequence followed a gradient of attentional weights. This means that more attention was allocated to the first saccade goal than at the second saccade goal, and so on and so forth. Instead, we saw an almost perfectly equal level of preferential processing at both saccade landing points during oculomotor capture sequences (when dwell times were short), reflecting a slight perceptual disadvantage a capturing distractor may have, in comparison to the first intended target in a sequence of saccades. It is highly possible that with the build-up of attention occurring later in time at the capturing distractor, perceptual performance did not acquire the overall advantage it should have had, compared to performance found at the second intended location. Another possible explanation of an entirely speculative nature derives from electrophysiology. The lateral intraparietal area (LIP) is believed to play an important role in regards to both allocation of visual attention and saccadic eye movements (Colby & Goldberg, 1999; Bisley & Goldberg, 2010). Gottlieb, Kusunoki, & Goldberg (1998), through single cell-recoding, showed that the neurons in LIP only responded when the presented stimuli were task relevant or abrupt onsets. The capturing distractor in our study, was neither task relevant, nor an abruptly appearing stimulus. Perhaps the lack of distractor-associated neuronal activation in the LIP may have contributed to the reduced attentional deployment, to the distractor location, compared to the enhancement found at the first saccade goal in a sequence of goal-directed saccades.

### 6.2 Presence of Visual Objects before saccadic shifts of attention

Once established that the shift of attention that precedes eye movements is probably a signature of all saccades, regardless of task goals, we turn to better assess the role visual objects have in shaping the distribution of attention. While the next section discusses how changes in signal (bottom-up and top-down) associated with non-target visual objects and locations, affect attention, this section discusses whether presenting an object at all shapes pre-saccadic attention. We saw that when a goal-directed saccade was made to a saccade target attention focused almost exclusively on the saccade target, mirroring the findings by Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Deubel, 2008; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011. By requiring participants to execute memory-guided saccades (Study 3 & 4) and saccades with differing arrangements of visual objects (Study 3) we obtained evidence that the pre-saccadic shift is in fact a malleable process, highly shaped by the structure of the visual field. This confirmed recent views by Taylor et al. (2015) and Lisi et al. (2015) who demonstrated that the use of placeholders substantially alters patterns of attention and pre-saccadic related mechanisms. Similarly, Woodman, Arita, & Luck (2009) used event-related potentials to test how visual attention is deployed in a symbolic-cuing paradigm and focused on a component named N2pc. This component is known to index lateralized shifts of perceptual attention. A cue stimulus cued attention to locations, which were either demarked by object stimuli or no objects at all. The anticipatory N2pc activation emerged only when visual objects were present, disappearing when cued locations were not marked by placeholders. Their findings suggest that early contralateral negativity was driven by the cuing stimulus and not by the hemifield that was being cued. This once again shows the importance of visual objects in attentional tasks and draws attention to the fact their use has been largely taken for granted when designing studies exploring attention-related effects. Our findings support the notion, proposed by the above authors, that attention-related effects are greatly altered by the presence of visual objects. However, the pre-saccadic shift of attention in our studies did not vanish; rather attentional resources spread wider and appeared to be far less unbound to the target location, compared to when an object was present at that location. This could prove to be a difference between attentional effects in cueing (Woodman et al., 2009; Taylor et al., 2015) and remapping paradigms (Lisi et al., 2015) on one side, and pre-saccadic shifts of attention, on the other. With our studies highlighting a degree of flexibility in the allocation of pre-saccadic attention we turned to focus on the neural mechanisms that might be at play. Receptive fields (RF) of a neuron are defined as the part of stimulus space within which a stimulus elicits a response from the neuron (Lennie, 2003). RFs are sensitive to stimuli being presented at their area of reception and stimuli elicit the strongest response from the centre of the RF. Presenting the same stimulus further away from the centre of the RF elicits a weaker response that gradually degrades the further the stimulus is presented. It has been shown that the allocation of attention affects the RFs by shrinking and enlarging their area of focus (for a review see Anton-Erxleben & Carrasco, 2013) which, in turn modifies integration area between multiple RFs. Since attending to a defined location demarked by an object selectively increases the sensitivity of the smallest RFs, tuned to high spatial frequency, at that location (Gobell & Carrasco, 2005) it is very likely that the absence of a saccade stimulus does not cause the shrinkage of RFs. It must be said that the link between RFs and the deployment of attention is still in the process of being accurately understood. However, it would be expected that RFs not shrinking due to the absence of a saccade stimulus would have direct attentional consequences, particularly to the area of perceptual enhancement. Visual targets, and the associated movement plans towards these targets, are automatically computed by the visual system. We saw evidence of this in Study 2, whereby merely altering the set-size and requiring observers to perform saccades towards a revealed target affected time of saccade initiation. Even though the observers in the study performed exogenous driven saccades to a pop-out target, the number of possible motor alternatives associated with the presented objects affected performance. The SC (discussed in the Introduction) is responsible for the automatic encoding of visual targets, and generating towards these targets movement plans (Basso et al., 1999). In a study explicitly investigating SC response based on the presence (or not) of visual targets Edelman & Goldberg (2001) found that saccade-related discharge decreased as time between the target disappearance and saccade initiation increased. Sommer & Wurtz, (2004) investigated SC and FEF activation in a battery of eye movement tasks, included memory saccades and delayed saccades, and obtained very similar findings. The decrease in SC activation could be a likely candidate to explain why pre-saccadic shifts of attention become unbound to the saccade target and spread increasingly to the periphery, when the saccade target is no longer present. Other cortical brain regions have also displayed a stark reduction in activity when saccades were being prepared in the absence of a visual object (e.g. LIP area, Bisley & Goldberg, 2003). An important scientific task will be to unify these relatively separate contributions, arriving from behavioural data, such as that described in the current project, and the brain areas described.

## 6.3 Residual Attention: Bottom-Up and To-Down Allocation to Visual Objects

As was briefly touched upon in the introduction, attention is allocated to regions of the visual field based entirely on the colour, orientation, size, luminance, motion, closure, shape and depth of perceived visual attributes, in what is known as bottom-up allocation of attention ("undoubted" and "probable" attributes that guide attention, from Wolfe & Horowitz, 2004). Immediate goals and intentions also lead to attention favouring one location over another, even when all visual attributes are kept equal, and this is known as top-down allocation of attention. The distinction within the literature proves, at times, to be schematic and likely, an oversimplification of the underlying processes, possibly encapsulating other independent processes (e.g. selection history attention by Belopolsky, 2015). Nonetheless, the concepts have been linked to two distinct systems operating independently (Pinto, van der Leij, Sligte, Lamme, & Scholte, 2013) and the dichotomy still proves “central to theories of attentional processing” (Martin Eimer, Kiss, Press, & Sauter, 2009). We will focus on attention being allocated in top-down and bottom-up fashion to non-saccade targets, and to better understand the topic it is worth discussing a study by Montagnini & Castet (2007). The authors had observers perform a traditional saccadic dual-task, where eye movements to a target were executed and the tilt of Gabor patches, acting as the perceptual probe, discriminated. The probability of the perceptual probe appearing at the saccade target was modified in each block, and the observers were explicitly given these probabilities. The findings showed that perceptual performance was highly affected by the probabilities. Indeed, an independent component of attention, as the authors called it, could be allocated freely to different locations, even on the opposite side of the saccade target (12 dva away from the saccade target and 6 dva away from the fixation stimulus). The author’s results suggested that the independent component was subtracted from the attention intended to be shifted to the saccade target. They argued the subtraction occurred voluntarily, based on the observer’s goals (top down set) to attend to locations where the probability was higher the probe would appear. While the authors address an interesting issue, which is the usage of residual pre-saccadic attention, their belief that attentional resources were subtracted from the pre-saccadic shift to the saccade target however, remains highly questionable. This finding likely emerged from the task design, as observers were trained over blocks of conditions to allocate attention according to the task demands, resulting in an “artificial” modulation of attention at the saccade target location. Also, the findings in the current project do not support this suggestion. In Study 4 we examined the spatial distribution of attention by measuring attention at a large number of locations, just before saccades were made towards a sustained visual target, or to a transient target which had disappeared. Large differences emerged in the spread of attention between conditions, with activation in the sustained condition narrowly centred around the saccade target, while that in the transient condition was wide, spreading up to 4.7

dva away from the target. Despite these differences in spread of attention, the shift of attention to the most central eccentricity in both conditions remained identical. That is to say, that the wide spread of attention in the transient condition did not come at the expense of discrimination performance around the centre of the target location. The pre-saccadic shift of attention had therefore not been "diluted" in this condition, rather it appeared that residual attentional resources had been allocated to the periphery. Our findings from Study 1 also offer insight in the matter. The data suggested that changes in luminosity at the saccade target did not in any way affect performance at this location. When the same changes in luminosity were applied to a colour singleton distractor, they caused large differences in performance at the distractor location. Also strikingly, these modulations in performance at the distractor location did not lead to changes in the preferential processing of the saccade target. A natural conclusion would be that the shift of attention to the saccade target is not modulated by visual attributes. A possible explanation for this comes from a study by Theeuwes & Van der Burg, (2007), who found that top-down knowledge of where a target could appear, modulated preferential processing at the target location. Top-down knowledge of what the target would be, on the other hand, did not. Perhaps an active shift of attention to a target, therefore under the observer's volition, is simply not modulated by a target's visual attributes. An alternative explanation emerges from the findings of Carrasco, Ling, & Read (2004), who found that spatial cueing increased the apparent contrast at the cued location, thus enhancing appearance. The data was consistent with a contrast gain change, where the deployment of attention caused a shift in the psychometric function of contrast sensitivity, rendering stimuli at cued locations easier to discriminate. If the shift of attention that precedes eye movements acts the same way, heightening perception of bottom-up attributes such as contrast, perhaps additional bottom-up modulations of the saccade target stimulus go largely unnoticed. That is to say, perhaps perceptual sensitivity is already close to ceiling at the saccade target. Important to note that our data on luminosity changes at the distractor and target locations were only a secondary aspect of Study 1, which provided interesting preliminary findings and should be treated as a stepping stone for more exhaustive work on the subject matter. In both sets of findings from the current project (“undiluted” pre-saccadic attention and luminosity findings), the pre-saccadic shift of attention to the saccade target appeared to be obligatory and unaltered, while visual attributes such as distractor luminosity (Study 1), and presence of a target shape (Study 4), modulated the allocation of the residual attention (bottom-up allocation). These findings are clearly in stark contrast to the aforementioned subtraction argument by Montagnini & Castet (2007). It is however possible, that when there are incentives or task requirements to attend to non-saccade target locations, then top-down signals allocate attention to these locations, at the expense of a portion of the pre-saccadic shift of attention to the saccade target. We cannot rule this out. Our findings, on the other hand, focused on bottom-up driven attention to non-saccade-target locations. It would be very useful if this issue were addressed in the future, in order to establish the relationship between performance at the saccade target and at non-saccade target locations, where attention is driven either in bottom-up or top-down fashion to these locations. Lastly, while not agreeing with the Montagnini & Castet (2007) subtraction argument their work makes an important point. It emphasizes a degree of flexibility in the allocation of pre-saccadic attention, and that, despite the obligatory shift to the saccade target, some attentional resources (either residual, as our data suggests, or subtracted) are available for the visual system to make use of.

We observed how bottom-up signals allocated the residual pre-saccadic attention to non-saccade target objects, with the strength of the signal determining the extent of the preferential processing. However, in one experiment conducted, a distractor onset appearing before the saccade did not capture attention. This is surprising because luminance increments, which drew substantial attentional resources to the distractor object in the aforementioned experiment, have been shown to exert less capture (Irwin et al., 2000). Visual onsets, in fact, are known to reliably and automatically capture attention and gaze (e.g. Theeuwes, 1994; Yantis & Jonides, 1990; Mulckhuyse et al., 2008; Schreij, Theeuwes & Olivers, 2010). Our distractor onset was perceived by the observers, highlighted by the fact its presence affected SRTs and caused an overall decrement to perceptual performance at the non-distractor locations. It, however, did not draw attentional resources to itself, nor did it capture gaze (< 3% of trials). Because the distractor was perceived, but did not lead to capture, it can be assumed it was inhibited, and that this inhibition occurred at an early stage of the distractor appearance (a point of view promoted by Lamy, Tsal, & Egeth (2003). Several findings support this explanation. Firstly the distractor's colour feature was predictable, and remained so throughout all the sessions. Over trials observers likely became efficient at applying top-down inhibition at the distractor onset location (suggested in Müller, Geyer, Zehetleitner, & Krummenacher, 2009; Zehetleitner, Proulx, & Müller, 2009). The high frequency of distractor present trials likely added to making inhibition of the distractor easy to achieve. Thus, participants in our study could have acquired a suppression strategy (Müller et al., 2009), limiting distractor processing at the initial stages. Moher, Abrams, Egeth, Yantis & Stuphorn (2013) found that when observers knew the probability that a distractor would appear was high, rapid suppression of the distractor occurred. Very similarly, Geyer, Müller, & Krummenacher (2008) found that when it was expected that a distractor would appear on screen, the observer's was not captured. These findings, of course, apply directly to our experimental design and could explain why the residual pre-saccadic attention was not allocated to the onset. Lastly, it is worth considering that the visual impact of the onset may have been greatly reduced. The distractor onset appeared at a fixed time, during the colour change that revealed the saccade target. This means that two of the three initially presented items changed colour simultaneously with the onset's appearance, likely reducing its capturing power.

## 6.4 Residual Attention: Mechanical Allocation to Visual Objects

Part of the residual pre-saccadic attention not allocated to the upcoming saccade target is predictively remapped (see "Predictive Remapping" in the introduction), in order to maintain attention at locations of interest across eye movements. This therefore means that the visual system accounts for the retinal displacement caused by upcoming eye movements. There is evidence of successfully remapped visual elements that were initially attended by bottom-up signals (a salient green blob in Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013) or by top-down signals (locations associated with fruit juice rewards in Mirpour & Bisely, 2012). However, the remapping of this activation, whereby it is shifted to a novel location, appears mechanically driven by the saccade. In fact, we view this process as a mechanical allocation of attention, as it is neither driven by the observers' goals, nor can it be attributed to visual attributes. Rather, attention seems to be allocated to the remapped location based on the size and direction of the saccade vector, using these movement coordinates to shift attention in retinotopic space. A goal of the project, was to determine whether the visual system accounts for the retinal displacement caused by involuntary movements, just as it does for goal-directed saccades (e.g. Duhamel, Colby, & Goldberg, 1992; Rolfs et al., 2011; Szinte, Carrasco, Cavanagh, & Rolfs, 2015). Our findings showed that when a sequence of two saccades was carried out, the second saccade target was remapped, so as to maintain attention at its location, even once the initial capture saccade has been completed. Enhancement at the remapped location was only found when the two saccades were programmed largely in parallel, highlighted by the length of their dwell time (short in this case). These findings mirrored those of Rolfs et al., (2011) who showed behaviourally for the first time, that perceptual enhancement could be found at the remapped location of a second saccade goal, when a sequence of two saccades was planned. The neurons in retinotopically organized spatial areas that control for saccades and attention have been shown to become pre-activated in anticipation of the soon-to-arrive stimulus (Sommer & Wurtz, 2006). As the visual system must ignore saccade-induced visual changes (Wurtz, 2008), while acting in anticipatory fashion, it would be expected that attention is remapped prior to saccades, regardless of the level of volition driving the saccade. Our findings largely confirmed this prediction.

## 6.5 Conclusion

In a series of experiments it became apparent that the visual system is highly sensitive to the presence of visual objects, presented close to the time of the saccade. This sensitivity translated directly to attentional modulation. We saw that a pre-saccadic shift of attention was deployed to the saccade target even when this was a capturing distractor. This lead to speculation that pre-saccadic shifts of attention are the signature of all saccades types. Despite this seemingly obligatory shift we learned that attentional resources allocated prior to an eye movement are not fixed; rather they are highly shaped by the visual objects present in the visual field. How residual attentional resources, not allocated to the saccade target, were employed, was also observed in detail, along with how bottom-up and top-down signals shape this deployment.

# Résumé

Notre système visuel est ancré dans la fovéa, car le traitement profond des informations visuelles ne se produit que dans le centre de la rétine. Cela oblige les yeux à faire des mouvements constants afin d'apporter ces éléments visuels dans la fovéa. Malgré cela, les mouvements oculaires passent largement inaperçus et l'environnement est perçu comme visuellement stable. Les déplacements de l'attention avant le mouvement oculaire pourraient garantir cette stabilité en facilitant la transition d'une image à une autre dans la fovéa. Avant le mouvement oculaire, l'attention se déplace vers l'endroit où les yeux vont atterrir et les éléments visuels qui y sont présentés vont être traités préférentiellement. Un mécanisme similaire, également basé sur la répartition de l'attention dans les coordonnées « retinotopic » est connu sous le nom de « remapping ». Il permet de maintenir l'attention sur les lieux d'intérêt à travers les mouvements des yeux, tout en tenant compte du déplacement de la rétine causée par chaque mouvement à venir. Dans la thèse actuelle, nous nous intéressons à la façon dont les éléments visuels présents dans l'environnement influencent la répartition de l'attention avant les mouvements oculaires.

### 1.1 Introduction aux mouvements oculaires saccadés

Le système visuel humain est un outil extraordinaire et complexe, largement considéré comme le plus important de tous ces sens. Il a le plus grand nombre de zones dédiées dans le cerveau et la plus grande quantité de neurones qui produisent, au final, la vision. La priorité qui est mise sur le traitement visuel n'est pas spécifique pour l'homme, mais plutôt une caractéristique d'un grand nombre de mammifères. En effet, Sprague (1996) explique que le traitement neuronal dans le cortex visuel est largement distribué et comprend environ la moitié du cerveau de nombreux animaux mammifères, les plus intensément étudiés en laboratoire étant le rat, la gerbille, le hamster, le toupaye, le chat, le galagos,le hibou, le singe et le macaque. Chez le chat, 20 aires visuelles dédiées ont été identifiées dans le cortex, dont beaucoup sont organisé de manière rétinotopique et contenant des cartes spatiales allant, en termes de représentation de l'acuité de la structure de l'environnement, de grossière à fines. Cela signifie que l'information visuelle s'adapte de l'environnement de l'individu et est organisé en dans de nombreuses « cartes », ou des structures de base, à travers le cerveau, chacun différant en niveau de détail. Au centre de l'enquête globale que nous traitons est la façon dont cette information est obtenue. Les yeux reçoivent d'abord l'entrée visuelle et leur physiologie oblige le système visuel à fonctionner de façon très spécifique, afin de compenser ses faiblesses et exploiter ses points forts. Le plus haut niveau de clarté est offert uniquement dans le point centrale de fixation, i.e. à un ou deux degrés du champ visuel. Cela conduit les humains à changer leur regard à intervalles réguliers, généralement 3 ou 4 fois par seconde, afin de traiter et de comprendre l'environnement visuel (Findlay et Gilchrist, 2003). De ce fait, les mouvements oculaires saccadés servent principalement à apporter des images d'éléments d'intérêt dans la fovéa. Ils sont, comme expliqué par Reddi & Carpenter, (2000), souvent déclenchée par l'apparition soudaine d'un stimulus visuel dans la périphérie et peuvent atteindre des vitesses de 900 degrés par seconde, avec un cours à temps notamment standardise. Ils sont, en fait, les plus rapides de tous les mouvements du corps. Il y a trois muscles qui génèrent le mouvement du bulbe oculaire : le rectus latéral et médial (gauche et droite), le rectus supérieur et inférieur (haut et bas) et l'oblique supérieur et inférieur (principalement pour des mouvements de rotation obliques) (voir la figure 1). Les saccades sont connues comme balistiques, en ce que, une fois planifiée, leur destination a été établie. Même si cela a été considéré comme étant vrai durant de nombreuses années, les récentes découvertes de Mathot, Melmi, & Castet (2015) sur la base des travaux antérieurs de Castet, Jeanjean, et Masson (2002) ont démontré que la perception reste active pendant le mouvement saccades, à son tour, affecte la dilatation des pupilles.

### 1.3 Stabilité visuelle

Il a été discuté jusqu'à présent que les mouvements oculaires sont principalement déclancher pour « fovéiser » les objets, i.e apporté rapidement ceux-ci dans le domaine de la plus haute résolution pour un traitement en profondeur. Ceci, cependant, ouvre à un défaut de conception potentiel, qui sera précisé par l'analogie de la caméra vidéo suivante. Nous pouvons considérer nos yeux comme une caméra vidéo filmant le monde, tenu par un caméraman. Chaque déplacement de la caméra à un objet d'intérêt maintenant, et chaque poignée de main, correspondent à un mouvement des yeux. Même avec les caméras vidéo la plus haute résolution et les mains les plus stables de la qualité de l'information visuelle apparaissent saccadées au mieux, et aboutissent souvent à une image brouillée. Alors que la technologie n'a pas encore de surmonter ces limitations du système visuel humain réussi depuis longtemps. Malgré les saccade et le changement rapide de l'image dans nos rétines, le monde semble reste stable. Nous percevons le monde comme un flux régulier et continu de l'information visuelle, et non pas une séquence de clichés d'objets « fovéisés ». La façon dont la stabilité visuelle est atteinte étant donné ce que nous savons du système visuel, a suscité la recherche scientifique depuis des siècles. Déjà au 19ème siècle, Herrmann von Helmholtz a proposé que pour chaque mouvement des yeux, une copie efférente soit créée (une copie de la commande du moteur, également appelé décharge corollaire). La copie efférente nous permet d'anticiper les changements sensoriels du mouvement, et donc la distinction entre le mouvement et le mouvement de la rétine auto-induite dans le monde extérieur. Plus récemment, des expériences neurophysiologiques ont fourni des preuves solides pour cette idée (résumée dans Sommer & Wurtz, 2008a, 2008b). Une voie neuronale d'une saccade, liant les zones subcortical du SC à la FEF, a été identifiée. Les neurones de cette voie montrent un modèle de décharge remplissant les critères pour un signal de copie efférente. Le concept de copie efférente, avec une activité oculomotrice juste avant un mouvement oculaire fournissant des informations sur l'emplacement prévu d'un objet pertinent sur la rétine suite à une saccade, est donc un candidat de choix pour expliquer comment le système visuel va au-delà des clichés pour atteindre la stabilité visuelle.

### 1.4 Attention Visuelle : Traitement préférentiel

La quantité d'information visuelle reçue par le cerveau à un moment est trop grande être traité par notre système visuelle en entier. Une sélection est donc nécessaire pour traiter que les informations les plus pertinentes pour le comportement actuel. Ce mécanisme de sélection est appelé l'attention visuelle. Il est important de fournir d'abord une définition de l'attention visuelle. Nous définissons l'attention visuelle que le traitement préférentiel des parties de notre environnement visuel. On observe donc l'attention visuelle dans sa manifestation qui est le traitement préférentiel, ce qui conduit à la transformation en profondeur d'une position dans l'espace et non d'un autre. Cette position théorétique sur l'attention visuelle suggère des différences sémantiques mineures avec celle de Rizzolatti, Riggio, & Sheliga (1994), qui déclarent : « attention spatiale est la conséquence d'une facilitation des neurones dans les cartes spatiales pragmatiques ». Les cartes spatiales pragmatiques sont tout simplement des circuits neuronaux qui représentent l'espace dans un système de coordonnées d'attentionnel spatiale et sont lié à des emplacements dans cet espace. S'en dégage une manifestation, qui est la facilitation. Le traitement préférentiel n'est pas toujours dépendant de la volonté, avec d'innombrables exemples dans la littérature d'observateurs agissant un peu comme des détecteurs passifs de luminosité et de saillance (Theeuwes, 1992, 1993 ; 2010) et même de la récompense (Anderson, Laurent, et Yantis, 2011). Ici, l'attention visuelle est allouée à des endroits à la mode automatique apparente et est définie comme « bottom-up ». Lorsque l'attention visuelle est activement allouée par l'observateur, elle est plutôt appelé « top-down ». Les facteurs « bottom-up » et « top-down » influenceraient conjointement la distribution de l'attention covert (Cave & Wolfe, 1990 ; Wolfe, 1994). De ce point de vue, le bas niveau des caractéristiques visuelles des objets, ainsi que leur pertinence à la tâche, façonnent l'allocation de l'attention. Par exemple, un objet rouge vif saillant entre les objets verts attirera l'attention. De même, quand on nous dit de trouver des triangles dans un affichage, une attention covert sera attribuée principalement à des objets qui correspondent à la description. Les objets sont donc comparés à un ensemble de haut en bas notamment avec ceux qui portent une plus grande similitude avec la cible de recherche d'attirer une plus grande attention (Ansorge, Kiss, Worschech, & Eimer, 2011; Eimer & Kiss, 2008; Folk et al, 1992). L'allocation attentionnelle sélective, nous permet donc de surmonter l'incapacité de notre système à traiter efficacement de nombreuses cibles simultanément, ceci en structurant l'apport de l'environnement. Que le système visuel soit en mesure d'assister à plusieurs endroits distincts simultanément est une question qui a intéressé les chercheurs depuis de nombreuses années. Kramer & Hahn (1995) à condition que le premier aperçu du sujet en prouvant que l'attention pourrait être attribué à deux régions non contiguës, alors que l'attention ne pouvait être divisé entre stimuli apparition. Müller, Malinowski, Gruber, & Hillyard (2003), basés sur ces résultats, ont prouvé que l'attention pouvait être attribuée à des positions distinctes spatialement, ceci pour des périodes de temps prolongées. Surtout, ils montrent que les positions entres ces positions distinctes ne sont pas englobés par la propagation de l'attention et qu'il n'y avait aucun coût associé à porter son attention à deux positions distinctes par rapport à deux adjacents.

### 1.5 Attention Visuelle : « Shifts » d'attention pré-saccades

Un lien étroit a été démontré maintes et maintes fois entre les mouvements oculaires et l'attention visuelle, ce qui n'est pas surprenant puisque les mouvements oculaires ont comme but principal de collecter l'information du monde, au moyen d'un outil, la « fovéalisation ». L'un des effets les plus fiables et très étudiés dans la science de la vision est le changement d'attention fait, juste avant que le mouvement de l'œil ne soit fait, à l'endroit où les yeux vont se poser (Duebel & Schneider, 1996 ; Hoffman & Subramaniam, 1995 ; Kowler, Anderson, Dosher, & Blaser, 1995). Cela a été démontré que conduire à un traitement préférentiel à l'endroit où les yeux vont atterrir (Duebel & Schneider, 1996), avec une attention anticipant donc le mouvement des yeux se poser. C'est donc comme si les yeux commencent à voir avant de voir. Ceci signifie des niveaux élevés d'acuité perceptive à l'endroit où ils vont se poser, même si les yeux ne sont pas encore déplacer. En outre, le déploiement de l’attention visuelle suit une dynamique temporelle relativement stricte, en augmentant progressivement, à partir de plusieurs centaines de millisecondes avant que le mouvement (250 ms en Deubel 2008, 170 ms dans Rolfs et al, 2010) et atteint son apogée juste avant l’exécution. L’attention visuelle est donc le temps de verrouillage à l’apparition de la saccade. Seule une poignée de donnés à ce jour ont fourni des preuves de découplage (notamment Belopolsky & Theeuwes, 2009), et avec la version la plus forte d’une théorie très populaire, le théorie « prémotrice » de l’attention (Rizzolatti, Riggio, Dascola, & Umilta, 1987; Rizzolatti, Riggio, et Sheliga, 1994). Cette théorie suggère que les mouvements des yeux et les mouvements d’orientions de l’attention sont codés de façon identique dans des structures du cerveau. Il a, en effet, suggéré que l’attention et les mouvements oculaires peuvent faire partie du même système. Il est intéressant de noter que le décalage spécifique de l’emplacement de l’attention qui précède un but direct, retarde la saccade de l’attention implicite, distribuée étroitement (Zimba & Hughes, 1987) et centrée presque exclusivement autour de l’emplacement cible (Kowler, Anderson, Dosher, & Blaser, 1995). Il est largement accepté que quand une saccade cible dirigée est programmée, les emplacements non-cibles reçoivent peu ou pas de mise en valeur (voir Kowler, Anderson, Dosher, & Blaser, 1995), tout comme il est impossible d’effectuer une saccade vers une cible connue tout en déplaçant activement l’attention vers un autre emplacement (Deubel & Schneider, 1996). Le lien entre saccades et l’attention est considéré non seulement dans le comportement, mais aussi au niveau neurophysiologique, en particulier dans FEF, une région corticale discutée précédemment dans la section de la neurophysiologie. Moore & Fallah (2001) ont choisi une approche de microstimulation pour enquêter sur le lien entre la FEF et l’attention visuelle. Ils ont observé que lorsque les microstimulations ont été administrées sur des neurones en rapport avec l’emplacement du champ de mouvement associé, et maintenu en dessous du seuil saccades, la sensibilité au contraste fortement augmenté. Cela signifiait que, malgré les microstimulations étant insuffisantes pour déclencher la saccade, l’activité dans ce domaine a été intimement liée à l’attention visuelle. De même, Wardak et al., (2006) a injecté du « muscimol » à divers endroits autour de FEF, ce qui simulait une lésion dans la région. Des changements spectaculaires dans le comportement des saccades ont été accompagnés par une déficience allocation de l'attention visuelle, suite à l'inactivation de la région. Les mouvements oculaires et l'attention visuelle sont donc étroitement liés. En conséquence, beaucoup ont essayé d'établir quel rôle de ce mécanisme joue dans l'élaboration de la vision. Il a été avancé que le traitement préférentiel de l'objet sur le point d'être « fovéalisé » est relié à la perception de la stabilité visuelle. Dans cette perspective, le changement de l'attention pré-saccades fournit une prévision de la saccade à la cible, et ce modèle peut ensuite être comparé à l'entrée visuelle post-saccades. Informations sur la cible saccade semble jouer un rôle particulier dans la détection des déplacements de stimulation externes (Currie, McConkie, Carlson-Radvansky, et Irwin, 2000). Un certain nombre de chercheurs, en effet, croire que les changements pré-saccades de l'attention peuvent faciliter le maintien de la stabilité et de la continuité de la perception à travers les saccades (Deubel, Schneider, et Paprotta, 1998 ; Currie et al., 2000 ; Melcher, 2009). Ce mécanisme pourrait être le pont entre les « fovéation » instantanés du monde et la stabilité visuelle, chaque image étant « allégée » dans le système visuel avant que le mouvement des yeux soit déclenché.

### 1.6 Attention Visuelle : Predictive Remapping

Nous avons vu que des points d'intérêts dans le champ visuel peuvent attirer l'attention de manière considérable et ceci même avant l'exécution d'un mouvement des yeux, l'attention se déplaçant à l'endroit où le mouvement des yeux s'achève. Qu'arrive-t-il à alors à l'attention allouée à ces points d'intérêts quand un mouvement des yeux (modifiant inévitablement l'image sur la rétine) est effectué? Le système visuel parvient à maintenir un traitement préférentiel pour certains ces points d'intérêts, en prenant en compte les mouvements des yeux à venir. Ce traitement est appelé « remapping » et fait référence à un changement de profil spatial de champs récepteurs neuronaux précédant l'exécution d'une saccade (Hall & Colby 2011; Wurtz, Joiner & Berman, 2011). Ce transfert d'activité entre neurones organisés rétinotopiquement, documenté par Duhamel, Colby, et Goldberg (1992), nous permet de maintenir l'attention sur les points d'intérêt d'une scène visuelle tout en compensant pour les mouvements oculaires à venir (pour une revue de question sue ce thème, Cavanagh, Hunt, Afraz & Rolfs, 2010). Lors de la programmation d'un mouvement des yeux vers une cible, l'attention se déplace à l'endroit où les yeux sont amenés et environ 80 millisecondes avant l'initiation de la saccade, l'attention se trouvant aux positions d'intérêts est remappé de manière prédictive. Cela signifie que l'ajustement de l'attention juste avant les mouvements oculaires est fait de façon à ce que ce traitement préférentiel se maintient à la position des points d'intérêts même après la saccade. Ceci est réalisé en déplaçant temporairement l'attention déployée aux points d'intérêt dans la direction opposée du mouvement des yeux à venir. En d'autres termes, un déplacement de l'attention se produit dans la direction opposé aux points d'intérêt, un déplacement de taille équivalente à la future saccade. Des améliorations perceptive ont été observé à ces nouvelles positions (Rolfs et al., 2010). En déplaçant l'attention d'un point d'intérêt à un emplacement nouveau dans le sens opposé à la saccade, notre système visuel anticipe les conséquences des mouvement des yeux à venir, et garanti que l'attention sera à l'emplacement des points d'intérêts une fois la saccade achevée (Cavanagh, Hunt, Afraz & Rolfs, 2010).

### 1.7 Attention Visuelle : Capture attentionnelle

Nous avons vu jusqu'à présent que l'allocation de l'attention visuelle peut conduire à la transformation en profondeur des lieux d'intérêt et il peut commencer préférentiellement le traitement de l'endroit où les yeux vont atterrir avant que le mouvement soit réellement exécuté. Cependant, l'attention visuelle peut également améliorer le traitement de l'information inutile ou préjudiciable qui arrive à attirer des ressources attentionnelles. Le monde est rempli de distractions, allant de bannières publicitaires flashy à l'apparition soudaine d'un pop-up Internet. Un but principal de l'attention est de limiter le traitement à des éléments pertinents à notre comportement actuel, et de minimiser les interférences de distracteurs non pertinentes. La littérature attentionnelle-contrôle a mis l'accent sur les mécanismes de l'attraction de distracteurs, avec des cas où l'attention visuelle surmonte efficacement la distraction étant du côté opposé évident de la pièce de monnaie. Principalement deux positions ont été proposées, opposée radicalement. On propose que l'attention soit induite par des stimuli et que distracteurs saillants capturer l'attention quel que soit avec ses objectifs ou ensemble attentionnel (Theeuwes, 1992, 2010). Cette conceptualise distraction attentionnelle, principalement appelée capture comme attentionnelle, comme un processus presque entièrement réflexif. L'autre position propose que l'attention visuelle soit entraînée par les objectifs de l'observateur et que la capture attentionnelle soit contingente aux buts attentionnels d'un observateur (par exemple, Folk, Remington, & Johnston, 1992). Cela signifie que seuls les distracteurs qui portent une certaine similitude visuelle à un objet, ou des objets d'intérêt, donc correspondant à un ensemble attentionnel actuel, capteront l'attention. Bien qu'il y ait eu un débat au cours des 20 dernières années, au moment où l'attention est capturée et lorsque l'attention surmonte la distraction, il y a un accord général que lorsque les objets multiples sont affichés avec une cible de recherche, une compétition pour les ressources attentionnelles se pose, avec saillants objets provoquant une atteinte substantielle (Bacon & Egeth 1994 ; Becker, 2007 ; Fecteau, 2007 ; Folk & Remington, 1998 ; Folk, Remington, & Johnston, 1992 ; Lamy, tsal, & Egeth, 2003 ; Theeuwes, 1991, 1992 ; Yantis & Hillstrom, 1994) et que chaque objet perçu attire une certaine quantité d'attention secrète (Müller & Krummenacher, 2006;. Zehetleitner, Krummenacher, et al, 2011). L'effet est plus fort lorsque le distracteur est étroitement positionné à la cible (Bahcall & Kowler, 1999), il peut se produire même lorsque le distracteur est totalement indifférent à la tâche à accomplir (Theeuwes, 1994) et a été observé dans les milieux où les participants étaient demandés explicitement d'ignorer le distracteur (Remington et al., 1992).

## 1.8 Attention Visuelle : Inhibition

Bien que certains endroits ou caractéristiques peuvent être améliorés du point de vue de la perception, le système visuel a la capacité d'inhiber le traitement de certains éléments . Aussi, tout comme pour l'amélioration de la perception, il existe divers degrés de l'intentionnalité entourant le processus. Au niveau purement mécanique (c.-à-d "void of intention") l'inhibition peut être trouvée autour d'une région de traitement visuel amélioré (Cutzu & Tsotsos, 2003; Müller, Mollenhauer, Rösler, et Kleinschmidt, 2005; Serrano-pedraza, Gamonoso-cruz, & Derrington , 2013). Il a en effet été démontré que les formes d'inhibition d'un anneau suppressive dans le voisinage immédiat d'un élément ciblé. Ceci est connu comme la "suppression surround" et a été montré pour être plus marqué pour les objets présents à la périphérie (Xing & Heeger, 2000). Müller et al. (2005) ajoute un aperçu de la forme spécifique de l'anneau suppressif. Les auteurs ont manipulé la difficulté d'une tâche visuelle et observé qu'une plus grande quantité de ressources attentionnelles allouées à une cible (ex: seuil de facilitation plus élevé) a conduit à une immersion plus profonde de l'inhibition entourant la cible. D'autre part, lorsque la cible était facile à distinguer, elle a été également moins améliorée et a conduit à une immersion inhibitrice moins profonde de l'entourage. Ici, l'inhibition semble démarquer l'endroit où la facilitation se termine. D'une manière similaire, l'inhibition est souvent appelée à modifier l'équilibre des ressources attentionnelles allouées à des stimuli en compétition les uns avec les autres. La concurrence peut en effet être biaisée en inhibant les distractions concurrentes de manière à favoriser un stimulus particulier cible (Desimone & Duncan, 1995; Mathot, Hickey, et Theeuwes, 2010). Les objets distrayants proéminents peuvent en effet être efficacement ignorés, afin d'assister à une cible moins saillante. Est-ce que le système visuel atteint cet objectif en supprimant activement les distractions ou en donnant plus d'importance aux caractéristiques des cibles? Gaspar & McDonald (2014) ont observé que les distractions saillantes ont été supprimées, même quand ils étaient tous les deux singletons de couleur, ce qui signifie que leur poids volumétrique ne permettrait pas la sélection de la cible. Les auteurs concluent que les distractions saillantes inutiles sont activement supprimées et que cela ne se produit que lorsque la distraction n'a pas réussi à accéder à la mémoire de travail. La suppression active a été vu de non seulement empêcher la répartition de l'attention, mais aussi de mettre fin à l'activation d'un élément déjà ciblé (Sawaki, Geng, et Chance, 2012). Cet ensemble de résultats montre que l'inhibition joue un rôle essentiel dans la formation de l'allocation d'attention aux cibles visées. Enfin, tout comme la *facilitation* qui est un terme également lié au processus de l'allocation d'attention et aux processus moteurs, la même chose s'applique pour l'inhibition. Il a récemment été démontré que l'inhibition d'une réponse motrice particulière dans une tâche d'arrêt ne portait pas de conséquences sur la réponse choisie (Xu, Westrick, et Ivry, 2015), ce qui suggère que les processus inhibiteurs sont indépendants des processus de facilitation.

### 1.9 Résumé de l'état de la recherche et un aperçu de la thèse actuelle

Les sujets abordés à ce point figureront dans les documents scientifiques énoncés dans les chapitres suivants. Certains sujets ne seront pas seulement abordés brièvement, mais seront les piliers de l'enquête. L'accent sera mis sur les processus perceptifs qui se produisent avant les mouvements oculaires, afin de mieux comprendre à la fois leur fonctionnement et comment cela pourrait aider à parvenir à la stabilité visuelle. L'introduction a abordé le débat de longue date sur la façon dont le système visuel atteint la perception d'un flux cohérent et stable de l'information, en dépit de l'exploration visuelle menée par les mouvements oculaires ayant une grande clarté que dans la fovéa. Les changements d'attention à la cible saccade ont été observés avant les mouvements oculaires, et il a été suggéré qu'ils facilitent la transition entre chaque «capture» de la fovéa, comblant l'image pré et post-saccades. Il a été démontré que l'attention visuelle est retracée d'une manière prédictive à partir d'endroits fréquentés, juste avant l'exécution de mouvement oculaire, afin de maintenir l'attention à ces endroits durant les mouvements oculaires. Nous visons d'abord de déterminer si ces processus attentionnels ne se produisent que pour les mouvements ciblés, où l'intention de bouger les yeux peut induire les changements décrits et de retraçage d'attention. En outre, ces processus attentionnels pourraient être une caractéristique déterminante de toutes les saccades, indépendamment de l'intentionnalité. Cette possibilité serait une condition préalable à un ensemble de processus étroitement liés en charge de la réalisation, ou tout au moins aider, la stabilité visuelle. Considérant que la recherche précédente a évalué avec succès le déplacement de l'attention avant une saccade dirigée vers un but volontaire à un emplacement cible, notre étude initiale examinera si une capture oculomotrice conduit aux mêmes avantages perceptifs à un emplacement de capture de distraction. Nous visons également à déterminer si le retraçage prédictif d'objets aperçus est réalisée également lorsque les saccades involontaires sont faites, ce qui signifie que les conséquences de la perception d'une saccade involontaire sont également pris en compte. Une grande partie du projet aura pour but de déterminer si les changements d'attention sont standardisés pour tous les mouvements oculaires saccadés, où l'attention est attribuée au point de la prochaine saccade. D'autre part, l'environnement visuel, qui est la relation spatiale entre les objets visuels présents au et autour du point d'atterrissage de la saccade, pourrait façonner le déplacement des ressources attentionnelles. Si tel est le cas, il sera intéressant de tracer la propagation de l'attention pré-saccades quand un objet est présent et quand il ne l'est pas. Les différences dans la propagation attentionnelle pourraient aider à déterminer le comportement de la dégradation de la mémoire par rapport au temps de l'attention visuelle associée à l'emplacement du stimulus. Comme l'ensemble de l'enquête tourne autour des processus qui se produisent au moment précédant le mouvement des yeux, une partie du projet visera à évaluer la façon dont la planification des saccades est affectée par le nombre variable de stimuli présentés. L'enquête va donc aborder le sujet de l'accumulation des informations de pré-saccades, en vue d'atteindre un seuil de décision, comme un lien entre la planification et l'exécution des mouvements oculaires saccadés.

En somme, l'état actuel de la recherche postule que la planification des saccades est étroitement couplé avec l'attention. Ceci est basé sur le fait que l'attention est spatialement et temporellement le temps de verrouillage du mouvement de l'oeil mis à venir; un mécanisme proposé comme explication de la façon dont le système visuel relie les captures continues de la Fovéa. Cependant, nous ne savons pas si ce processus se produit pour toutes les saccades, si elle est influencée par les éléments visuels présentés, si les cibles présentent uniquement dans la mémoire conduisent à un autre déplacement de l'attention, ou si la planification des saccades se produit automatiquement lorsque les cibles sont présentées. Dans les chapitres suivants quatre études seront présentées:

*Étude 1 : Enhancement Perceptual avant prévu et Involuntary Saccades*

Cette étude a examiné les changements pré-saccades de l'attention faite à une cible déterminée ou faite à un écarteur de capture. La preuve a été obtenue que les déplacements de l'attention visuelle sont relativement indifférents par des objectifs saccade, et que les séquences de saccades de capture-corrective aussi conduire à remappage attentionnel. L'étude a été publiée dans le Journal of Vision (Puntiroli, Kerzel, & Born, 2015).

*Étude 2 : Course d'accumuler des preuves de décision saccade : une exception pour accélérer précision compromis*

Cette étude a examiné la planification des saccades dans les grandes et petites tailles set. Nous avons constaté que l'exécution de saccades à une cible dans un grand format de jeu peut conduire à des latences réduites par rapport à une petite taille de set. Cette différence ne vient pas au détriment de la précision et ne prédit par un modèle d'accumulateur populaire. L'étude a été soumise pour publication, et des révisions mineures sont nécessaires.

*Étude 3 : Les objets et leur disposition affectent visuelle Attention avant les mouvements oculaires*

Cette étude a examiné si le traitement préférentiel trouvé à l'endroit où les yeux vont atterrir est purement dicté par des mesures saccade. À cette fin, nous avons présenté un nombre différent de placeholders à et autour de l'emplacement cible saccade. Les résultats montrent que les objets visuels et leur arrangement influent sur les emplacements choisis pour le traitement préférentiel. L'étude a été soumise pour publication.

*Etude 4 : Changements pré-saccades malléables d'attention*

Cette étude a examiné l'évolution pré-saccades d'attention lorsque l'objet cible saccade était présent et quand il avait disparu peu de temps avant que le mouvement (à savoir présente uniquement dans la mémoire de travail visuelle). Des cartes détaillées de la propagation de l'attention ont été obtenues dans les deux conditions. Le résultat montre que lorsqu'un objet cible est présent l'attention se déplace spécifiquement à cet endroit et quand l'objet cible est plus présent l'attention se propage à partir du point d'atterrissage et en outre aux endroits environnants. L'étude est en cours de préparation pour la soumission.

# Discussion sur les points principaux

### 2.1 Attribution classique de l'attention pré-saccadique à les Objets Visuel Pas-Bout

Dans une série d'études (1,2 et 4) nous avons reproduit l'effet classique du déplacement de l'attention avant le mouvement oculaire, de sorte que l'attention visuelle se déplace vers l'emplacement de la cible de la saccade avant le mouvement des yeux (comportemental : Duebel & Schneider, 1996 ; Hoffman & Subramaniam, 1995 ; Kowler, Anderson, Dosher, & Blaser, 1995 ; neurophysiologique : Tolias et al 2001 ; Zirnsak et al, 2014) et continue d'augmenter jusqu'au moment où le mouvement est initié (Deubel, 2008 ; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Le traitement préférentiel était étroitement et presque exclusivement concentré autour de l'objet cible de la saccade, c'est-à-dire lorsque ces saccades étaient effectivement exécutées et allaient directement à la cible prévue, avec la présence d'un distracteur saillant (Etude 1), de distracteurs adjacents non saillants (Etude 3) ou sans objets distracteurs (Etude 4). Néanmoins, le même phénomène a été observé pour les saccades de capture (Etude 1). Autrement dit, un déplacement de l'attention pré-saccade, à l'endroit d'atterrissage de la saccade, a eu lieu même si cette saccade avait été capturée par un objet distracteur saillant au lieu de la cible. Tout comme pour les saccades dirigées vers un but, des éléments visuels présents à l’emplacement du point d’atterrissage d’une saccade de capture font l’objet d’un traitement en profondeur, avec une attention croissante jusqu’au moment où la saccade est lancée. En effet, le traitement préférentiel a été observé à l’emplacement du distracteur et des cibles de la saccade, reflétant les conclusions de Godijn & Theeuwes (2003), Baldauf & Deubel (2008) et Rolfs et al. (2011) qui ont constaté que l’attention pourrait se déplacer vers deux cibles de saccade lorsqu’une séquence de saccades prédéterminée est exécutée. Ces différentsauteurs constatent tous que la planification de séquences de saccades vers deux, voire même trois endroits conduits à des avantages perceptifs aux emplacements des buts des saccades, comparés aux endroits où les mouvements oculaires n’arrivent jamais. Cela se voit aussi dans nos conclusions. Il y a de fortes raisons de croire que l’attention pré-saccadique est allouée de façon indépendante à ces points d’atterrissage séquentiels, tels que l’emplacement du distracteur et de la cible de la saccade dans l’Etude 1 dans le cas d’une capture oculomotrice. L’hypothèse ici est que l’attention peut se déplacer de façon divisée vers des emplacements spatiaux non-contigus, plutôt que de s’élargir afin d’envelopper les deux endroits (comme suggéré par Pan & Eriksen, 1993 ; Posner, Snyder, et Davidson, 1980 ; McCormik, Klein, & Johnston, 1998 ; Eriksen et Yeh, 1985). Les résultats de Baldauf et Deubel (2008) confirment cette hypothèse. Les auteurs demandent aux participants d’exécuter des séquences de deux ou trois saccades et mesurent la performance attentionnelle aux endroits ciblés et également aux endroits intermédiaires non-ciblés. Bien que les performances perceptives aux endroits ciblés se trouvent améliorées, les performances chutent au niveau de la chance aux endroits intermédiaires. Ces résultats ne peuvent pas être expliqués par des modèles postulant un seul foyer élargi de l’attention. Des résultats comportementaux très similaires ont été obtenus par Klapetek, Jonikaitis, et Deubel (2016), qui employaient un paradigme d’antisaccade et qui ont observé que l’attention était divisée entre l’emplacement de l’indice (« cue ») et de la cible de l’antisaccade, lorsque de saccades erronées ont été apportées à l’indice. Müller, Malinowski, Gruber, et Hillyard (2003) ont également mis en évidence que l’attention pourrait être divisée entre des endroits non-contigus, en regardant le « steady-state visual evoked potentials » (SSVEP), en l’absence de mouvements oculaires. Les auteurs demandent aux participants de prêter attention à des séquences de symboles présentés à deux emplacements sur quatre, et appuyer sur un bouton lorsque les symboles appariés aux deux endroits visités par l'attention. Il est important de noter que les SSVEP sont plus importants pour les stimuli visités par l'attention visuelle. Les principales conclusions étaient que les amplitudes SSVEP aux endroits intermédiaires (entre deux endroits visités par l'attention visuelle) étaient considérablement réduites par rapport à lorsque ces mêmes endroits étaient visités par l'attention visuelle. Étonnamment, il n'y avait pas de coût apparent de la division de l'attention entre de multiples endroits, étant donné que la focalisation sur deux emplacements adjacents ou deux emplacements non-adjacents ne provoquait pas de différences en termes de SSVEP. Il y a de fortes raisons de croire que l'attention a été allouée en parallèle aux deux points d'atterrissage de saccade dans notre Etude 1, comme dans les études de Godijn et Theeuwes (2003), Baldauf et Deubel (2008), Rolfs et al., (2011) et Müller et al., (2003). Nos résultats vont à l'encontre d'un modèle séquentiel d'allocation d'attention pré-saccadique, puisque les TRs sur les essais de capture (entre 200 et 250 ms) n'étaient pas suffisamment longs afin de permettre l'identification des objets visuels, le désengagement attentionnel, et finalement le transfert de l'attention en fonction de la tâche, un ensemble de processus qui exigerait entre 200 et 500 ms selon Duncan, Ward, et Shapiro, 1994 (voir aussi Moore, Egeth, Berglan, et chance, 1996 ; Peterson & Juola, 2000 ; Reeves & Sperling, 1986). Cette répartition attentionnelle entre des emplacements spatiaux non-contigus, attribuée de façon parallèle au distracteur et à la cible de la saccade, a des implications importantes pour d'autres endroits non visités par une saccade, que nous discuterons ultérieurement (dans la partie « Attention résiduelle : Allocation mécanique »). Dans leur ensemble, nos résultats mettent en évidence qu'une quantité importante de ressources attentionnelles est obligatoirement attribuée à tous les endroits visités par les mouvements oculaires, et les stimuli présents dans ces endroits sont traités préférentiellement, indépendamment du « top-down set » de l'observateur. L'étude de l'allocation attentionnelle précédant les saccades de capture oculomotrice (Etude 1), suivies par les saccades dirigées vers le but, et avant les saccades guidées par la mémoire (Etude 4), a souligné encore une fois le couplage fort entre saccades et attention. Ces résultats soutiennent la théorie prémotrice de l'attention (Rizzolatti, Riggio, Dascola, & umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994), qui stipule que l'activation du système moteur, dans le but d'effectuer un mouvement des yeux, conduit à un déplacement obligatoire de l'attention. En d'autres termes, la théorie considère l'attention comme fonctionnellement équivalente à la préparation de la saccade. Ici, nous voyons des preuves à l'appui du deuxième principe, les mouvements oculaires planifiés dans les expériences mentionnées ont déclenché un déplacement de l'attention, même en l'absence d'intention de la part des observateurs. Un grand nombre d'études ont montré que les actions dirigées vers un but sont précédées par des déplacements de l'attention (par exemple Duebel & Schneider, 1996 ; Hoffman & Subramaniam, 1995 ; Kowler, Anderson, Dosher, & Blaser, 1995 ; Rolfs et al, 2011, pour n'en citer que quelques-uns), de sorte que le lien étroit entre l'attention et la préparation du mouvement ne sont pas remis en cause. Il est toutefois intéressant de noter qu'un nombre croissant d'études interrogent cette théorie (e. g Gregoriou, Gotts, & Desimone, 2012 ; McPeek et Keller, 2002 ; Sato et Schall, 2003). La théorie prémotrice peut toutefois être utile en tant que cadre théorique et reste une théorie populaire, sous une forme considérablement modifiée (voir Smith & Schenk, 2012).

## 2.2 Attention résiduelle : Allocation mécanique aux Objets Visuel

Une partie de l'attention pré-saccadique résiduelle est redistribuée de façon prédictive (voir « Predictive Remapping » dans l'introduction), afin de maintenir l'attention sur les principaux sites d'intérêt à travers les mouvements oculaires. Cela signifie donc que le système visuel contient une représentation du déplacement de la rétine provoquée par les mouvements oculaires à venir. Il existe des preuves d'éléments visuels remappés avec succès qui ont été initialement assistés par des signaux de bas en haut (un blob vert saillant dans Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013) ou par des signaux de haut en bas (emplacements associés à des récompenses de jus de fruits dans Mirpour & Bisely, 2012). Cependant, le remappage de cette activation, par laquelle il est déplacé vers un emplacement roman, apparaît entraîné mécaniquement par la saccade. En fait, nous considérons ce processus comme une répartition mécanique de l'attention, car il est ni entraîné par les objectifs des observateurs, il ne peut pas être attribuée à des attributs visuels. Au contraire, l'attention semble être attribuée à l'emplacement remapped en fonction de la taille et la direction du vecteur saccade, en utilisant ces mouvements coordonnés de détourner l'attention dans l'espace rétinotopique. était un objectif du projet afin de déterminer si le système visuel représente le déplacement de la rétine causée par des mouvements involontaires, comme il le fait pour les saccades dirigées vers un but (par exemple Duhamel, Colby, & Goldberg, 1992;. Rolfs et al, 2011 ; Szinte , Carrasco, Cavanagh, & Rolfs, 2015). Nos résultats ont montré que, lorsqu'une séquence de deux saccades a été réalisée la deuxième cible a été remappé saccades, de manière à maintenir l'attention sur son emplacement, même une fois la saccade de capture initiale a été achevée. Amélioration à l'emplacement remapped n'a été trouvé que lorsque les deux saccades ont été programmées en grande partie en parallèle, mis en évidence par la durée de leur temps de séjour (courte dans ce cas). Ces résultats reflètent ceux de Rolfs et al., (2011) qui a montré comportemental pour la première fois que l'amélioration de la perception pourrait être trouvé à l'emplacement remapped d'un deuxième but saccade, quand une séquence de deux saccades était prévue. Les neurones dans les zones spatiales rétinotopique organisées qui contrôlent des saccades et l'attention a été démontré que pour devenir pré-activés en prévision de la relance bientôt à arriver (Sommer & Wurtz, 2006). Comme le système visuel doit ignorer les changements visuels saccade-induite (Wurtz, 2008) tout en agissant de façon anticipée, il serait prévu que l'attention est recartographiée avant saccades, quel que soit le niveau de la volonté de conduire la saccade. Nos résultats ont largement confirmé cette prédiction.

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