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# The link between covert attention and saccade programming: Evidence from competitive tasks

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## Summary

The present dissertation investigates the link between visuospatial attention, saccade decisions and saccade programming in the human brain, mainly relying on psychophysical methods, but also with the help of transcranial magnetic stimulation (TMS).

Several lines of evidence indicate that attention is automatically allocated to the goals of saccades in preparation (e.g., Deubel & Schneider, 1996; Moore & Fallah, 2004) and a number of studies of our research group have proven that visual discrimination performance, as a measure of attention deployment, can be used as an index of target selection in early saccade planning (Baldauf & Deubel, 2008; Dhawan, Deubel, & Jonikaitis, 2013; Jonikaitis & Deubel, 2011; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). The studies reported in this thesis also made use of this method and the second study extends it by showing that visual performance also indexes saccadic decision making.

The first study (**Chapter 2.1**) examines attentional dynamics in the antisaccade task. We measured visual discrimination performance at both the cue location (the most salient visual stimulus) and the antisaccade goal while participants programmed antisaccades and found evidence for a parallel attentional selection of both locations. The pre-saccadic visual selection of the antisaccade goal was associated with correct saccade performance, suggesting that visual and oculomotor selection in the antisaccade task are mediated by a common attentional process. The analysis of error trials provided evidence that the antisaccade task may involve the automatic parallel programming of two competing saccade programs.

The second study (**Chapter 2.2**) investigates how perceptual selection is modulated during the course of decisions between two alternative saccade targets, in a rule-based and in a free choice condition. We tracked visual selection at both possible saccade targets as well as at saccade-irrelevant locations and observed a parallel selection of both possible targets, with a clear perceptual advantage at the final saccade goal. This saccade-related bias was evident both before correct and before incorrect rule-based responses, which shows that the pattern of perceptual facilitation reflects the ongoing motor decision.

The third study (**Chapter 2.3**) studies how TMS of the frontal eye fields (FEF) affects the coupling between visual selection and saccade programming. We delivered TMS to three possible scalp locations while participants were performing a dual visual-saccadic task and found that TMS of the left FEF facilitated endogenous attention to the right visual hemifield and reduced attention at the goal of leftwards saccades, most likely through interhemispheric competition. This indicates that endogenous attention and saccade programming are separable within the FEF.



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## General Introduction

The first part of the Introduction contains a review of the most important theories and findings concerning the relationship between covert attention, saccade programming and saccadic decisions. In the second part, I will explain our motivation for the three studies that constitute this cumulative thesis.

### 1.1 Covert and overt attention: Two sides of the same coin?

When inspecting a visual scene, humans frequently make rapid goal-directed eye movements, so-called saccades, with the purpose to bring objects of interest into their fovea, where visual acuity is highest. However, it is also known that we can allocate visual attention without making an overt eye movement and that such covert attentional shifts result in enhanced visual processing at the attended location (Posner, 1980). The relation between both types of visual orienting has been a matter of scientific debate for the last three decades and no consensus has been reached to date.

In the following sections, I will first introduce the most important theories regarding the coupling between covert attention and saccades, including evidence for and against these views. I will continue by discussing findings regarding the potentially different relation of exogenous and endogenous orienting to the oculomotor system and the relation between attention and saccadic decision making. Finally, I will review evidence on how visual attention, saccade programming and saccadic decisions could be linked at the level of the brain. I hope to convince the reader that the debate whether covert and overt attention are linked or independent is obsolete, as they are simply two different consequences of the same competitive processes.

#### 1.1.1 The link between covert attention and saccade programming

Findings on neural correlates of saccade programming and attention in the superior colliculus (Goldberg & Wurtz, 1972; Schiller & Koerner, 1971; Schiller & Stryker, 1972; Wurtz & Mohler, 1976) led to the view that attention might be equivalent to the readiness to make a motor response (Wurtz & Mohler, 1976). This idea was taken up in the *oculomotor readiness hypothesis* (Klein, 1980), which states that covert visual orienting equals to the programming of an eye movement that is never executed.

Klein (1980; Klein & Pontefract, 1994) did not find empirical support for the two main predictions of their hypothesis (perceptual facilitation at planned saccade goals and speeded saccade latencies to the attended locations) and hence rejected it. Other authors also adopted the view that attentional shifts are independent from eye movement planning and that their relationship is at best functional, in terms that they often share a common goal (e.g., Remington, 1980; Posner, 1980).

The oculomotor readiness hypothesis was transformed into the very influential *premotor theory of attention* (Rizzolatti, Riggio, Dascola, & Umiltà, 1987), which vindicates the idea that visual attention reflects eye movement programming (on the basis of the authors' own behavioral experiments and by revealing weak points in Klein's methodology) and extends it to all other effector systems (Rizzolatti, Riggio, & Sheliga, 1994).

Further evidence in favor of a tight link between eye movements and covert visual attention comes from dual-task studies, in which subjects had to prepare a saccade to a location in space and make perceptual judgments about stimuli presented at that same or at different locations. Their results demonstrate that in the preparatory phase of a saccade visual processing is best at the future saccade endpoint (Deubel & Schneider, 1996; Hoffmann & Subramaniam, 1995; Kowler, Anderson, Doshier, & Blaser, 1995). This suggests that during saccade preparation visual attention automatically shifts to the movement goal and cannot be allocated to saccade-irrelevant locations, except for very special circumstances under which a part of the attentional resources can be split off (Kowler et al., 1995; Montagnini & Castet, 2007).

More recent results on the temporal dynamics of the pre-saccadic attentional deployment have shown that attention can only be diverted away from the saccade target at the very beginning of saccade preparation (Doré-Mazars, Pouget, & Beauvillain, 2004; Montagnini & Castet, 2007), as attentional engagement at the saccade target evolves gradually over time and is strongest shortly before the onset of the saccade (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel, 2008; Doré-Mazars et al., 2004; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007). The aforementioned findings demonstrate that saccade programming is sufficient for attention allocation, which is one claim of the premotor theory of attention, but they do not support its second claim that saccade programming is also mandatory for attention, in the sense that visual orienting can only take place when a saccade is being planned. The fact that visual selection is not independent from saccade programming does not necessarily imply a shared control mechanism, but could instead mean that both processes compete for some common resources.

Along these lines, Schneider (1995) argued that saccade programming is only one realm where visual attention plays a functional role, the other being object recognition, and proposed an alternative theoretical account of the relationship between visual perception and motor action. His *visual attention model (VAM)* postulates that selection for visual perception and selection for space-based motor action are performed by a single attention mechanism, which always selects one object at a time. Low-level visual representations in area V1 that correspond to the selected object receive prioritized processing in higher-level areas of the ventral and dorsal pathways (see Goodale & Milner, 1992; Mishkin, Ungerleider, & Macko, 1983). This leads to faster recognition and conscious perception of the selected object and to the computation of one or several motor programs towards the object, which are not necessarily executed. The first prediction of the theory (that motor programming facilitates visual perception) is supported by a substantial body of empirical evidence and has been discussed on the previous page. The second prediction (that visual selection also facilitates motor programming) is supported by findings that allocating covert attention improves saccadic performance towards the attended location (Hoffman & Subramaniam, 1995; Kowler et al., 1995) and biases saccade trajectories (e.g., Sheliga, Riggio, Craighero, & Rizzolatti, 1995; Sheliga, Riggio, & Rizzolatti, 1994; Van der Stigchel & Theeuwes, 2007).

Belopolsky and Theeuwes (2009, 2012) proposed that the relation between covert attention and saccade programming depends on whether shifting or maintenance of attention are considered. In their view, shifts of covert attention are always accompanied by the corresponding saccade program, while maintenance of covert attention at a location can either lead to activation or to suppression of a saccade program, depending on the situation.

### 1.1.2 Differences between endogenous and exogenous attention

A growing body of evidence suggests that the relationship between covert and overt orienting may depend on the way the attention shift or the saccade program are triggered. Covert attention and saccades can be guided through external events, such as a sudden onset or change in the visual periphery (“exogenous”, “stimulus-driven”, or “reflexive” orienting), or by internal processes, such as a behavioral goal or a task instruction (“endogenous”, “goal-driven”, or “voluntary” orienting. Endogenous and exogenous orienting differ in a number of aspects (e.g., Jonides, 1981, Müller & Rabbit, 1989; also see Berger, Henik, & Rafal, 2005) and are controlled through partially separate neural circuits (see **Chapter 1.1.4**).

A number of lesion studies have investigated whether exogenous and endogenous attention differ with respect to their dependence on the oculomotor system. This question was motivated by the assumption that the phylogenetically old midbrain system might be necessary only for reflexive orienting (as is the case in most vertebrates), while endogenous orienting might depend on cortical regions not so directly involved in the control of eye movements. Rafal, Posner, Friedman, Inhoff, and Bernstein (1988) investigated attentional orienting in patients with progressive supranuclear palsy (a disease that affects brainstem oculomotor neurons as well as the superior colliculus) and observed deficits in both exogenous and endogenous attention. Subsequent studies on patients with peripheral ocular motility disorders found impairments in endogenous (Craighero, Carta, & Fadiga, 2001) or only in exogenous orienting (Gabay, Henik, & Gradstein, 2010; Smith, Rorden, & Jackson, 2004).

The results of a second group of studies, which disrupted the ability to make eye movements experimentally (through abduction of the eye into the temporal hemifield), also give a mixed picture: some found evidence for a selective impairment of exogenous orienting at locations to which no saccade could be made (Smith, Rorden, & Schenk, 2012; Smith, Ball & Ellison, 2014), while others observed deficits in endogenous (Craighero, Nascimben, & Fadiga, 2004) or in both exogenous and endogenous (Smith, Ball, Ellison, & Schenk, 2010) attention. In summary, the above mentioned findings unanimously suggest that exogenous attention relies on the ability to make (or to program) eye movements (except for the work of Craighero and her colleagues, in which exogenous attention was not explicitly tested), but they do not support any clear conclusion concerning the dependence of endogenous attention on oculomotor programming.

Regardless of the controversy, Smith and his collaborators argue that saccade preparation is mandatory for exogenous but not for endogenous attention (Smith et al., 2012, 2014; Smith & Schenk, 2012) and attempt to integrate this notion into a broader framework given by the biased competition model of attention (Desimone & Duncan, 1995). According to their view, saccade preparation is just one form of bias, which relies on the functioning of premotor brain structures and which can be outweighed or completely replaced by top-down cognitive biases that are independent of the eye movement system (Smith & Schenk, 2012). Their position is compatible with a reduced version of the premotor theory of attention (valid only for exogenous attention) and can also be reconciled with the results of the dual-task experiments that showed an obligatory coupling between saccade programming and endogenous attention shortly before a saccade is executed (the motor system has increasing weight towards the onset of the movement).

Most dual-task studies showing an influence of saccade programming on visual perception employed endogenous (central or symbolic) saccade cues, eventually in combination with endogenous attention cues. Given the different characteristics of endogenous and exogenous cueing, it could be possible that perceptual and motor selection can be decoupled if one relies on exogenous and the other on endogenous control. Schneider and Deubel (2002) demonstrated that this is not the case, as the strong coupling of visual discrimination performance to the goal of endogenously cued saccades (Deubel & Schneider, 1996) also holds for exogenously triggered saccades. Instead, their findings suggest that attention cannot be voluntarily decoupled while it is engaged by saccade programming, regardless of the mechanism that led to the saccade program.

Godijn and Theeuwes (2003) argue that genuine exogenous saccades have to occur against the will of the observer, which means that they can only be investigated in situations where an endogenous saccade goal competes with an eye-capturing exogenous stimulus. The two paradigms that fulfill these requirements are the antisaccade task (Hallett, 1978), which was used in the present thesis (see **Chapters 1.2** and **2.1**), and the oculomotor capture paradigm (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999), in which endogenous saccades to a color-defined target compete with involuntary saccades to an onset distractor. The results of several studies (Godijn & Theeuwes, 2002; Irwin, Colcombe, Kramer & Hahn, 2000; Theeuwes et al., 1998, 1999) revealed that in as much as a third of all trials, participants initially made a saccade to the irrelevant distractor (oculomotor capture), before they redirected their gaze to the correct target. Theeuwes et al. (1999) argued that the irrelevant singleton always captured attention and led to the initiation of a saccade program, which, if fast enough, could win the competition against the voluntary saccade program. Attentional deployment was inferred from discrimination performance at the distractor location, but unfortunately it was impossible to rule out that attention was allocated to the distractor due to the salience or task relevance of the discrimination stimulus. A subsequent study (Godijn & Theeuwes, 2003) showed inhibition-of-return at the distractor location, even in trials with no oculomotor capture, and thus provided indirect evidence that attention was automatically captured by the distractor.

So while the oculomotor capture task is, at least in theory, well suited to elucidate the nature of the link between exogenous attention and saccade programming, the studies that used it were unable to provide a convincing or direct measure of attention.

### 1.1.3 Saccade decisions and their relation to attention

Whenever we move our eyes to a new position in space, this action has to be preceded by some kind of decision process that determines why we want to look to that particular location and not to a different one. Saccadic decisions usually involve a competition between multiple spatial locations, as visual scenes rarely contain just one plausible eye movement target.

It is assumed that such decision processes consist of a gradual accumulation of visual evidence in favor of the most conspicuous objects or spatial locations, and whichever of them first reaches a decision boundary, becomes the target of the following saccade (e.g., Brown & Heathcote, 2007; Carpenter & Williams, 1995; Ratcliff & McKoon, 2008). While the existence of decision-related sensory accumulation in the brain is supported by a wealth of neurophysiological evidence (e.g., Hanes & Schall, 1996; Munoz & Wurtz, 1995; Newsome, Britten, & Movshon, 1989; Schall, 2003; Shadlen & Newsome, 1996, 2001; Wurtz & Goldberg, 1972), it remains unclear if the resulting neural activation directly leads to an eye movement or if motor programming represents a separate consecutive processing stage.

According to the *affordance competition hypothesis* (Cisek, 2007), motor decisions consist of a biased competition between parallel representations of possible actions in sensorimotor brain areas. In other words, it is assumed that the brain begins to plan all possible movements, before it reaches a decision which of them to execute. These motor plans are not to be confused with motor programs that control the execution of movements, they rather have to be understood as representations of motor goals or difference vectors between the current state and the intended state (Buneo, Jarvis, Batista, & Andersen, 2002; Cisek, 2005).

In the oculomotor domain, some evidence for the parallel encoding of multiple saccade plans has come from recordings from the monkey superior colliculus (Basso & Wurtz, 1998; McPeck, Han, & Keller, 2003) as well as from behavioral results on how saccade trajectories are influenced by the presence of a distractor (e.g., Godijn & Theeuwes, 2002; McPeck et al., 2003; Nummenmaa & Hietanen, 2006; Theeuwes et al., 1998) or by a choice between two saccade targets (McSorley & McCloy, 2009). Unfortunately, the observed effects might also be consequences of the parallel visual selection of multiple spatial locations and the only way to rule this possibility out is to spatially dissociate visual and oculomotor targets. Klaes, Westendorff, Chakrabarti, and Gail (2011) did this for reaching movements by employing a rule-selection task, where a peripheral visual target was combined with a color cue that determined whether a reach towards or away from the target was required.

They found that neural activity in the parietal reach region and in dorsal premotor cortex simultaneously represented the two possible reach goals, even though only one visual target was present. We are not aware of the existence of a comparable study focusing on eye movements, so we can only speculate that it could reveal a parallel representation of saccade goals in parts of the brain's oculomotor network. While this would demonstrate that saccade goal selection goes a step beyond visual target selection, it would not prove that the representations of the two spatial locations reflected competing saccade programs, as there are probably neurons that do not distinguish between goals for visual perception and for eye movements and simply signal the behavioral priority of spatial locations (see next section for a detailed explanation of the concept).

#### 1.1.4 Attention and saccade programming in the brain

The tight coupling between saccades and visual attention is also evident at a neurophysiological level, since both are controlled by largely overlapping networks of brain areas (e.g., Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000; de Haan, Morgan & Rorden, 2008, Wardak, Olivier, & Duhamel, 2011). Three central nodes of this network, which have been extensively investigated in electrophysiological and microstimulation studies in monkeys, are the superior colliculus, the lateral intraparietal area, and the frontal eye fields, and recent studies also increasingly focus on the basal ganglia.

The **superior colliculus (SC)** is a structure in the midbrain that contains a retinotopically organized motor map for the control of saccades. The main function of the SC is to translate sensory information into saccadic commands (Sparks, 1986) and to select targets for saccades (McPeck & Keller, 2004), but SC neurons have also been found to mediate covert spatial attention in purely perceptual tasks (Cavanaugh & Wurtz, 2004; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Lovejoy & Krauzlis, 2010; Müller, Philiastrides, & Newsome, 2005). Kustov and Robinson (1996) provided a first proof for crosstalk between attention and saccade programming in the SC by demonstrating that shifts of covert attention influence the direction of collicular saccade programs. Further evidence was provided by Ignashchenkova et al. (2004), who showed that collicular visuomotor neurons that are known to participate in the preparation of saccades are also active during covert shifts of attention.

The **lateral intraparietal area (LIP)** is a region of the posterior parietal cortex that was long thought to contribute to the forming of oculomotor plans and was therefore named the “parietal eye field” (Andersen, Brotchie, & Mazzoni, 1992). More recent evidence suggests that LIP is not directly involved in saccade programming, but rather functions as a “priority map” (Fecteau & Munoz, 2006; Serences & Yantis, 2006) that integrates bottom-up visual saliency with top-down biases into a spatial representation of behavioral relevance, which is the used to guide eye movements (Bisley & Goldberg, 2010; Bisley, Ipata, Krishna, Gee, & Goldberg, 2009; Ipata, Gee, Bisley, & Goldberg, 2009; Goldberg, Bisley, Powell, & Gottlieb, 2006; Paré & Dorris, 2011). Consistent with this view, LIP neurons strongly respond to stimulus salience (Arcizet, Mirpour, & Bisley, 2011; Balan & Gottlieb, 2006; Constantinidis & Steinmetz, 2005; Gottlieb, Kusunoki & Goldberg, 1998; Kusunoki, Gottlieb, & Goldberg, 2000) and these responses are modulated by task relevance, including information about planned saccades (Buschman & Miller, 2007; Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Toth & Assad, 2002).

Studies that investigated how LIP neurons convert sensory information into perceptual or motor choices arrived at the conclusion that the cells accumulate sensory evidence in support of the target in their response field and thus carry out a perceptual or premotor decision process (Hanks, Ditterich, & Shadlen, 2006; Platt & Glimcher, 1999; Shadlen & Newsome, 2001; Roitman & Shadlen, 2002). This process is modulated by reward associated with visual targets or movement goals (Bendiksby & Platt, 2006; Coe, Tomihara, Matsuzawa, & Hikosaka, 2002; Dorris & Glimcher, 2004; Peck, Jangraw, Suzuki, Efem, & Gottlieb, 2009; Platt & Glimcher, 1999; Sugrue, Corrado, & Newsome, 2004) and by their novelty (Foley, Jangraw, Peck, & Gottlieb, 2014).

A question that remains debated is whether LIP neurons represent visual selection or saccade planning. However, the distinction makes little sense in the light of the likely role of the LIP as a priority map that guides both overt and covert selection. If LIP is a priority map, its neurons simply carry a priority signal that results from a combination of visual, oculomotor and other biases and is used to guide both overt and covert selection. Depending on the timing and relative strength of the visual and oculomotor biases, the priority signal may sometimes give the appearance of a pure visual or saccade-related activation. Consistent with this view, Bennur and Gold (2011) provided evidence that LIP neurons act very flexibly and can represent perceptual decisions as well as saccade plans, depending on the momentary task requirements.



The **frontal eye fields (FEF)** is a bilateral structure in the left and right frontal lobes that plays a key role in the control of visually guided saccades.

FEF motor neurons form a topographic representation of the visual field (Bruce, Goldberg, Bushnell, & Stanton, 1985; Robinson & Fuchs, 1969) and their output signal is directly transmitted to the SC (Segraves & Goldberg, 1987; Sommer & Wurtz, 2000, 2001) and to the saccade generating network in the brainstem (Dassonville, Schlag, & Schlag-Rey, 1992; Segraves, 1992). Lesion studies in both monkeys and humans have shown that FEF involvement is necessary for the programming of endogenous saccades and for complex oculomotor behavior, such as memory-guided saccades, saccadic sequences or the suppression of inappropriate saccades (Pierrot-Deseilligny, Ploner, Müri, Gaymard, & Rivaud-Pechoux, 2002; Tehovnik, Sommer, Chou, Slocum, & Schiller, 2000), but also for a normal functioning of covert spatial attention (Wardak, Ibos, Duhamel, & Olivier, 2006).

Findings by Schall and his colleagues that visually responsive FEF neurons select the targets of upcoming saccades (Schall & Hanes, 1993; Schall, Hanes, Thompson, & King, 1995; Thompson, Hanes, Bichot, & Schall, 1996) suggested that visual selection and saccade programming might be linked within the FEF. Later findings of the same research group, however, showed that both processes can be dissociated within the FEF (Juan, Shorter-Jacobi, & Schall, 2004; Murthy, Thompson, & Schall, 2001; Sato & Schall, 2003; Thompson, Bichot, & Schall, 1997). Juan et al. (2004), for instance, employed an antisaccade task to examine whether target selection by FEF neurons requires saccade preparation or if both processes are independent of each other. They trained monkeys to saccade towards or away from a color singleton, depending on its orientation, and tested saccade preparation by measuring the direction of saccades evoked by FEF microstimulation at variable times after presentation of the search array. The results demonstrated that FEF neurons selected the singleton even though there was no saccade preparation towards it, which proves that visual selection and saccade programming are not obligatorily coupled within the FEF.

The importance of the FEF for the control of endogenous attention comes from the fact that activity of FEF neurons can modulate the sensitivity of other visual cortical areas through top-down connections and thereby enhance the strength of the target representation, especially in the presence of competing distractors (Armstrong, Fitzgerald, & Moore, 2006; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008; Ekstrom, Roelfsema, Arsenault, Kolster, & Vanduffel, 2009; Moore & Armstrong, 2003; Premereur, Vanduffel, & Janssen, 2014).

While this contribution of the FEF to the control of endogenous attention is well established, its role in exogenous orienting is still a matter of debate. Several fMRI studies demonstrated that endogenous and exogenous orienting engage the same large-scale network of brain areas, including the FEF and the human homologue of area LIP (Kim et al., 1999; Mayer, Dorflinger, Rao, & Seidenberg, 2004; Peelen, Heslenfeld, & Theeuwes, 2004; Rosen et al., 1999), but a weakness of these studies was that the blocked design did not allow to distinguish between cue-related and target-related activity. To overcome this problem, Kincade, Abrams, Astafiev, Shulman, and Corbetta (2005) used an event-related approach that separated preparatory and target-related activity and found that endogenous attention led to greater preparatory activity in both FEF and LIP, while exogenous attention recruited additional regions in the occipitotemporal cortex.

Research findings on monkeys suggest that exogenous attention mainly depends on area LIP, but there is some evidence that easy visual search for “pop-out” targets activates the FEF (Wardak, Vaduffel, & Orban, 2010) and that FEF inactivation leads to deficits in visual search that do not depend on search difficulty (Wardak et al., 2006). Moreover, it has been shown that FEF neurons automatically select the location of targets that differ from distractors in a single feature (Schall & Hanes, 1993). Researchers have also tried to understand the roles of LIP and FEF in the control of exogenous attention by comparing their time courses of activation in bottom-up attention tasks. While Buschman and Miller (2007) observed that LIP neurons signal the target before FEF neurons (also see Ibos, Duhamel & Ben Hamed, 2013), Katsuki, Saito, and Constantinidis (2014) found that the LIP and FEF are activated in parallel (with a slight temporal advantage for the FEF), which raises the possibility that exogenous attention results from the joint activity of both areas.

The **basal ganglia (BG)** are a collection of subcortical nuclei, comprising the caudate nucleus and putamen (together called striatum), the globus pallidus, the substantia nigra, and the subthalamic nucleus. These distributed nuclei act as a functional entity and one of their crucial roles is the selection of voluntary movements, including eye movements. The BG are interconnected with all cortical and subcortical areas that play a role in visual selection and oculomotor control (Hikosaka, Takikawa, & Kawagoe, 2000) and have been shown to mediate top-down attention (Van Schouwenburg, den Ouden, & Cools, 2010, 2015; Tommasi et al., 2015) and saccade selection based on memory (Bayer, Handel, & Glimcher, 2004; Hikosaka & Wurtz, 1983) and on reward expectancy (see Hikosaka, Nakamura, & Nakahara, 2006 for a review).

The crucial output node of the BG for saccadic control is the substantia nigra pars reticulata (SNr), which exerts tonic inhibitory influence on saccade-related neurons in the superior colliculus that can be removed or strengthened dependent on task requirements and behavioral context (for reviews, see Hikosaka et al., 2000; Shires, Joshi, & Basso, 2010). Saccade-related decisions are thought to emerge mostly from the combination of sensory and cognitive information in a cortico-striatal loop through the caudate nucleus (Vokoun, Mahamed, & Basso, 2011), but only little is known about the neural mechanisms so far.

## 1.2 Aims of this thesis

The goal of this dissertation was to investigate the relation between visual selection, saccade decisions, and saccade programming in humans by tracking these processes with the help of classical behavioral methods and by trying to influence the activity of frontal eye field neurons by transcranial magnetic stimulation (TMS). To assess the time courses of covert visual selection and saccade execution in great detail, we used a dual-task cueing paradigm, in which we measured eye movements as well as probe discrimination at different locations in space and different times relative to saccade or decision cues. We deliberately employed tasks that lead to a high degree of spatial competition, as we reasoned that the distribution of attention during such tasks would be maximally informative about the momentary priority of spatial locations and would thus allow the most valid conclusions about ongoing cognitive processes.

The aim of the first study (**Chapter 2.1**) was to investigate the competition between endogenous and exogenous spatial orienting. One way to induce such a competition in a laboratory setting is the use of the antisaccade task (Hallett, 1978), in which observers are presented with a visual stimulus on one side of a visual display and are asked to make a saccade to the mirror identical location on the contralateral side. The antisaccade task is particularly well suited for the investigation of the competition between exogenous and endogenous orienting, as it spatially dissociates the goals of both processes. The dissociation results from the fact that the sudden appearance of a visual stimulus automatically captures attention, while an eye movement has to be planned to the contralateral side.

Several authors have suggested that the programming of an antisaccade involves the parallel generation of two competing motor plans - one towards the cue/stimulus and a second towards the antisaccade target (Massen, 2004; Munoz & Everling, 2004; Noorani & Carpenter, 2013).

Despite its face plausibility, this claim has only been supported by indirect evidence on error rates and processing speeds of the competing components (Massen, 2004; Mokler & Fischer, 1999). To our knowledge, only one study (Smith & Schenk, 2007) measured attention allocation in the antisaccade task, but at a very early time interval relative to saccade execution, where no saccade preparation was in progress and only reflexive attention towards the visual cue was observed. Our main goal was therefore to track the deployment of attention to the cue and to the antisaccade goal during the whole period of saccade preparation.

The second study (**Chapter 2.2**) set out to examine attentional dynamics during the choice between two memorized saccade goals. We were particularly interested in whether the representation of saccade goals during the decision process would be paralleled by visual selection and how this sensory representation would change over time. We employed a rule-based choice task (similar to the one Klaes and his colleagues used with monkeys - see **Chapter 1.1.3**), but instead of recording brain activity, we measured visual discrimination performance at both possible saccade targets as well as at saccade-irrelevant locations. Since we also wanted to know whether the pattern of results would differ between rule-based and free choice, we additionally included a condition where participants could choose to which of the targets they would look.

The goal of the third study (**Chapter 2.3**) was to investigate the role of the human FEF in the control of exogenously and endogenously cued saccades and corresponding presaccadic attention shifts. While the FEF is undoubtedly involved in the control of endogenous orienting, it is much less clear if it also participates in exogenous orienting (see **Chapter 1.1.4**).

A suitable method to non-invasively influence human cortical activity is transcranial magnetic stimulation (TMS), which uses an electromagnetic coil to induce electric currents in underlying brain tissue. When applied on-line at previously defined time points during a trial, TMS permits causal inferences about the temporal dynamics of neural processes in the targeted brain areas, which makes it a valuable tool for the study of attentional and oculomotor processes.

Two previous studies have investigated how FEF-TMS affects the coupling between visual selection and saccade preparation in Deubel & Schneider's (1996) dual-task paradigm, yielding inconsistent results (Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009). The third study of this cumulative thesis examines the same question with the help of an improved dual-task paradigm, additionally comparing conditions with endogenous and exogenous saccades.



## 2 Cumulative Thesis

This doctoral thesis consists of three individual studies: One peer-reviewed and published article (2.1) and two manuscripts (2.2 and 2.3). The following chapter consists of these studies, each accompanied by a statement clarifying the contributions of the involved authors.

### 2.1 Study 1: Attention allocation before antisaccades

#### Contributions:

A version of this chapter has been published as Klapetek, A., Jonikaitis, D., & Deubel, H. (2016). Attention allocation before antisaccades. *Journal of Vision*, 16(1):11.

The author of this dissertation participated in designing the experiments, programmed the experiments, collected and analyzed the data, created plots, interpreted the results and wrote the journal article.

Donatas Jonikaitis participated in designing the experiments, in analyzing and interpreting the results, and he commented on and helped revising the manuscript.

Heiner Deubel conceived and supervised the project, participated in designing the experiments and interpreting the results, and commented on the manuscript.

## Attention allocation before antisaccades

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### Abstract

In the present study, we investigated the distribution of attention before antisaccades. We used a dual task paradigm, in which participants made prosaccades or antisaccades and discriminated the orientation of a visual probe shown at the saccade goal, the visual cue location (antisaccade condition), or a neutral location. Moreover, participants indicated whether they had made a correct antisaccade or an erroneous prosaccade. We observed that, while spatial attention in the prosaccade task was allocated only to the saccade goal, attention in the antisaccade task was allocated both to the cued location and to the antisaccade goal. This suggests parallel attentional selection of the cued and anti-saccade locations. We further observed that in error trials – in which participants made an incorrect prosaccade instead of an antisaccade, spatial attention was biased towards the prosaccade goal. These erroneous prosaccades were mostly unnoticed and were often followed by corrective antisaccades with very short latencies ( $< 100$  ms). Data from error trials therefore provide further evidence for the parallel programming of the reflexive prosaccade to the cue and the antisaccade to the intended location. Taken together, our results suggest that attention allocation and saccade goal selection in the antisaccade task are mediated by a common competitive process.



## INTRODUCTION

The ability of humans to flexibly control their behavior can be studied in the antisaccade paradigm (Hallett, 1978; Hallett & Adams, 1980). In this task, a visual stimulus is presented in one visual hemifield and the observer is asked to make a saccade to its mirror position in the opposite hemifield. Thus, instead of making a reflexive eye movement to a visually salient stimulus location, one has to program an eye movement towards the opposite location. For this reason, the antisaccade task provides a unique situation, in which the visual stimulus is dissociated from the final oculomotor command.

Earlier research has focused mainly on motor aspects of performance in the antisaccade task in order to understand the mechanisms underlying antisaccade preparation. It has been suggested that after onset of the visual stimulus, two motor plans are initiated – one towards the stimulus and one towards the antisaccade target (Massen, 2004; Munoz & Everling, 2004; Noorani & Carpenter, 2013). These two plans compete in reaching a threshold at which the winning motor program is executed. The idea of parallel prosaccade and antisaccade programming in the antisaccade task is empirically supported by observations that the inter-saccadic interval between an erroneous primary saccade and the secondary, corrective saccades directed to the antisaccade goal is often very short (Massen, 2004; Mokler & Fischer, 1999). Moreover, by introducing experimental manipulations that selectively influenced the processing speed of the exogenous prosaccade or the endogenous antisaccade component, Massen (2004) demonstrated that a slowing of the exogenous component (slowing prosaccade preparation) resulted in a reduced error rate, while a slowing of the endogenous component (slowing antisaccade preparation) led to more errors.

However, as earlier research has mainly focused on motor performance in the antisaccade task, only little is known about the distribution of attention before antisaccades. This is surprising, especially if we consider that the antisaccade task offers the possibility to investigate competitive interactions between exogenous and endogenous attention. On the one hand, salient visual cues capture attention even if such cues are task-irrelevant (Carrasco, 2011; Carrasco, Ling, & Read, 2004; Müller & Rabbit, 1989; Nakayama & Mackeben, 1989). On the other hand, during the preparation of goal-directed saccades, spatial attention inevitably shifts to the saccade target (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Jonikaitis & Theeuwes, 2013; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011). Therefore, there are two potential attentional targets in the antisaccade task – attention is likely to be drawn towards the visual stimulus location and/or towards the antisaccade target.

Given that saccade target selection and spatial attention are thought to be closely coupled (Awh, Armstrong, & Moore, 2006; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995), measuring spatial attention during the antisaccade task should help us to understand covert visual and motor selection during the task even before the eyes move.

Exact attentional effects in the antisaccade task are difficult to predict. Earlier observations contrasting endogenously cued spatial attention and attention at saccade targets found attentional costs either at the attended location (Deubel, 2008; Deubel & Schneider, 1996; Jonikaitis & Theeuwes, 2013; Kowler et al., 1995; Wilder, Kowler, Schnitzer, Gersch, & Doshier, 2009) or at the saccade target (Montagnini & Castet, 2007). Therefore, one could expect attention to be biased either towards the antisaccade target or towards the visual stimulus. The only direct measure of attention allocation before saccades was provided by Mokler, Deubel and Fischer (2000), who showed that attention shifts in parallel to both locations. However, this study used a spatial pre-cue to increase the percentage of saccade errors, which may have influenced attention in an unforeseeable way.

In order to investigate the relationship between attention and antisaccade programming in as much detail as possible, we completed two experiments that allowed to measure attention at the visual stimulus location as well as at the antisaccade goal. Making use of the fact that probe discrimination at exogenously or endogenously cued locations can be used as a reliable measure of spatial attention (see Carrasco, 2006; Deubel & Schneider, 1996), we employed a dual task, in which observers made prosaccades or antisaccades and simultaneously discriminated visual probes at these locations. Throughout the course of a trial, there were always two (in Experiment 1) or six (in Experiment 2) squares present on the display, one of which was briefly marked by a visual onset cue that signaled to the observer to make a saccade towards this square, or an antisaccade to the diagonally opposite square. At a randomly selected point in time during saccade preparation, a perceptual probe was shown in any of the squares. This allowed us to track spatial attention allocation to different locations during saccade preparation. We were further interested how spatial attention was allocated on error trials - that is when participants made erroneous prosaccades instead of antisaccades. We increased the number of errors by introducing a temporal gap between fixation offset and visual cue appearance (Bell, Everling, & Munoz, 2000; Fischer & Weber, 1997; Forbes & Klein, 1996). Last, we also asked participants to report whether they had made an incorrect saccade or not, as we planned to test whether error awareness would be linked to attention allocation, as was reported by Mokler et al. (2000).

## METHODS

### *Participants*

Eighteen observers (most of them students) participated in the present study, after giving written informed consent. The participants had normal or corrected-to-normal vision and all except for two of the authors were naïve with respect to the goals of the study. Ten observers (5 male, 5 female, age 21-31) took part in Experiment 1 and sixteen observers (4 male, 12 female, age 21-31). The experiments were carried out in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

### *Apparatus*

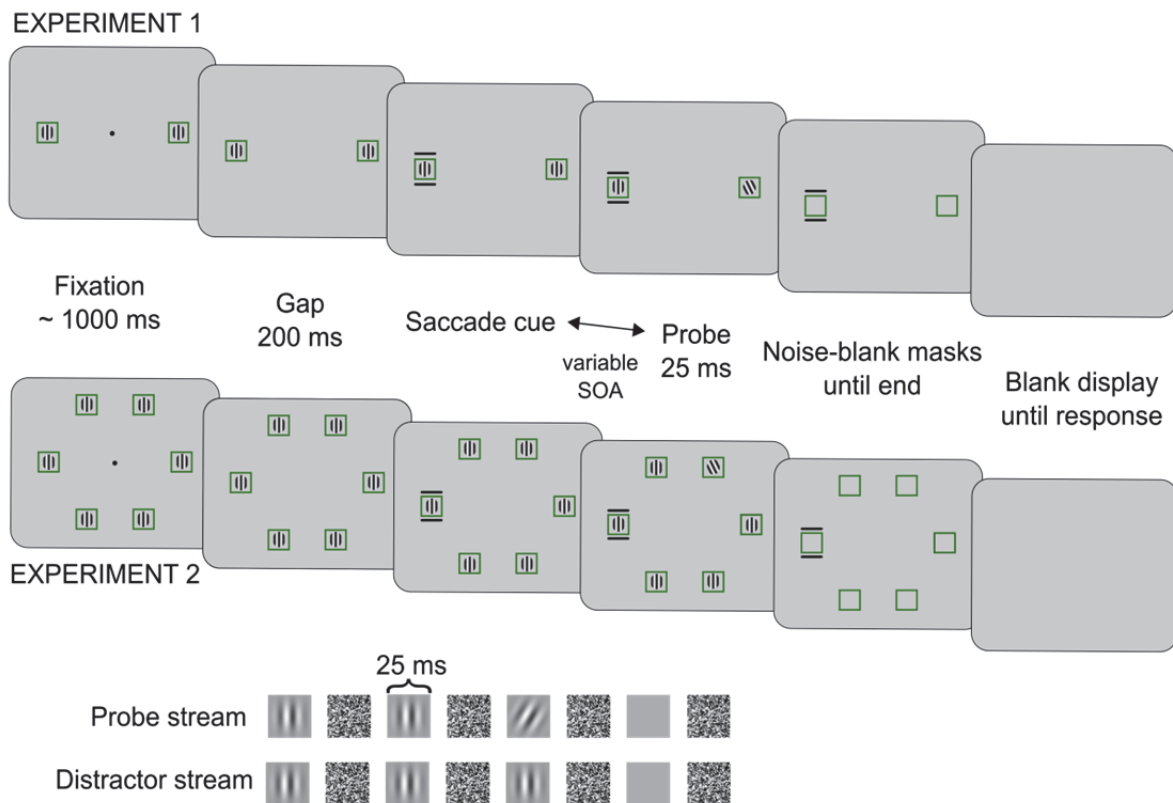
The observers were seated in a dimly illuminated room in front of a 19-inch CRT monitor (ViewSonic G90fB, screen refresh rate: 120 Hz, spatial resolution: 1024 x 768 pixels), positioned at a viewing distance of 70 cm. Their head position was stabilized by a chin and forehead rest. Eye movements were recorded with an EyeLink 1000 desktop mounted eye tracker (SR Research, Canada) with a spatial resolution below 0.25 degrees, at a sampling rate of 1000 Hz. The eye tracker was calibrated in the beginning of the experiment, before each new block and whenever it was necessary. Stimulus presentation and response collection were controlled by an Apple Mac Mini, using MATLAB software (MathWorks, USA) and the Psychophysics and Eyelink Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997; see <http://psychtoolbox.org>). Manual responses were recorded via the arrow keys on the right hand side of a standard computer keyboard.

### *Stimuli and Task*

The visual display contained a central black fixation dot (diameter: 0.5 degrees of visual angle) and two (Experiment 1) or six (Experiment 2) green frames (edge length: 2 deg), positioned symmetrically on the outline of an imaginary circle (radius: 7 deg) centered on the fixation dot. The frame objects contained interleaved sequences of vertically oriented Gabor patches (spatial frequency: 2.5 cpd, contrast: 100%, random phase on each presentation) and white noise masks, alternating every 3 frames (25 ms). The probe, a brief (25 ms) leftward or rightward tilt of the Gabor patch, could appear in any of the squares at different SOAs relative to cue onset.

The SOA range differed between experiments and is specified later. The angular of the Gabor pattern was chosen for each observer individually, based on the results of a short visual pretest at the beginning of each experimental session (see Pretests section below).

After a random fixation interval of 800 to 1200 ms, the fixation dot disappeared and the saccade cue (two 0.2 degrees thick horizontal black lines above and below one of the squares) appeared 180 to 220 ms later. Depending on the instruction screen at the beginning of each block, observers were asked to make a saccade to the cued square (prosaccade blocks) or to the diagonally opposite square (antisaccade blocks) as quickly as possible. After probe offset, all Gabor patches were replaced by empty squares, so that all objects contained noise-blank masks until the blackening of the display 700 ms after onset of the saccade cue. Observers had as much time as they needed to indicate the perceived tilt direction by pressing the left arrow key for a leftward tilt or the right arrow key for a rightward tilt. A new trial started 200 ms after their response. In Experiment 2, observers were additionally asked to indicate by a second button press at the very end of each trial whether their initial saccade was correct (up arrow key) or incorrect (down arrow key). They were instructed to use the index and ring fingers of their right hand for the left and right responses and the middle finger for the up and down responses.



**Figure 1.** Schematic representation of the stimulus sequences in both experiments and examples for the probe and distractor streams.

## ***Design***

### *Experiment 1*

The first experiment consisted of 1440 trials, divided into 24 blocks of 60 trials. Observers were instructed to make prosaccades in one half of the blocks and antisaccades in the other half. The experiment was divided into four sessions (on separate days), so that each session consisted of three prosaccade and three antisaccade blocks in randomized order. For each trial within a session, the locations of the saccade target and the probe were determined randomly and the cue-to-probe SOA was drawn from 36 time points between -100 and 250 ms.

### *Experiment 2*

Our second experiment consisted of 2160 trials, divided into 36 blocks of 60 trials each, spread over six sessions. The design was analogous to Experiment 1, but the display now contained six instead of two squares, which made it possible to show the probe at a neutral location in one third of the trials, the remaining two thirds being randomly split between saccade goal and the diagonally opposite location. The position of the cued square was randomly selected in every trial, so that all six squares were equally likely to be the saccade target. For the first six observers, the cue to probe SOA was randomly drawn from 36 time points between -100 and 250 ms. For the remaining participants, the cue to probe SOA was limited to 11 time points between 100 and 200 ms. The trial number was accordingly reduced to 1440 trials (24 blocks of 60 trials, divided into four sessions, each consisting of three pro- and three antisaccade blocks in randomized order).

## ***Pretests***

The pretests consisted of 60 trials with identical visual stimuli as in the main experiments, except that the probe was always presented at the cued location 100 ms after cue onset. Observers were instructed to covertly attend to the cued square while maintaining central fixation and to discriminate the orientation of the probe at the end of the trial. A modified version of the QUEST procedure (King-Smith et al., 1994; Watson & Pelli, 1983) was used to determine the two tilt angles at which observers reached 82% correct probe discrimination in the left and right half of the display. Tilt angles ranged between 4 and 21 degrees in Experiment 1 ( $M = 9.7$ ,  $SD = 6.7$ ) and between 3 and 27 degrees in Experiment 2 ( $M = 11.0$ ,  $SD = 4.3$ ). Angles for the left and right display half were comparable.

## ***Data analyses***

All eye movement and behavioral data were analyzed using Matlab software (MathWorks, USA) and the Psychophysics and Eyelink toolboxes (Brainard, 1997; Cornelissen et al., 2002; Kleiner et al., 2007; Pelli, 1997; see <http://psychtoolbox.org>). Eye movements were recorded online during sessions and evaluated offline using Eyelink's built-in saccade detection algorithm (Experiment 1), or our own customized velocity-space algorithm that corrected for glissades (Experiment 2). In a direct comparison, both algorithms detected identical saccade beginning times, but the Eyelink algorithm tended to include glissades at the end of saccades into the saccade duration and thus tended to yield unrealistically short intersaccadic intervals. Primary saccades with latencies below 100 ms or above 600 ms were removed from analysis. In total, we had to reject 5% of all trials due to blinks, missing data or not clearly separable saccades.

Statistical analyses consisted of repeated-measures analyses of variance (ANOVA) and post-hoc comparisons using t-tests with a Bonferroni correction. The Greenhouse-Geisser correction was applied whenever sphericity was violated. All analyses were based on a minimum of five trials per participant and condition.

## **RESULTS**

### **Experiment 1**

#### ***Saccade latency and direction errors***

The initial saccade direction was incorrect in 3% of all prosaccade trials and in 18% of the antisaccade trials. To assess whether saccade latencies differed between prosaccades and antisaccades and whether they were affected by probe location and timing, we performed a repeated-measures ANOVA with saccade type (prosaccade, antisaccade), probe location (at cue, opposite cue) and probe presentation time (six 50 ms wide time bins between -100 and 200 ms) as the within-subjects factors.

We found that antisaccade latencies were longer than prosaccade latencies ( $M = 218$  ms,  $SD = 55$  ms for antisaccades vs.  $M = 163$  ms,  $SD = 45$  ms for prosaccades,  $F(1,9) = 138.0$ ,  $p < .001$ ). This latency difference is one of the typical characteristics of antisaccades (Hallett, 1978), that has been robustly replicated in many different versions of the antisaccade task. Furthermore, we observed that neither the location nor the timing of the probe had any effect on saccade latency (no significant main effects of these two factors).

This indicates that the probe discrimination task did not alter saccade preparation and can be used as an effective measure of attention allocation during saccade programming.

### *Saccade amplitude*

In order to assess saccade accuracy, we calculated the gains of primary saccades as the ratio between saccade amplitude and target amplitude. We were mainly interested in whether gains would differ between prosaccades and antisaccades and between correct saccades and erroneous prosaccades. Since saccade gains did not vary as a function of probe presentation time, we decided to exclude this factor from analysis in order to have a sufficient number of trials per participant and condition (before exclusion, many bins had less than five trials, afterwards the minimum was 19).

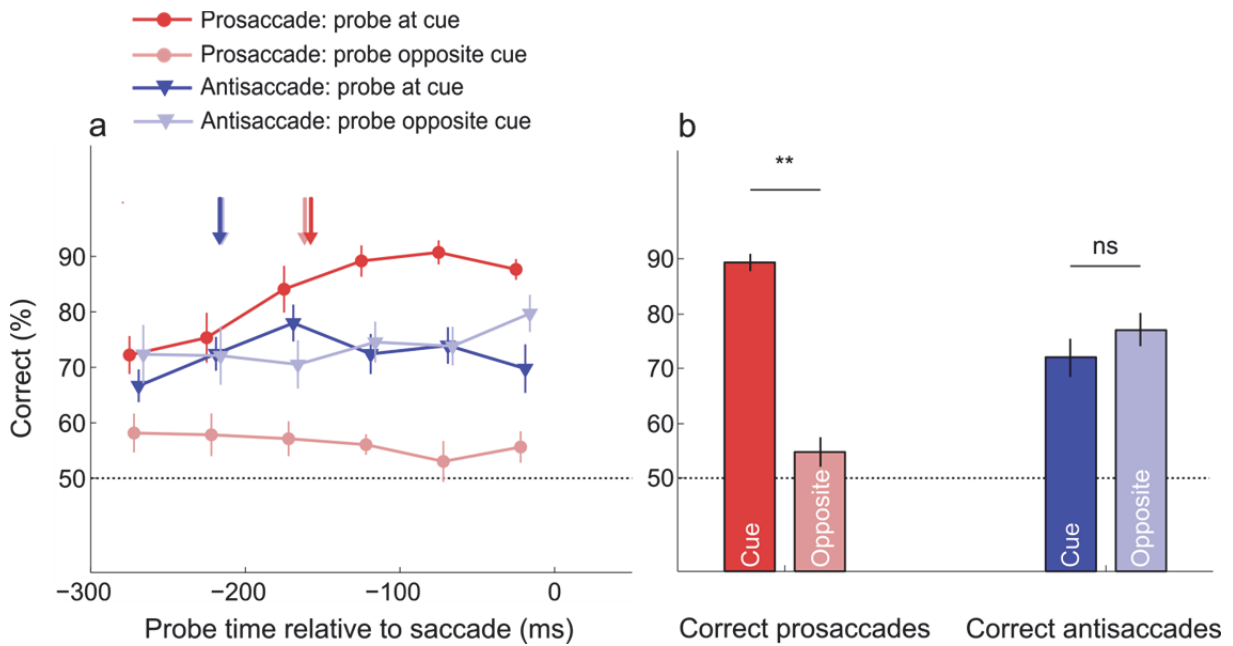
The ANOVA of the gains with saccade type (correct prosaccade, correct antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue) as the between-subjects factors revealed a significant main effect of saccade type,  $F(2,18) = 46.1$ ,  $p < .001$ , and no significant effect of probe location. While amplitudes of correct prosaccades and antisaccades were both very accurate (mean gain = 1.0), erroneous prosaccades tended to undershoot the target (mean gain = .86) and thus differed significantly from correct saccades (as revealed by post-hoc comparisons).

### *Discrimination performance*

Since we presented the probe at different SOAs with respect to the saccade cue, it was possible to determine the time course of attentional deployment to both probe locations. For this purpose, we sorted all SOAs into 50 ms-wide bins and calculated the proportion of correct probe discriminations for each saccade condition and probe location in each time bin (see **Figure 2a**).

Discrimination performance in the prosaccade condition was clearly superior for probes presented at the cued location (saccade goal) compared to the opposite location, where it was just slightly above chance level. In the antisaccade condition, in contrast, performance was about equally good at the cued and the opposite location (antisaccade goal), but generally worse than at the prosaccade goal in the prosaccade condition, which suggests that attentional resources were split over both locations. Interestingly, the benefits at the saccade goal in the prosaccade condition and at the cued location and antisaccade goal in the antisaccade condition can already be seen before saccade cue onset.

This is likely due to a retro-active attentional effect, which can extend into the pre-cue period (Sergent et al., 2013; Thibault, Cavanagh, & Sergent, 2015). The most likely explanation is that shifts of spatial attention to the cued location or to saccade goals retroactively trigger conscious access to previously unconscious sensory representations. Unfortunately, this effect limits the tracking of the temporal profile of spatial attention. For this reason, we decided to focus in our further analyses on the spatial distribution of attention shortly before the saccade (the last two bins pooled together).



**Figure 2.** Discrimination performance in Experiment 1. Correct discrimination (in %) is plotted as a function of saccade type (prosaccade or antisaccade) and probe location (at the cued location or opposite from it). Error bars represent standard errors of the mean. The dashed line denotes the chance performance level. (a) Discrimination performance for probes appearing at various times before saccade onset. Only trials with correct saccades were included and each bin contains at least 10 trials per participant and condition ( $M = 37$ ). The vertical arrows indicate the average times when the saccade cues were presented. (b) Discrimination performance for probes presented less than 100 ms before saccade onset as a function of saccade type (prosaccade or antisaccade) and probe location (at the visual cue or opposite from the cue). At least 40 trials per participant and condition were analyzed ( $M = 79$  for prosaccades and  $M = 63$  for antisaccades).

We performed a repeated measures ANOVA with saccade type (prosaccade, antisaccade) and probe location (at cue, opposite cue) as the within-subjects factors (see **Figure 2b** for a graphical summary of the results). The results show that probe discrimination performance depended upon probe location (main effect of probe location,  $F(1,9) = 30.0$ ,  $p < .001$ , and interaction between probe location and saccade type,  $F(1,9) = 32.7$ ,  $p < .001$ ).



In the prosaccade task, discrimination performance (% correct) was significantly better at the cued location, which was the saccade goal, ( $M = 89.4\%$ ,  $SD = 5.0\%$ ) than at the task-irrelevant opposite location ( $M = 54.7\%$ ,  $SD = 8.7\%$ ; post-hoc comparisons). In contrast to this, in correct trials of the antisaccade task, discrimination at the cued location ( $M = 72.0\%$ ,  $SD = 10.7\%$ ) and at the antisaccade goal ( $M = 77.1\%$ ,  $SD = 9.8\%$ ) were not significantly different.

We were also interested in whether attention allocation to the saccade goal would differ as a function of saccade type. The analysis revealed that discrimination performance at the goal of correct prosaccades ( $M = 89.4\%$ ,  $SD = 5.0\%$ ) was significantly better than at the goal of correct antisaccades ( $M = 77.1\%$ ,  $SD = 9.8\%$ ).

Taken together, the results on discrimination performance demonstrate that during the programming of antisaccades, attention was about equally allocated to the visual cue and to the future saccade goal. Discrimination performance was clearly best at the goal of voluntary prosaccades, which could be explained by the summation of the effects of reflexive and endogenous attention. An alternative reason for this advantage could be the absence of attentional competition in this condition, as the opposite location was completely irrelevant for the saccade task.

## Experiment 2

It is well possible that the parallel allocation of attention in Experiment 1 was, at least in part, a consequence of having only two possible probe locations, which may have allowed observers to split their attention. One of the goals of Experiment 2 therefore was to control for this potential bias by adding four saccade-irrelevant probe locations, thus introducing more visual competition. In addition, we wanted to test whether attention allocation would be related to awareness of direction errors and therefore added a measure of error awareness at the end of each trial. In contrast to Experiment 1, where we were interested in the time course of attention allocation, we decided to focus on the interval between 100 ms post-cue and the beginning of the saccade, where we had previously found the strongest attentional cueing effects.

### *Direction errors and awareness*

While saccade accuracy was very high in prosaccade blocks (98% correct), participants made a considerable amount of direction errors in antisaccade blocks.

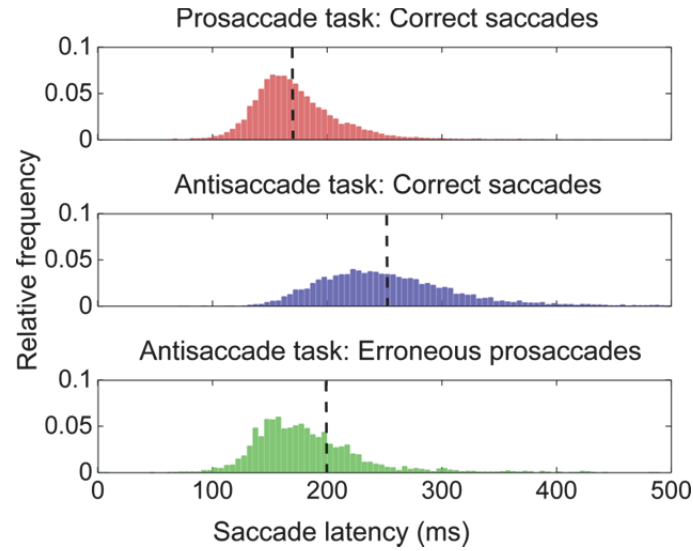
In 16% of all antisaccade trials, the first saccade went to the visual cue (erroneous prosaccade), in 12% it went to one of the squares adjacent to the antisaccade target and in 3% it went elsewhere. 61% of the erroneous prosaccades were not declared by the observers, which is consistent with the 62% reported by Mokler and Fischer (1999).

According to signal detection theory (Green & Swets, 1966), detection performance is a function of the detectability of the signal and the response strategy of the observer. To understand how these two variables influenced our results, we calculated discrimination sensitivity ( $d'$ ) and response bias ( $C$ ) for each of our participants. Sensitivity ranged between 0.8 and 3.4 ( $M = 1.9$ ), which means that observers could discriminate between trials with correct saccades and those with direction errors way above chance level.  $C$  ranged between 0.3 and 1.7 ( $M = 1.2$ ), which indicates that all observers adopted a conservative criterion and tended to prefer “no” responses over “yes” responses. This was most likely a consequence of the low base rate of errors ( $< 10\%$ ) and the payoff characteristics (no benefits, but rather expected costs associated with correct error detection) in our experiments. In sum, the analysis of discrimination sensitivity and response bias revealed that observers were reasonably good at detecting errors (some even very good), but they tended to report only errors that they felt certain about.

### *Saccade latency*

Saccade latencies were analyzed in the same way as amplitudes (ANOVA with the factors saccade type and probe location). **Figure 3** shows the saccadic latency distributions for correct prosaccades in the prosaccade task, and for correct antisaccades and erroneous prosaccades in the antisaccade task.

Saccade latencies for correct antisaccades ( $M = 253$  ms,  $SD = 63$  ms) were longer than for correct prosaccades ( $M = 170$  ms,  $SD = 39$  ms) and for erroneous prosaccades ( $M = 199$  ms,  $SD = 79$  ms), this difference being significant (main effect of saccade type:  $F(2,14) = 16.6$ ,  $p < .001$ , and post-hoc comparisons).



**Figure 3.** Saccade latencies in Experiment 2. The histograms represent relative frequency distributions of saccade latencies (bin size: 5 ms) of correct prosaccades ( $N = 13003$ ), correct antisaccades ( $N = 9665$ ) and erroneous prosaccades ( $N = 2298$ ). The vertical dotted lines correspond to the means.

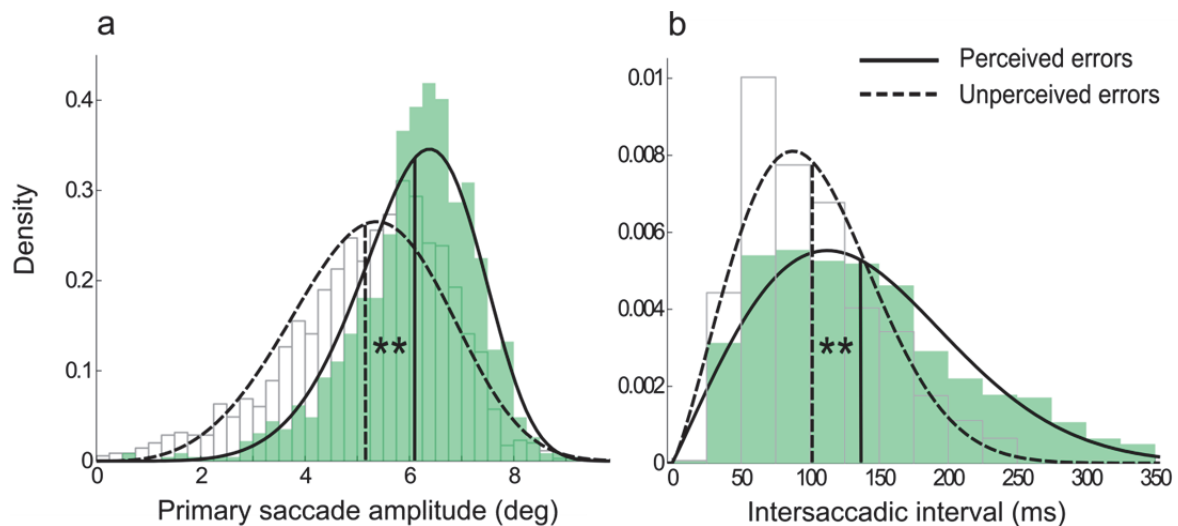
### *Saccade amplitude*

Amplitudes of primary saccades were subjected to a repeated measures ANOVA with the factors saccade type (prosaccade, antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue). As in Experiment 1, erroneous prosaccades (in the antisaccade task) had significantly shorter amplitudes ( $M = 5.7$  deg,  $SD = 1.5$  deg) than both correct prosaccades ( $M = 6.7$  deg,  $SD = 0.8$  deg) and correct antisaccades ( $M = 6.7$  deg,  $SD = 1.1$  deg). The difference was statistically significant (main effect of saccade type,  $F(2,26) = 63.0$ ,  $p < .001$  and post-hoc comparisons). Within the group of erroneous prosaccades, amplitudes were significantly shorter for unperceived errors ( $M = 5.2$  deg,  $SD = 1.5$  deg) than for perceived errors ( $M = 6.1$  deg,  $SD = 1.2$  deg),  $t(15) = 6.7$ ,  $p < .001$ .

### *Corrective saccades*

Erroneous prosaccades having wrong direction and shorter amplitudes than the correct saccades were often followed by corrective saccades. Indeed, our analysis revealed that 71% of all prosaccade errors were corrected in the direction of the intended antisaccade goal (only saccades that crossed the midline were counted as corrective saccades). The proportion of corrective saccades was considerably higher after unperceived errors (87%) than after perceived errors (47%).

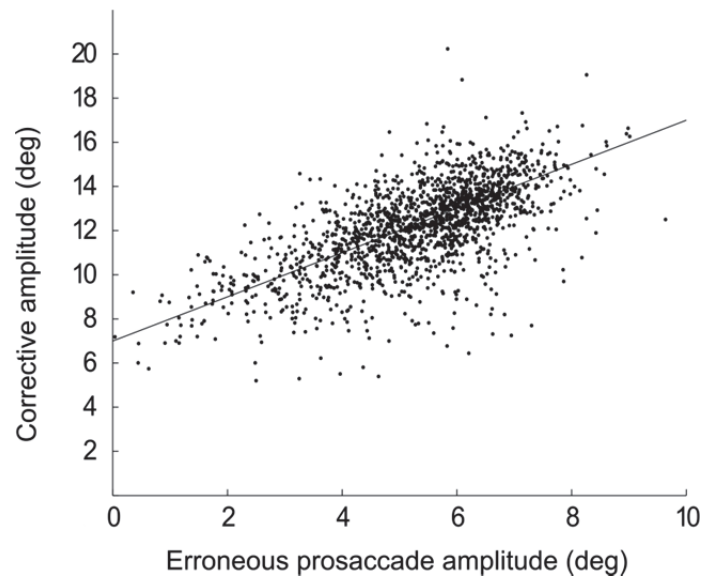
**Figure 4** displays the distributions of primary saccade amplitudes and correction times (intersaccadic intervals) for trials with perceived and unperceived prosaccade errors. About half of the corrective saccades (49%) occurred within less than 100 ms after the end of the erroneous prosaccade. The very short latency suggests that these secondary saccades were programmed partly in parallel with the primary saccade. Correction times were significantly shorter after unperceived ( $M = 101$  ms,  $SD = 48$  ms) than after perceived ( $M = 139$  ms,  $SD = 73$  ms) errors,  $t(15) = 3.5$ ,  $p < .01$ . There was also a significant correlation between the amplitude of the initial saccade and the correction time of the second saccade, meaning that hypometric errors tended to be corrected faster than errors that landed closer to the target (Spearman correlation:  $p < .001$  for all but one subject).



**Figure 4.** Amplitudes (a) and correction times (b) of perceived vs. unperceived erroneous prosaccades. The histograms plot scaled relative frequency, the curves represent Weibull functions fitted to the data and the vertical lines correspond to the means. (a) Amplitudes of perceived ( $N = 907$ ) compared to unperceived ( $N = 1391$ ) saccades; bin size=5 deg. (b) Correction times of perceived ( $N = 563$ ) compared to unperceived ( $N = 1229$ ) errors, bin size: 25 ms.

**Figure 5** illustrates the linear relationship between amplitudes of primary and corrective saccades, which proves that most corrective saccades landed on the target or close to it. The line represents perfect error compensation, where the corrective gain (i.e., the sum of the amplitudes of both saccades, with leftward amplitudes reversed in sign) equals the target distance. This gain was higher following unperceived errors ( $M = 7.0$  deg,  $SD = 0.1$  deg) than after perceived errors ( $M = 6.6$  deg,  $SD = 0.1$  deg) and the difference was statistically significant,  $t(15) = 28.9$ ,  $p < .001$ .

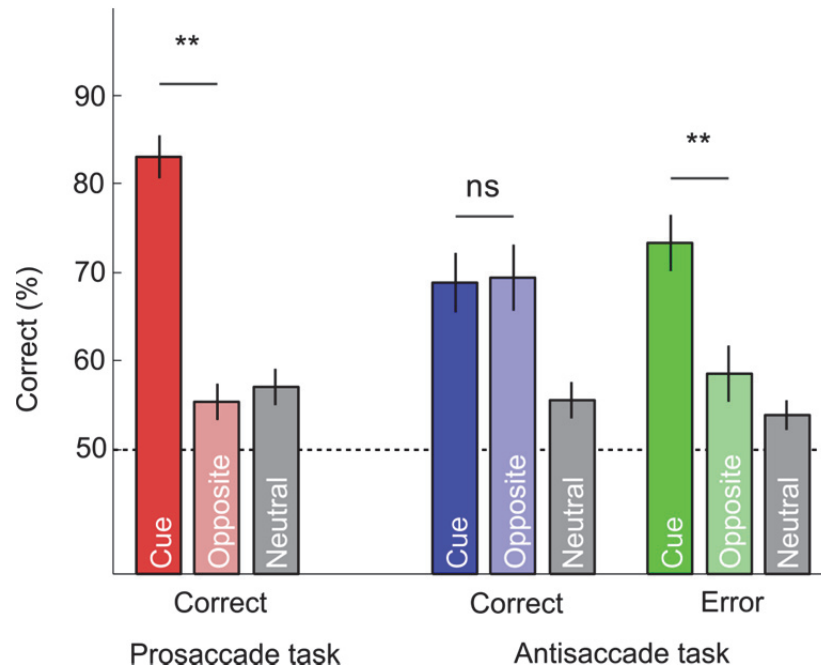
Interestingly, this effect remained present in the subgroup of very quickly corrected saccades, which means that it cannot be explained by differences in correction time.



**Figure 5.** Scatterplot of the amplitudes of erroneous prosaccades and their corrections. The diagonal line represents full correction to the intended antisaccade target.

### *Discrimination performance*

We performed a repeated measures ANOVA with saccade type (prosaccade, antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue, neutral) as the within-subjects factors (see **Figure 6** for a graphical summary of the results). The results showed that probe discrimination mainly depended on the location of the probe (main effect of probe location,  $F(2,26) = 28.7$ ,  $p < .001$ , and revealed a significant interaction between saccade type and probe location,  $F(4,52) = 10.7$ ,  $p < .001$ ). Before correct prosaccades, discrimination performance was significantly better at the cued location, which was the saccade goal, ( $M = 83.4\%$ ,  $SD = 8.3\%$ ) than both at the opposite location ( $M = 55.1\%$ ,  $SD = 7.7\%$ ) and at the neutral location ( $M = 57.2\%$ ,  $SD = 7.4\%$ ), which were task-irrelevant. Before correct antisaccades, discrimination at the cued location ( $M = 68.9\%$ ,  $SD = 12.8\%$ ) and at the antisaccade goal ( $M = 69.4\%$ ,  $SD = 15.1\%$ ) were almost equal and were both significantly better than at the neutral location ( $M = 55.3\%$ ,  $SD = 7.9\%$ ). In contrast to this, probe discrimination before erroneous prosaccades was significantly better at the cued location ( $M = 74.4\%$ ,  $SD = 13.9\%$ ) than at the opposite ( $M = 57.5\%$ ,  $SD = 14.8\%$ ) and neutral ( $M = 51.4\%$ ,  $SD = 11.7\%$ ) locations.



**Figure 6.** Discrimination performance in Experiment 2. The graph compares discrimination rates for probes presented between 100 and 200 ms after cue onset as a function of saccade type (correct prosaccade, correct antisaccade, erroneous prosaccade) and probe location (at cue, opposite cue, neutral). Error bars represent standard errors of the mean. The dashed line denotes the chance performance level. The analysis was based on at least five trials per participant and condition ( $M = 98$  for correct prosaccades,  $M = 102$  for correct antisaccades,  $M = 19$  for erroneous prosaccades).

In summary, the results on discrimination performance in Experiment 2 tell the same story as in Experiment 1: Correct antisaccades were associated with pre-saccadic attention at both locations. We further observed that errors were associated with more attention at the cued location, where the saccade was made to, and less attention at the correct antisaccade goal. Moreover, the significant difference between performance at the antisaccade goal and at the neutral location before correct antisaccades proves that attention allocation to the antisaccade goal is mediated by oculomotor preparation rather than by some strategy for maximizing discrimination performance.

As we were interested in whether the enhanced attention at the cued location or rather the reduced amount of attention at the correct antisaccade goal was predictive of errors, we performed post-hoc comparisons of discrimination performance at the cued and opposite locations before correct antisaccades and before errors. The results revealed that only the error-related decline in performance at the correct antisaccade goal, but not the increase at the cued location, was statistically significant. This suggests that attention at the antisaccade goal is crucial for correct antisaccade programming.

To investigate the question of whether error awareness is related to attention allocation, as has been proposed in previous work (e.g., Deubel et al., 1999; Godijn & Theeuwes, 2003b; Mokler & Fischer, 1999), we compared discrimination performance in trials with perceived and with unperceived errors. The results did not reveal any differences, except for a non-significant trend towards better discrimination performance (at all locations) in trials with unperceived errors. To see whether the allocation of attention in trials with corrected errors depended on the latency of the corrective saccade, we compared discrimination performance in trials with very fast ( $\leq 90$  ms) and longer ( $> 90$  ms) correction times. The results did not reveal any consistent differences.

## DISCUSSION

The goal of this study was to investigate the allocation of spatial attention during the programming of antisaccades. We employed a dual task, in which participants made prosaccades or antisaccades and concurrently discriminated visual probes at the cued location, the opposite location (i.e., the antisaccade goal), or at task-irrelevant locations.

First, we replicated the findings of previous antisaccade studies, such as the substantially longer latency of antisaccades in comparison to prosaccades (Everling, Dorris, & Munoz, 1998; Hallett, 1978) and the higher error rate in the antisaccade condition (Hallett, 1978; Heath, Dunham, Binsted, & Godbolt, 2010). Second, we found that most erroneous prosaccades were not perceived and were rapidly corrected, suggesting that a large proportion of corrective antisaccades was programmed in parallel with the erroneous prosaccades (Massen, 2004; Mokler et al., 2000; Mokler & Fischer, 1999). Our third and most important finding was that before antisaccades, attention was allocated in parallel to the visual cue and the antisaccade goal, rather than being first allocated to the cue and then to the antisaccade goal. Prosaccade errors were associated with an attentional bias towards the prosaccade goal, which has important implications concerning the relationship between attention and saccade programming.

In the following sections, we will discuss our results in the context of existing theories and previous findings in this field and propose a model of how attention and saccades could be influenced by a common competitive process.

### ***Parallel programming of prosaccades and antisaccades***

Parallel programming of two subsequent saccades can be inferred from very short intersaccadic intervals (Becker & Jürgens, 1979) and has been reported not only in the antisaccade task (Massen, 2004; Mokler & Fischer, 1999), but also in other tasks, such as reading (Morrison, 1984), double-step paradigms (Becker & Jürgens, 1979; Walker & McSorley, 2006), visual search (McPeck, Skavenski & Nakayama, 2000) and in the oculomotor capture paradigm (Godijn & Theeuwes, 2002, Irwin, Colcombe, Kramer, & Hahn, 2000; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999).

Recent investigations into this topic mainly focused on situations where an endogenous saccade is programmed along with an initial involuntary saccade to a visual distractor. McPeck et al. (2000), for instance, asked their subjects to saccade to a red or green color singleton presented along with two distractors of the opponent color (e.g., green or red). The fact that the same colors were used for target and distractors led to many erroneous saccades towards one of the distractors, especially when the distractors had the same color as the target in the previous trial. These erroneous saccades were often hypometric and many were followed by short-latency corrective saccades to the target. Based on these observations, McPeck et al. (2000) proposed a competition model of saccade programming, in which both saccade goals were represented in a common motor map, supposedly located in the superior colliculus. Mutual inhibitory connections between neurons would make sure that any increase in neural activity at one location would result in a decrease in activity at the other.

Investigations using the oculomotor capture paradigm (Godijn & Theeuwes, 2002; Irwin et al., 2000; Theeuwes et al., 1998, 1999), where endogenous saccades to a color-defined target compete with involuntary saccades to an onset distractor, yielded very similar results: a substantial proportion of initial erroneous saccades to the distractor, many of them followed by corrective saccades after less than 100 ms of fixation.

After the initial assumption that exogenous and endogenous saccades were programmed in separate brain circuits and simply race towards a threshold (Theeuwes et al., 1998, 1999), Godijn & Theeuwes (2002) formulated their *competitive integration model* (also see Meeter, Van der Stigchel, & Theeuwes, 2010), which also postulates that the rivalry takes place on a common collicular map with lateral inhibitory connections.

The idea of a parallel competition between erroneous prosaccades and subsequent corrective saccades in the antisaccade task was first addressed by Mokler and Fischer (1999) and further elaborated by Massen (2004).



Although Massen assumed mutual inhibition between the pro- and antisaccade programs, her findings (see **Introduction**) could not rule out an independent race model (the only evidence for mutual inhibition between prosaccades and antisaccades came from her observation that slower and faster corrected erroneous prosaccades tended to have shorter amplitudes, which could be due to interference from the second saccade program). Kristjánsson and colleagues (Kristjánsson, Chen, & Nakayama, 2001; Kristjánsson, Vandenbroucke, & Driver, 2004) showed that manipulations that slow down the prosaccade component can lead to faster antisaccades, which is more compatible with a model that assumes competitive interactions between both.

The results of the present study confirm many of the above mentioned findings, such as the shorter amplitudes of erroneous saccades and the significant proportion of very short correction times. In agreement with McPeck et al. (2000), we found a significant correlation between the amplitudes of initial erroneous saccades and their correction times: The faster a saccade was corrected, the smaller tended to be its amplitude. This suggests that the first saccade was influenced or even disrupted by the programming of the second saccade. Slower errors also tended to have shorter amplitudes (although this relationship was less consistent). Taken together, our findings provide further evidence that reflexive and endogenous saccades compete within the same or overlapping neural networks.

### ***Parallel attentional selection***

The results of our experiments revealed that antisaccades are preceded by attention allocation to both the visual cue and the antisaccade goal, thus suggesting that both locations compete for attentional resources. Our findings are consistent with previous evidence that visuospatial attention can be divided when this is beneficial for the task (Awh & Pashler, 2000; Baldauf & Deubel, 2008a, 2008b, 2009; Baldauf, Wolf, & Deubel, 2006; Deubel, 2014; Godijn & Theeuwes, 2003a; Jefferies, Enns, & DiLollo, 2014; Jonikaitis & Deubel, 2011). Moreover, our data rule out the serial hypothesis, according to which attention first needs to be disengaged from the visual target, before it can shift to the antisaccade goal (e.g., Crawford, Kean, Klein, & Hamm, 2006; Olk & Kingstone, 2003). If the serial hypothesis was true, we would have observed improved performance at the antisaccade target and poor performance at the cued location shortly before saccade onset. Instead, we found comparable performance at both locations.

### *The link between attention and (anti)saccades*

Our findings on attention allocation before correct antisaccades and before prosaccade errors have some important implications concerning the link between attention and saccade programming. The fact that attention before correct antisaccades was equally distributed among the cued location and the antisaccade goal is in conflict with the premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Rizzolatti, Riggio, & Sheliga, 1994), which regards attention as functionally equivalent to saccade preparation. If this theory was correct, correct antisaccades would be associated with more attention at the antisaccade goal than at the cued location, which was clearly not the case. Nevertheless, our results suggest that attention and saccade programming are closely linked, as attentional distribution was predictive of prosaccade errors.

Current views of visual attention are tied to the concept of priority maps (Fecteau & Munoz, 2006; Serences & Yantis, 2006), which are thought to integrate information about bottom-up saliency with top-down influences into a single real-time representation of behavioral relevance. In agreement with this concept, we believe that during the preparation of antisaccades, cue-related and antisaccade-related activity compete on such a map (or several related maps) and that the resulting priority signal influences both saccade programming (through modulatory influences on the oculomotor system) and visual perception (through feedback to early visual areas).

Our findings are compatible with such a model, as discrimination performance was clearly modulated by the saccade task and the ratio between cue-related and antisaccade-related attention was predictive of erroneous prosaccades. Research indicates that such a priority map could be represented in posterior parietal cortex. Single cell recording studies in monkeys have shown that neurons in area LIP (lateral intraparietal area) combine visual, cognitive and saccadic signals – and possibly others, such as information about reward – into a topographic representation of behavioral priority, which can be used to guide eye movements and attention (Bisley & Goldberg, 2010; Bisley, Ipata, Krishna, Gee, & Goldberg, 2009; Ipata, Gee, Bisley, & Goldberg, 2009). Gottlieb and Goldberg (1999) investigated LIP activity while monkeys performed antisaccades and found that most neurons strongly responded to the visual stimulus, when it fell in their receptive field, and some also fired in response to the antisaccade target. Recently, LIP has been shown to implement center-surround suppression mechanisms that can account for the type of competitive interactions between an endogenous saccade plan and a visually salient distractor, as we assume are happening in the antisaccade task.

In humans, researchers have identified topographically organized areas within the intraparietal sulcus (IPS) that most likely are the human homologues to monkey LIP (Schluppeck, Glimcher, & Heeger, 2005; Sereno, Pitzalis, & Martinez, 2001; Silver, Ress, & Heeger, 2005). Corbetta and Shulman (2002) identified IPS as a central part of the brain's network for endogenous attention. At the same time, IPS seems to play a role in selection for perception, as it has been shown to modulate activity in primary visual cortex via top-down attentional signals (Lauritzen, D'Esposito, Heeger, & Silver, 2009). A recent study by Khan et al. (2009) established a link between these two roles by showing that the well-documented facilitation of visual perception at the goal of a planned saccade crucially depends on the parietal cortex. IPS lesions lead to prolonged antisaccade latencies (Machado & Rafal, 2004) and a number of fMRI studies have found enhanced IPS activation in antisaccades as compared to prosaccades (see a recent meta-analysis by Jamadar, Fielding, & Egan, 2013). Of particular interest are the results of a study by Anderson, Husain, and Sumner (2008), which suggest that human IPS importantly contributes to the resolution of competition in the antisaccade task.

The idea that we try to convey here, namely that competitive integration can be generalized beyond the eye movement system and could occur on a parietal priority map, is not new, as it was already suggested by Hunt, von Mühlenen, and Kingstone (2007), based on their results on parallels between attentional and oculomotor capture.

We would like to emphasize that this proposal does not contradict the idea that saccade programs compete on a common collicular motor map (e.g., Findlay & Walker, 1999; Godijn & Theeuwes, 2002; McPeck et al., 2000; Trappenberg, Dorris, Munoz, & Klein, 2001), since we do not assume that our putative priority signal can directly drive eye movements. It rather seems that the SC motor map consists of a further competitive stage, even more specialized on oculomotor selection. Interestingly, findings from neurophysiological studies in monkeys revealed that stimulus-related activity bursts can be larger than antisaccade-related bursts even in FEF and SC, which are known to directly trigger eye movements (Everling, Dorris, Klein, & Munoz, 1999; Everling & Munoz, 2000). This indicates that the final threshold for saccade generation is not localized in SC or FEF, but rather in the brainstem saccade generator, where outputs from the whole oculomotor network are integrated (see Jantz, Watanabe, Everling, & Munoz, 2013, for further evidence). The brain employs several strategies to down-weight target-related activity and up-weight antisaccade-related activity, both at the level of the SC and downstream from it. Examples are the increase in fixation-related and decrease in visual SC activity in the preparation of an antisaccade (Everling, Dorris, & Munoz, 1998) or the transient increase in omnipause neuron activity following the appearance of the visual stimulus (Everling, Paré, Dorris, & Munoz, 1998).

It has also been suggested that input from other oculomotor areas, such as the supplementary eye field (SEF), could boost the relatively weak antisaccade-related activity downstream from the SC (Jantz et al., 2013; Munoz & Everling, 2004). The question whether the antisaccade target is also favored by signals from a parietal priority map remains to be clarified by further research.

Taken together, our results, as well as the research reviewed here, suggest that attention and saccade programming are both inherently parallel processes in which different spatial locations are selected along each other, rather than one after the other. Although attentional and oculomotor selection seem to be linked, they are not identical, as perceptual benefits are not limited to the goal of the upcoming saccade. In terms of brain economy, such a distinction makes sense: While it may often be beneficial to attend to several objects or locations at the same time, the eyes cannot go to more than one target. This constraint, along with the relatively high costs associated with an erroneous eye movement, entails a greater need to favor task demands over salience for saccade programming. Nevertheless, a parallel accumulation of information until a very late stage of oculomotor programming is still advantageous, as it allows the system to act fast and flexibly and dramatically reduces planning costs, for example when several eye movements are made in sequence.

### ***Error awareness and attention***

Some authors (Deubel, Irwin & Schneider, 1999; Mokler & Fischer, 1999) have proposed that error recognition in the antisaccade task is mediated by visuospatial attention, in the sense that our mind falsely attributes eye position to the current locus of attention. If, according to this hypothesis, attention first moves to the visual cue, the participant would recognize the saccade direction error. If, however, attention first shifts to the antisaccade goal and only the eyes initially make a reflexive saccade in the wrong direction, the error would not reach awareness and can be corrected faster, as attention does not need to move to the correct location anymore. Mokler et al. (2000) observed that unperceived erroneous prosaccades were associated with better visual discrimination performance at the antisaccade goal than at the visual target, while the opposite was true for perceived errors. From this they concluded that reflexive prosaccades can occur without a prior attention shift to the target.

In our study, discrimination performance in error trials was always best at the cue location and error perception was associated with slightly worse performance on the discrimination task.

One attempt to explain these contradictory findings could be through the exact comparison of the experimental designs used in their study and ours. Notably, Mokler and her collaborators did not present probes at a neutral location, which makes it impossible to judge the amount of task-related attention at the antisaccade goal. Second, the 100% valid exogenous pre-cue shown 100-200 ms before the probe, which was intended to increase the rate of erroneous prosaccades (see Fischer & Weber, 1996), may have led to better discrimination performance at the cued location. Alternatively, the process of error monitoring may have drawn attentional resources away from the discrimination task.

Such an account could explain both the better discrimination performance in association with unperceived errors and the shorter latencies of subsequent corrective saccades observed in the present study. The results of a study by Taylor and Hutton (2011) support this hypothesis by showing that error perception in the antisaccade task may require top-down attentional control. The lower frequency and reduced gain of corrective saccades that we observed following perceived errors would also be consistent with such an explanation.

Based on their findings from the oculomotor capture paradigm, Godijn & Theeuwes (2003b) proposed a weaker form of Mokler's hypothesis, which states that involuntary saccades to distractors may not be perceived when attention remains on the distractor for too little time. Our results do not support any of the two accounts, since we found neither a proof for attention being disengaged from the cued location nor for less cue-related attention before unperceived errors. Rather, the main problem associated with both hypotheses may be that they presume that attentional processes are strictly serial, which reflects the persistent influence of the attentional spotlight metaphor. Only recently, the notion of a single attentional focus that needs to be shifted in space has been replaced by newer theories, in which activations corresponding to spatial locations can be enhanced or suppressed through mutual interactions or through external modulatory influences, leading to dynamic "attentional landscapes" that are adapted to the current sensorimotor task (Baldauf & Deubel, 2010).

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## 2.2 Study 2: Attention reflects saccade decisions

### Contributions:

The author of this dissertation participated in data collection and analysis, interpreted the results and wrote the manuscript.

Donatas Jonikaitis designed and programmed the experiment, collected and analyzed data, created plots, interpreted the results and participated in writing the manuscript.

Heiner Deubel supervised the project, interpreted results and commented on the manuscript.

## **Attention reflects saccade decisions**

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### **Abstract**

The present study investigated the allocation of visuospatial attention during free or rule-based decisions between two memorized saccade targets. Participants were asked to memorize two spatial locations, highlighted by different colors. After a delay period, the color of the central fixation changed and either indicated one of the memorized locations as the saccade target (rule-based choice), or indicated to freely choose between the two locations. By probing discrimination performance at variable SOAs relative to this cue, we were able to measure the time course of the attentional selection of both targets. In both rule-based and free choice trials, we observed a parallel selection of the chosen and the non-chosen saccade target, with a clear bias towards the chosen target. This bias was evident before correct and before erroneous rule-based responses. Perceptual performance during the memory delay was influenced by top-down and bottom-up factors as well as by selection history and predicted the direction of saccades. During saccade programming, performance increased at both potential saccade goals, consistent with a race of both saccade programs towards a decision threshold. Our findings demonstrate that saccade decisions have direct visual consequences and show that decision making can be traced in the human oculomotor system well before choices are made.

## INTRODUCTION

Despite the fact that we, seemingly automatically, move our eyes several times per second, each of our saccades has to be preceded by some kind of decision making process, in which the saccade goal is selected amongst other possible goals. While traditional theories of decision making postulated that decisions are first made by cognitive systems and only then implemented in the form of motor actions, recent neurophysiological findings challenge these serial models by supporting the view that motor decisions consist of a biased competition between alternative motor plans that are represented in parallel in sensorimotor brain areas (Andersen & Cui, 2009; Cisek, 2007; Cisek & Kalaska, 2010).

Computational models of the decision process assume that sensory evidence in favor of each movement alternative is integrated over time and gradually accumulated towards a threshold, at which the corresponding action is initiated (e.g., Brown & Heathcote, 2007; Carpenter & Williams, 1995; Ratcliff & McKoon, 2008). The starting point – or baseline – of the accumulation depends on the prior probability that the given movement will be executed (Ludwig, 2011), while the rate of accumulation depends on the strength of the sensory evidence and other variables, such as the value associated with the given response (Gold & Shadlen, 2007).

Numerous single cell recordings from the monkey brain have supported these assumptions by showing that the outcome of saccadic decisions directly depends on sensory information (Newsome, Britten, & Movshon, 1989; Salzman, Britten, & Newsome, 1990) and that this decision-related sensory evidence is accumulated in visuo-motor brain areas, such as LIP (Gold & Shadlen, 2000; Ipata, Gee, Goldberg, & Bisley, 2009; Roitman & Shadlen, 2002; Shadlen & Newsome, 1996, 2001), FEF (Hanes & Schall, 1996; Kim & Shadlen, 1999; Schall, 2003) and SC (Glimcher & Sparks, 1992; Horwitz & Newsome, 2001; Munoz & Wurtz, 1995; Sparks, 1978; Wurtz & Goldberg, 1972). An fMRI study in humans, in which two eye movements had to be planned in sequence, also provided evidence that the posterior parietal cortex (containing the human homologue of LIP) represents goals of upcoming saccades (Medendorp, Goltz, & Vilis, 2006).

When monkeys have to decide between two saccade targets, neurons in visuo-motor brain areas represent both response alternatives – with a stronger signal corresponding to the selected goal (Kim & Basso, 2008; Platt & Glimcher, 1997) – and the representations are modulated by the perceived probability or value of the responses (Basso & Wurtz, 1998; Sugrue, Corrado, & Newsome, 2004).

Consistent with this, behavioral studies show that competitive visual environments not seldom lead to the parallel programming of two, or possibly even more, saccades (Becker & Jürgens, 1979; Godijn & Theeuwes, 2002; Irwin, Colcombe, Kramer & Hahn, 2000; Klapetek, Jonikaitis, & Deubel, 2016; Massen, 2004; McPeck, Skavenski & Nakayama, 2000; Morrison, 1984; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Walker & McSorley, 2006).

Unfortunately, many of the studies that supposedly demonstrated decision-related neural activity investigated saccades to visual targets, which makes it difficult to judge whether the neural signals reflected perceptual decision making or saccade planning. A possible way to distinguish between the two processes is to dissociate visual information and saccade planning spatially (as for example in the antisaccade task, where saccades have to be directed away from a visual stimulus) or temporally (by presenting the saccade cue after the disappearance of the visual information). A few researchers recorded from LIP neurons while monkeys performed antisaccades (Gottlieb & Goldberg, 1999; Zhang & Barash, 2000, 2004), their results being contradictory. While Gottlieb and Goldberg found that only few LIP neurons represented purely saccade-related activity and most cells showed visual responses, Zhang and Barash (2000, 2004) observed that most neurons could carry visual as well as motor activity, depending on the context.

To investigate saccade decisions in humans, one can take advantage of the tight coupling between oculomotor and perceptual selection. During saccade preparation, perception is automatically enhanced at the saccade target (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Klapetek et al., 2016; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Jonikaitis & Theeuwes, 2013). On the other hand, the presentation of salient visual events, such as irrelevant distractors, often leads to involuntary saccades in the direction of these stimuli, which has been termed oculomotor capture (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). Such observations, along with a wealth of other findings in monkeys and humans (for a review, see Ptak, 2012) corroborate the hypothesis that oculomotor and visual selection are coupled through a common attentional priority mechanism, which always selects the behaviorally most relevant location (Fecteau & Munoz, 2006; Serences & Yantis, 2006). If this is true, we should expect that any saccadic decision (reflected in accumulation of evidence in favor of a particular location on the priority map) should also be reflected in gradually improving perceptual performance at the corresponding spatial location.

In order to test this hypothesis, we designed an experiment, in which human observers had to choose between two memorized saccade targets (either freely or on the basis of a color rule) and simultaneously discriminate visual probes at the two competing



target locations or elsewhere in the display. By probing discrimination performance at variable times during the trial, we were able to measure the time course of the perceptual selection of both target locations. Consistent with the previously reviewed evidence on the coupling between saccadic and perceptual selection, we expected to see a clear perceptual benefit at the chosen target. We were also interested whether a perceptual benefit would be evident at the competing (non-chosen) target location as well. It is possible that both saccade targets (or the oculomotor programs towards them) are simultaneously represented in visuomotor brain areas and facilitate perception at both corresponding spatial locations. A second possibility, however, is that the non-chosen target is treated as an irrelevant distractor and can be ignored or even inhibited from early on. A third possibility is that the pattern of perceptual facilitation would differ in the rule-based and in the free-choice conditions, for example due to smaller competition of the non-chosen target in the rule-based condition than in the free-choice condition.

## METHODS

### *Participants*

Twelve observers (age 21-29, seven female) completed the experiment for payment. All participants were naive as to the predictions of the study. The experiments were carried out with the approval of the department's ethic guidelines committee and in accordance to the Declaration of Helsinki, and participants gave written informed consent.

### *Apparatus*

The observers were seated in a quiet and dimly illuminated room in front of a gamma-linearized 21-in CRT monitor (Sony GDM-F500R, 1024 x 768 pixels, 120 Hz), positioned at a viewing distance of 60 cm. Right-eye gaze position was recorded with an EyeLink 1000 desktop mounted eye tracker (SR Research, Canada) at a sampling rate of 1000 Hz while head movements were minimized through the use of a chin and forehead rest. The eye tracker was calibrated before each new block and whenever it was necessary. Stimulus presentation and response collection were controlled by an Apple Mac Mini, using MATLAB software (MathWorks, Natick, USA) and the Psychophysics and EYELINK Toolbox extensions (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997; see <http://psychtoolbox.org>). Manual responses were collected via the arrow keys on the right hand side of the computer keyboard.

## Procedure

### *Main task*

Each trial started with a fixation target (black dot, diameter:  $0.75^\circ$  of visual angle) presented on a gray background. Five square objects (diameter:  $2.8^\circ$ ), were positioned on an imaginary circle around the fixation (radius:  $7^\circ$ ), the angular position of the first object was  $30^\circ$  plus a random jitter between  $-10$  to  $10^\circ$  and the distance between objects was  $72^\circ$  (see **Figure 1**). Each square object consisted of an alternating stream of vertically oriented Gabor patches (spatial frequency: 2.5 cycles per degree, 100% contrast, random phase selected on each presentation) and grayscale noise masks (pixel luminance values randomly drawn from a Gaussian distribution with minimum 0 (black) and maximum 255 (white),  $M = 128$  and  $SD = 128$ ). Gabor patches and noise masks alternated every 4 display refresh frames (33 ms).

During an initial memory cueing phase (Gaussian distribution with  $M = 2000$  ms and  $SD = 100$  ms), two of the streams were highlighted by color frames (one blue and the other green) and participants were asked to memorize their locations. The memory cueing phase was followed by a delay of 500 to 1500 ms (selected randomly from a uniform distribution), during which the colored frames were extinguished. After the delay, a central saccade cue was presented for 700 ms: the fixation target changed color to an equiluminant blue, green or orange color with equal probability. A green or blue fixation instructed a saccade to the corresponding memorized green or blue target location (rule-based choice), whereas an orange fixation indicated to saccade to either of the two memorized locations (free choice). After 700 ms, the fixation and all square objects were removed.

A probe display was presented -300 to 400 ms relative to saccade cue onset (time selected randomly from a uniform distribution). The probe was a Gabor patch tilted clockwise or counterclockwise (angle of tilt determined for each participant, see below) and was presented for 33 ms in one of the five object streams (selected randomly with equal probability).

After probe offset, no Gabor patches were further shown, so the object streams consisted of alternating noise masks and blank sequences. Observers reported the perceived probe orientation by pressing the left (counterclockwise tilt) or right (clockwise tilt) arrow key. We instructed observers to focus on making fast and accurate saccades and to guess whenever they were unsure about the probe orientation. Discrimination responses were not speeded. A new trial started 200 ms after the discrimination response.

### ***Pretest***

We determined the probe tilt angle for each participant at the beginning of each recording day. The visual stimuli in the pretest were identical as in the main task, except that only one memory target was presented and it always predicted the location of the probe (100% valid cue).

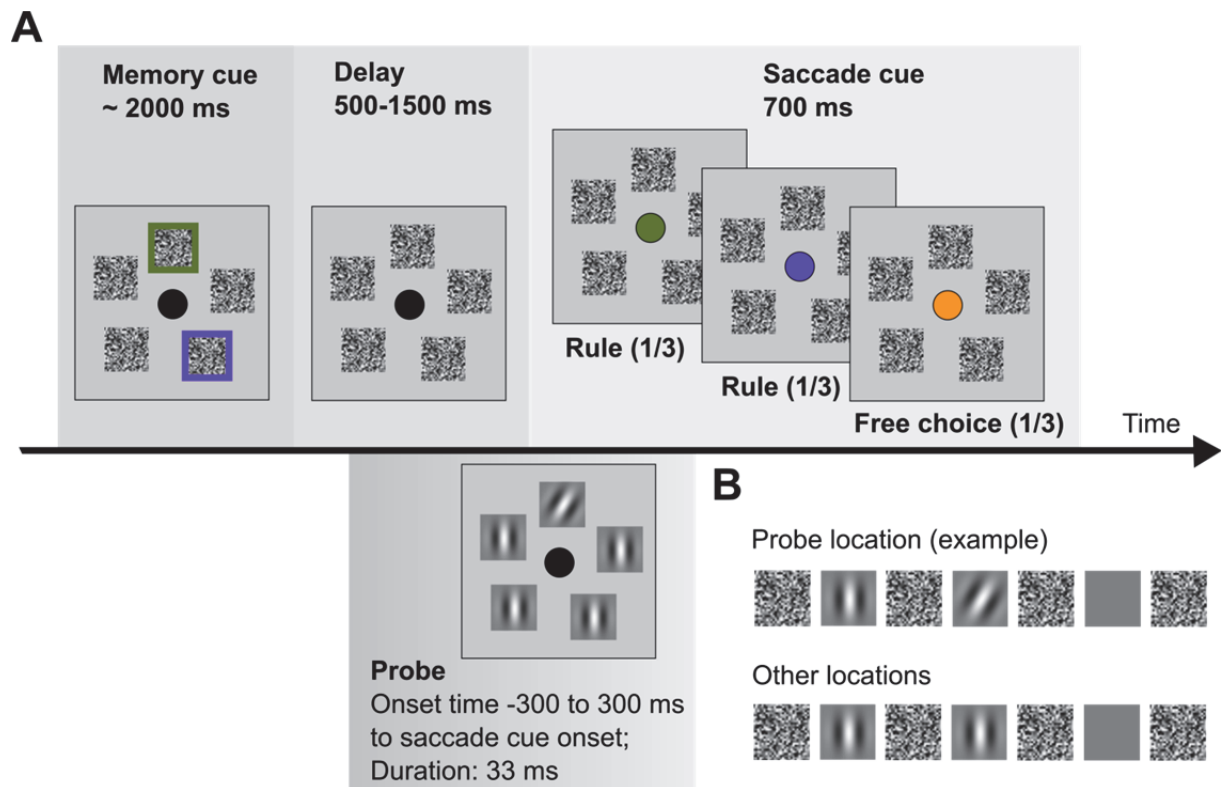
Observers were instructed to covertly attend to the memory target while maintaining central fixation and to report the orientation of the probe. The tilt angle at which observers reached 80% correct probe discrimination was determined using a modified version of the QUEST staircase procedure (King-Smith, Grigsby, Vingrys, Benes, & Supowit, 1994; Watson & Pelli, 1983) implemented in MATLAB Psychophysics toolbox.

Observers participated in a minimum of 14 main task sessions, each consisting of eight blocks of 50 trials. They usually performed one or two sessions on a single day.

### **Data analyses**

Drift correction was performed offline using the average gaze direction (given that no saccades of amplitude larger than  $0.5^\circ$  occurred) between 100 and 10 ms before memory delay onset. Saccades were detected offline using an algorithm that evaluates eye velocity changes (Engbert & Mergenthaler, 2006) with a velocity threshold of 6 SD to detect saccade onset and a minimum saccade duration of 6 ms. We classified saccades as correct if the starting point was less than  $2^\circ$  away from fixation, the endpoint was less than  $3^\circ$  away from the target center and the onset latency was between 50 and 700 ms. We removed trials due to breaking of fixation if a saccade larger than  $2^\circ$  occurred during the last 200 ms before saccade cue onset or between cue onset and correct saccade initiation. Trials were also removed if blinks occurred in the interval starting 100 ms before saccade cue onset and ending with saccade onset. On trials where the two target locations were adjacent (distance  $72^\circ$  of arc), the saccade was classified as either correct or incorrect, depending on whether the first saccade landed closer to the cued or to the non-cued location. Data from each participant was inspected manually for saccade and micro-saccade detection accuracy and data recording noise. In total, participants selected the correct target on 80155 and the erroneous target on 14912 out of the total 102451 recorded trials (7% of trials had to be removed for reasons mentioned above).

Statistical comparisons consisted of the calculation of the means of 10,000 bootstrap samples that were drawn with replacement from each condition's data set. Differences between the means were computed and two-tailed p-values were derived from the distribution of these differences. For each comparison, Cohen's  $d$  was calculated as a measure of effect size (difference between the means divided by the pooled standard deviation). Effect sizes of  $d = .20$  can be cautiously interpreted as "small",  $d = .50$  as "medium", and  $d = .80$  as "large" (Cohen, 1988).



**Figure 1.** (A) Schematic depiction of the sequence of stimuli. During the memory cueing period, two colored frames indicated the memory target locations. After a memory delay the saccade cue was presented. The saccade cue was a color change of the fixation: blue (1/3 of trials) or green (1/3 of trials) indicated that participants had to make a saccade towards the previously blue or green target (rule-based choice), whereas orange (1/3 of trials) indicated that either of the two targets could be selected (free choice). (B) During the entire trial, each of the five locations contained a rapidly alternating stream of white noise masks and vertically oriented Gabor patches. A probe was presented in one of the locations. The probe consisted of a tilt of one of the Gabors clockwise or counterclockwise from the vertical for 33 ms and appeared between -300 and 300 ms relative to the onset of the saccade cue.

## RESULTS

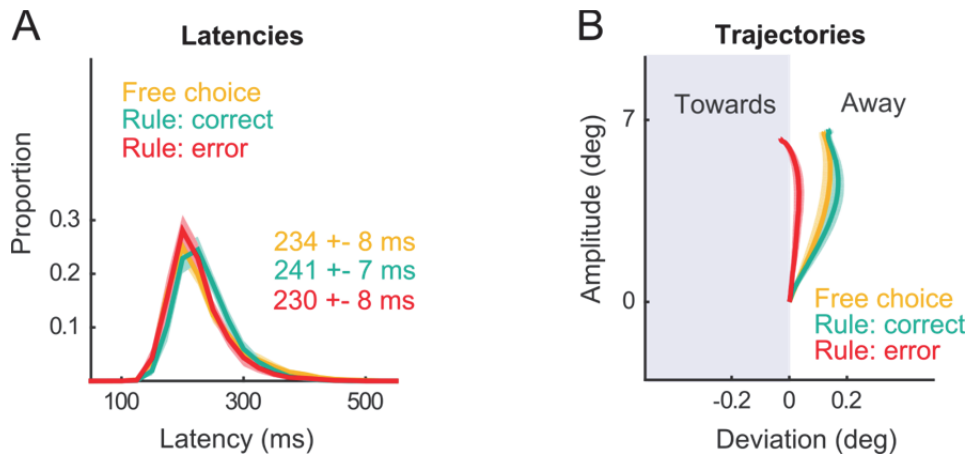
### *Properties of saccades*

Response latency and accuracy are the two main measures of the outcome of any decision making process. Further measures of motor performance, such as trajectory deviations, have also been used as a basis for inferences about competitive processes underlying choices between multiple motor plans (e.g., Chapman et al., 2010; McSorley & McCloy, 2009; Song & Nakayama, 2008; Welsh & Elliott, 2004).

**Figure 2A** shows the distributions of saccade latencies. Latencies (mean  $\pm$  SE) were shorter in the free-choice condition ( $234 \pm 8$  ms) than in the rule-based condition ( $241 \pm 7$  ms,  $p = .004$ , *Cohen's d* = .27). A comparison of saccade latencies on correct and error trials in the rule-based condition (note that decision errors could not occur in the free-choice condition) revealed shorter latencies on error trials ( $230 \pm 8$  ms) than on correct trials ( $241 \pm 7$  ms,  $p < .001$ ,  $d = .44$ ).

**Figure 2B** shows the saccade trajectories. In human studies, saccade trajectories tend to deviate away from competing stimuli if they are successfully suppressed on the motor map of the superior colliculus, and towards distractors if this suppression fails (e.g., Sheliga, Riggio, Craighero & Rizzolatti, 1995; Van der Stigchel, Meeter, & Theeuwes, 2006).

We observed that saccade trajectories deviated away from the non-chosen target both in the free-choice and in the rule-based condition. Surprisingly, this deviation away was abolished on error trials. Saccade deviation on error trials ( $0.03 \pm 0.03$  deg) was smaller than on both correct rule-based trials ( $0.30 \pm 0.03$  deg,  $p < .001$ ,  $d = 2.56$ ) and on free-choice trials ( $0.26 \pm 0.05$  deg,  $p < .001$ ,  $d = 1.78$ ). This suggests that suppression of the non-chosen target was reduced on error trials. However, two different reasons could underlie this reduced suppression. First, it is possible that both targets were represented in the oculomotor system and that the representation of the non-chosen target was not suppressed. Second, only the erroneously chosen saccade target may have been represented on error trials, while the correct target may simply not have been considered from the beginning. Unfortunately, neither alternative can be ruled out, as motor responses only reflect the final state of competition between possible movement targets, shortly before or during movement execution.



**Figure 2.** (A) Saccade latency distributions in the free and rule-based choice tasks. Errors were defined as wrong saccade target selection during the rule-based condition. Shaded areas represent the standard error of the mean (SEM). (B) Saccade trajectories towards or away from the non-chosen target. Locations were rotated and flipped, so that all non-chosen targets appear to the left of the saccade goal in the figure. Saccade trajectories towards the non-chosen target fall on the shaded background area, whereas trajectories away from it fall on the white background area.

In summary, while the latency and trajectory differences observed in our study can be cautiously interpreted, they represent the final state of motor decisions and hence allow us to draw only limited conclusions on the decision making process itself. We will therefore focus on attention allocation during decision making, which will change or disambiguate some of the previously discussed interpretations.

### ***Attentional selection***

Based on the existing literature, we expected to find (a) that attention would be maintained at the locations held in working memory during the delay interval, and (b) that attention would shift to the saccade goal before saccade onset.

In order to measure attention allocation during the memory delay, we calculated visual sensitivity (d-prime) in the probe discrimination task at all locations in the range 300-200 ms before the onset of the saccade cue. Visual sensitivity ( $M \pm SE$ ) was superior at both memorized locations. When compared to the average of the three task-irrelevant locations ( $0.1 \pm 0.1$ ), d-primes were higher at the location of the first ( $0.7 \pm 0.1$ ,  $p < .001$ ,  $d = 2.01$ ), and the second memory target ( $0.8 \pm 0.1$ ,  $p < .001$ ,  $d = 2.28$ ).

This indicates that both locations were selected by visuospatial attention, possibly in order to strengthen their representation in working memory by spatial rehearsal (Awh & Jonides, 2001).

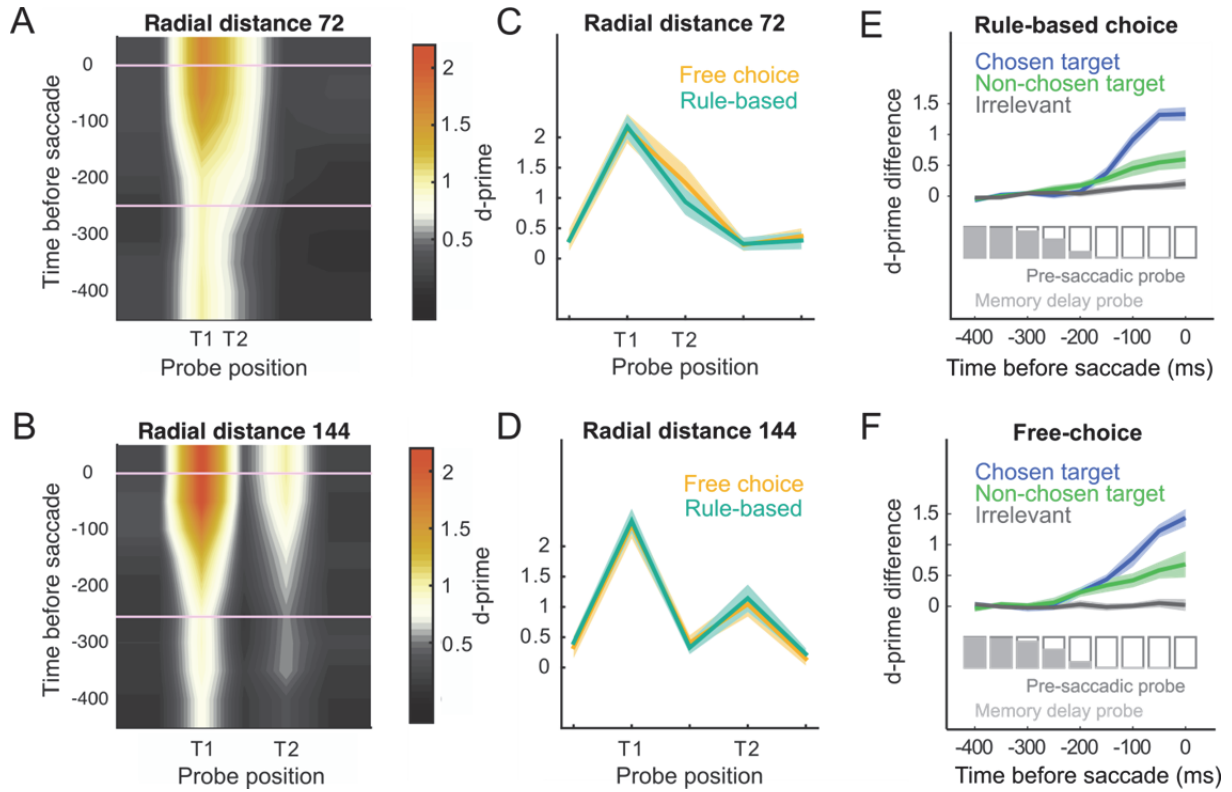
Next, we focused on discrimination performance after the appearance of the saccade cue. In line with earlier studies on saccade preparation and spatial attention (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Klapetek et al., 2016; Kowler et al., 1995; Rolfs et al., 2011; Jonikaitis & Theeuwes, 2013), we found that saccade preparation was associated with improved target discrimination at the future saccade goal. Visual sensitivity (100-0 ms before saccade onset) was higher at the chosen target ( $2.3 \pm 0.2$ ) than at the non-chosen target ( $1.1 \pm 0.2$ ,  $p < .001$ ,  $d = 1.64$ ), as well as at irrelevant locations ( $0.3 \pm 0.1$ ,  $p < .001$ ,  $d = 3.89$ ). Taken together, the pattern of perceptual discrimination performance suggests that spatial attention shifted to the saccade goal whenever a saccade was prepared.

### *Attentional selection is linked to decision making*

**Figure 3A-B** shows the spatiotemporal distribution of the pre-saccadic visual sensitivity. An increase in sensitivity occurred at both competing target locations, whereas there was little to no sensitivity increase at the irrelevant locations. Furthermore, sensitivity at the non-chosen location increased regardless of whether it was close to the chosen target (radial distance 72 degrees) or further away from it (radial distance 144 degrees), with no benefit at the location between the chosen and non-chosen target locations in the latter case (**Figure 3D**). This indicates that target selection is spatially specific and occurs before saccade onset.

To evaluate whether spatial attention reflects the process of saccadic decision making, we measured how visual sensitivity after saccade cue onset changed relative to visual sensitivity during the memory delay. For this purpose, we subtracted the average d-prime during the memory delay (-300 to -100 ms before saccade cue onset) from the d-prime in each time bin, separately for chosen, non-chosen, and task irrelevant locations as well as for both choice conditions. **Figure 3E-F** shows the change in visual sensitivity in the rule-based and free-choice conditions over time. Visual sensitivity increased at both the chosen target and the non-chosen target after the appearance of the saccade cue. Indeed, during rule-based decisions, the visual sensitivity increase relative to the memory delay (change in d-primes 100 to 0 ms before saccade onset) was larger at the chosen target ( $1.3 \pm 0.1$ ) than at irrelevant locations ( $0.2 \pm 0.1$ ,  $p < .001$ ,  $d = 4.20$ ) and this benefit was also present at the non-chosen target ( $0.5 \pm 0.1$ ,  $p < .001$ ,  $d = 1.20$ ).

Comparable results were observed during the free-choice task (chosen target:  $1.2 \pm 0.1$  vs. irrelevant:  $0.1 \pm 0.1$ ,  $p < .001$ ,  $d = 3.82$ ; non-chosen target:  $0.6 \pm 0.1$  vs. irrelevant,  $p < .001$ ,  $d = 1.52$ ). These results show that both target locations were selected by attention during the decision making period.



**Figure 3.** Attentional selection during decision making. **(A)** Visual sensitivity before saccade onset at all five measured locations. Memorized target locations are labeled as T1 (chosen target) and T2 (non-chosen target). Radial distance between both targets:  $72^\circ$ . **(B)** Visual sensitivity before saccade onset, radial distance between both targets:  $144^\circ$ . **(C)** Visual sensitivity in the free-choice and rule-based conditions between 100 and 0 ms before saccade onset, radial distance between both targets:  $72^\circ$ . **(D)** Visual sensitivity in the free-choice and rule-based conditions between 100 and 0 ms before saccade onset, radial distance between both targets:  $144^\circ$ . **(E)** Benefit in visual sensitivity in the rule-based condition relative to average performance 300 to 150 ms before saccade cue onset. The bars at the bottom of the figure indicate the ratio between probes presented before (gray) and after saccade cue onset (empty) within each time bin. Shaded areas represent SEM. **(F)** Benefit in visual sensitivity in the free-choice condition.

So far, the pattern of results supports the following conclusions: First, oculomotor decisions seem to interact with spatial attention, thus allowing us to track decision making before motor effects of decisions become observable. Second, memory-based saccade decisions involve attention allocation to both alternative saccade goals, despite the absence of visual information that could guide attention.



Both in the free-choice and surprisingly also in the rule-based choice condition, where the saccade target was defined by a simple stimulus-response mapping, we observed a simultaneous representation of both potential saccade goals during the entire decision making process.

### *Attentional selection is associated with saccade programming*

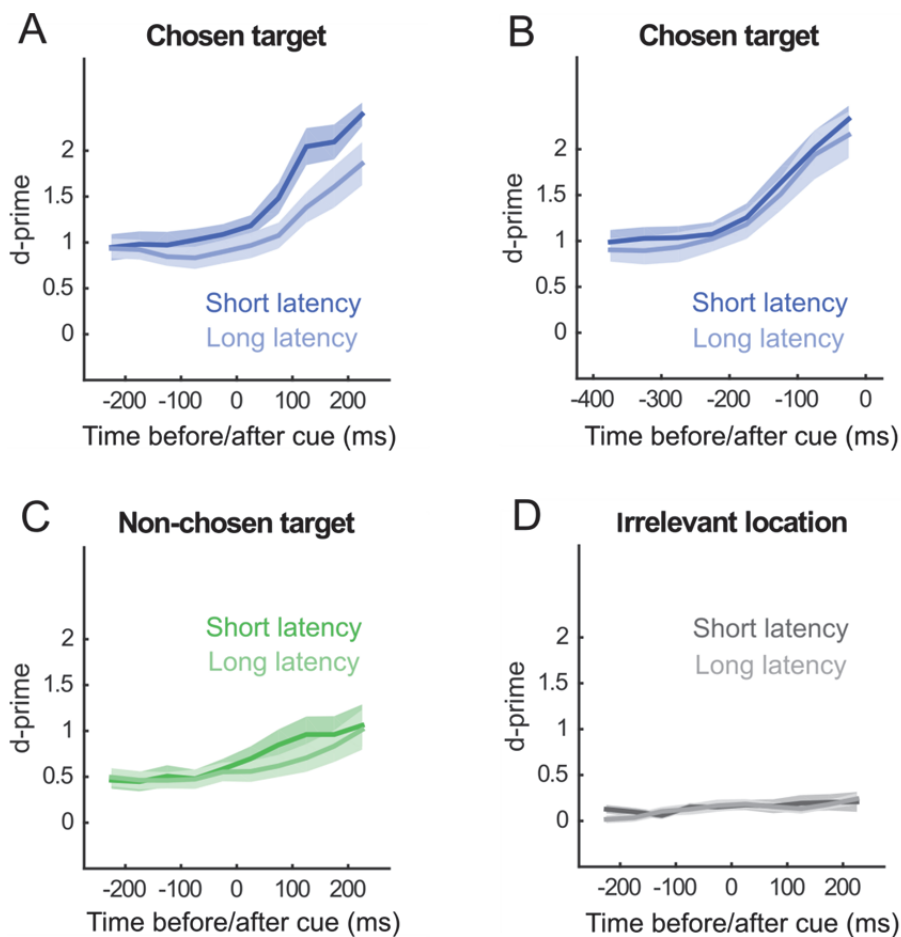
We next investigated whether the observed attentional selection was directly associated with saccade responses. For this purpose, we examined the relationship between saccade latencies and the time course of visual sensitivity (**Figure 4**). If covert attention indeed reflects decision making, then faster decisions, as indicated by saccade latencies, should be preceded by earlier attentional selection. However, in this context it is important to distinguish two factors that can influence the speed of decisions. One is the rate at which sensory evidence is accumulated towards the decision boundary, and the other is the starting point of the accumulation (or alternatively the threshold itself).

To compare trials with faster and slower saccades, we separated saccade latencies at the median for each participant (faster latencies were on average 217 ms and slower latencies were 269 ms). As can be seen in **Figure 4A**, we observed that after the onset of the saccade cue, visual sensitivity increased earlier during fast saccadic responses and improved later during slow saccadic responses. Visual sensitivity (averaged across 50-200 ms after saccade cue onset) was better during short latency trials ( $2.1 \pm 0.2$ ) than during long latency trials ( $1.6 \pm 0.2$ ,  $p < .001$ ,  $d = 1.04$ ). **Figure 4B** shows discrimination performance relative to saccade onset. We observed comparable rise rates for fast and slower decisions. Visual sensitivity for the interval 150-0 ms before saccade onset was comparable for short latency trials ( $2.0 \pm 0.2$ ) and long latency trials ( $1.9 \pm 0.3$ ),  $p = .52$ ,  $d = 0.09$ . These findings are compatible with the assumption that faster and slower decisions differ in the starting point of the accumulation, which depends on the prior probability of the associated movement vector (Ludwig, 2011), but not in the rate of the sensory evidence accumulation.

**Figure 4C** shows that saccade latency differences were also associated with discrimination performance differences at the non-chosen target. Visual sensitivity at the non-chosen target 50-200 ms after saccade cue onset was higher before short latency saccades ( $1.0 \pm 0.2$ ), than before long-latency saccades ( $0.7 \pm 0.2$ ,  $p = .006$ ,  $d = .42$ ), suggesting that the attention shift to the non-selected target was also linked to saccade onset. No such differences were present at task-irrelevant locations (**Figure 4D**).

Our results thus demonstrate that the timing of the attentional selection of the competing saccade targets is directly related to the timing of the saccade decision. An apparent interpretation is that participants were simply more alert on fast latency trials, which could lead to both an earlier increase in discrimination performance and to faster saccade programming. This explanation is unlikely, however, as discrimination performance at the irrelevant locations was not modulated by saccade latency.

Visual sensitivity at the irrelevant locations (50-200 ms after saccade cue onset) did not differ between short latency saccades ( $0.2 \pm 0.1$ ) and long latency saccades ( $0.1 \pm 0.1$ ,  $p = .53$ ,  $d = .24$ ). The effect of saccade latency on discrimination performance was instead restricted to the decision-relevant locations, suggesting that a spatially specific competition between these two locations had taken place.



**Figure 4.** Attentional selection before saccades with short and with long latencies. **(A)** Visual sensitivity at the chosen target relative to saccade cue onset. **(B)** Visual sensitivity at the chosen target relative to saccade onset. **(C)** Visual sensitivity at the non-chosen target relative to saccade cue onset. **(D)** Visual sensitivity at irrelevant locations relative to saccade cue onset.

### *Choice errors are related to attentional biases*

We observed that in the rule-based choice condition participants correctly selected the instructed target on 78% of the trials, and made an erroneous selection on 22%. Given the size of our data set, we recorded on average  $\sim 1200$  error trials per participant, which allowed us to perform an analysis of attentional selection during error trials. Our data on saccade trajectory deviations (**Figure 2B**) permitted two opposing hypotheses – either the non-chosen location was not suppressed, or it was not represented from the beginning.

**Figure 5A** compares visual sensitivity at the chosen target on correct and on error trials. It is evident that the target was selected later on error trials than on correct trials. Due to this, visual sensitivity (50-150 ms after saccade cue onset) was better at correctly chosen targets ( $1.4 \pm 0.2$ ) than at erroneously chosen targets ( $0.7 \pm 0.1$ ,  $p < .001$ ,  $d = 1.43$ ). However, discrimination performance at the non-chosen target also improved before saccade onset, indicating that both targets still competed on error trials. Indeed, discrimination performance at the non-chosen target (50-150 ms after saccade cue onset) was comparable on correct trials ( $0.7 \pm 0.1$ ) and on error trials ( $0.8 \pm 0.1$ ,  $p = .62$ ,  $d = .16$ ). This shows that due to later improvement at the chosen target locations on error trials, the competition between chosen and non-chosen locations was resolved later on error trials.

To determine whether saccade decisions were biased by selection history, we measured whether target choice was influenced by choice on the previous trial (**Figure 5B**). For this purpose, we calculated the selection bias as the difference between the percentages of same and different choices (target color or location) with respect to the previous trial. We observed that free choices tended to be biased by the color of the previously chosen target, as participants were less likely to choose the target of the same color (bias:  $-3.8 \pm 1.3$  %,  $p = .003$ ,  $d = 0.7$ ). Color did not affect rule-based choices, neither on correct (bias:  $0.4 \pm 0.4$  %,  $p = .26$ ,  $d = 0.26$ ) nor on error trials (bias:  $1.4 \pm 1.8$  %,  $p = .42$ ,  $d = .39$ ). The location of the previously chosen target also affected saccade choices, as participants were more likely to choose the same location as on the previous trial. This was true for both free choice trials (bias:  $4.4 \pm 1.0$  %,  $p < .001$ ,  $d = 1.28$ ) and error trials of the rule-based condition (bias:  $2.8 \pm 1.5$  %,  $p = .05$ ,  $d = .84$ ), but not for correct rule-based trials (bias:  $0.4 \pm 0.4$  %,  $p = .28$ ,  $d = .18$ ). Taken together, we observed some small but detectable biases by choice history.

We also checked whether participants were more likely to choose a saccade target when it coincided with the location of the discrimination probe (**Figure 5C**). Indeed, on trials where the probe was presented at the location of one of the two targets 50 ms or earlier before the saccade cue, saccades were more likely to be directed towards the probed target than towards the non-probed target. This bias was present in the free-choice condition ( $17 \pm 5\%$ ,  $p < .001$ ,  $d = 1.58$ ), as well as on correct trials of the rule-based condition ( $8 \pm 2\%$ ,  $p < .001$ ,  $d = 1.15$ ), and was strongest on error trials of the rule-based condition ( $32 \pm 9\%$ ,  $p < .001$ ,  $d = 1.96$ ). This suggests that the higher discrimination performance at the upcoming saccade goal during the memory delay (**Figure 5A**) results in large part from this bias.

The influence of the probe on decision making was greatly reduced when the probe was presented 50 ms or later after the onset of the saccade cue. In this case, the bias was not significant both on correct ( $0.3 \pm 0.1\%$ ,  $p = .78$ ,  $d = .03$ ) and on error trials ( $5 \pm 4\%$ ,  $p = .74$ ,  $d = 0.72$ ) of the rule-based condition ( $5 \pm 4\%$ ,  $p = .74$ ,  $d = 0.72$ ) and it was even reversed in the free choice condition ( $-6 \pm 3\%$ ,  $p = .04$ ,  $d = 0.78$ ). This can be expected, as it is progressively more difficult to capture attention as more information in favor of the saccade goal has been accumulated (Hunt, Von Mühlenen, & Kingstone, 2007).

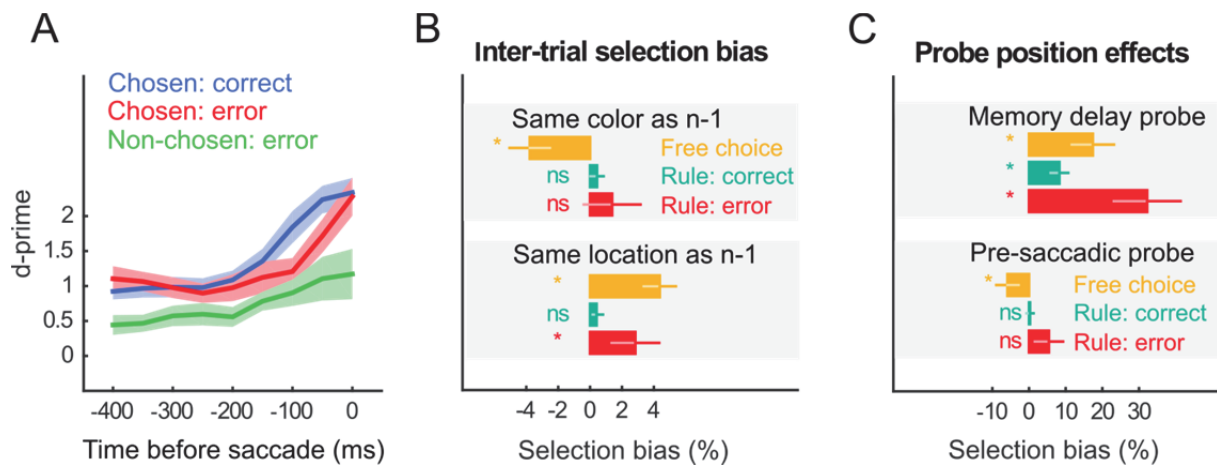


Figure 5. (A) Visual sensitivity during rule-based decisions relative to saccade onset. (B) Saccade choice as a function of previous choice. Selection bias is defined as the percentage of trials on which participants were more likely (positive bias) or less likely (negative bias) to choose a target of the same color (upper panel) or same location (lower panel) as in the preceding trial. Error bars represent the SEM. Bootstrap comparisons between two conditions: \* indicates  $p < 0.05$ , ns indicates  $p > 0.05$ . (C) Target selection as a function of probe location. Selection bias is defined as the percentage of trials on which participants were more likely or less likely to choose the target at the same location as a probe presented during the memory delay period (upper panel) or as a probe presented after the saccade cue (lower panel).

## DISCUSSION

The present study investigated the allocation of visuospatial attention during free or rule-based choices between memorized saccade targets. Decision making has been extensively studied in the presence of visual information, that is when one of two responses has to be chosen while the strength of visual information in favor of both response alternatives is being evaluated (for reviews see Glimcher, 2003; Gold & Shadlen, 2007; Schall, 2003), but to our knowledge this is the first examination of motor decisions between two goals stored in working memory. In our experiment, no external visuospatial information was available to guide the decision, but we still observed a parallel attentional selection of the competing saccade goals, both before and after the saccade cue.

To our surprise, we did not find any substantial differences between the rule-based and free-choice conditions, except for a shorter saccadic latency under free choice conditions.

### *Pre-selection during the memory delay*

The parallel selection of both saccade targets during the memory delay is consistent with evidence from other studies that spatial attention is allocated to locations maintained in working memory (Awh & Jonides, 2001; Awh, Jonides, & Reuter-Lorenz, 1998; Herwig, Beisert, & Schneider, 2010). The design of our experiment does not allow to disentangle the effects of attention and working memory on discrimination performance, as this was not one of our goals. Moreover, attention and visual working memory show so much overlap at the neural level that many authors consider them to be a unitary mechanism (Chun, 2011; Gazzaley & Nobre, 2012; Kiyonaga & Egner, 2013; Rensink, 2002; Theeuwes, Belopolsky, & Olivers, 2009; Wheeler & Treisman, 2002).

Interestingly, we did not observe a balanced selection of both targets during the memory delay, but one that was biased by future saccadic choice. This shows that on some trials, one target was clearly preferred over the other, and that this target was more likely to become the future saccade goal. Target selection was significantly biased by the appearance of the visual probe at one of the two remembered locations and, to a lesser degree, by the color of the saccade goal on the previous trial.

The finding that choice on the previous trial can bias motor decisions has been reported by a number of authors (Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015; Klaes, Westendorff, Chakrabarti, & Gail, 2011; de Lange, Rahnev, Donner, & Lau, 2013; Suriya-Arunroj & Gail, 2015) and it has been explained by the tendency of subjects to form probabilistic expectations that shift the starting point of the evidence accumulation closer to the decision boundary (de Lange et al., 2013; Suriya-Arunroj & Gail, 2015). Neurophysiological studies have shown that non-sensory variables, such as the prior probability that a certain response will be required (Basso & Wurtz, 1998; Dorris & Munoz, 1998; Platt & Glimcher, 1999), the reward associated with different response alternatives (Platt & Glimcher, 1999), or learned space-reward associations (Chelazzi et al., 2014), directly modulate the accumulation of saccade-related evidence in SC and LIP. It is becoming increasingly clear that the traditional dichotomy between top-down and bottom-up influences is not sufficient to explain how attention is allocated and that selection and reward history have to be considered as equally important attentional biases (Awh, Belopolsky, & Theeuwes, 2012). Our findings support this notion, as we observed that saccade goal selection was biased by choice on the previous trial, although this bias reduced performance.

We also observed that saccadic decisions in our study were biased by the appearance of the discrimination probe during the memory delay period, but not during saccade preparation. The latter finding is consistent with our earlier work, in which we did not observe any effects of discrimination probe appearance on saccade target selection (Rolfs et al., 2011, Jonikaitis, Szinte, Rolfs & Cavanagh, 2013, Jonikaitis & Theeuwes, 2013; Klapetek et al., 2016). In those studies, the probe did not capture attention, as neither the location nor the time of probe onset affected the direction or latency of saccades. Indeed, the reason we used continuous Gabor-mask streams was to prevent disruption of saccade preparation due to probe onset on a static display during saccade preparation. Therefore, the preferential selection of the probe location during the memory delay in the present study indicates that the probe was not salient enough to attract attention *per se*. Instead, it only affected decisions when participants were actively sampling the two memorized locations in search of any evidence that could help to decide for one of them. Such contingencies of attentional capture on endogenous attention have been previously reported by other authors (Anderson & Folk, 2010; Eimer & Kiss, 2008; Folk, Remington, & Johnston, 1992).

Taken together, our results on discrimination performance during the memory delay show that, instead of comprising a mere representation of the possible saccade goals, the memory interval involved some form of biased competition between the goals (Desimone & Duncan, 1995).

Choice on the previous trial, probe appearance, and possibly other intrinsic factors, biased participants to pre-select the saccade goal before the appearance of the saccade cue, even when this was not appropriate (such as in the rule-based condition, where the correct target was defined by the color of the cue).

### ***Perceptual selection reflects the decision process***

During the decision period, we observed an increase in visual sensitivity at the chosen saccade goal (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel, 2008; Doré-Mazars, Pouget, & Beauvillain, 2004; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007). The time course of this pre-saccadic visual sensitivity increase was linked to saccade onset regardless of the saccade latency, which indicates that it reflected the accumulation of sensory information in favor of the saccade goal and/or the saccade program. Surprisingly, we also observed a saccade-related increase in visual sensitivity at the non-chosen target, both in the free and rule-based choice tasks. The increase in visual sensitivity at both the chosen and the non-chosen targets indicates that both locations were evaluated in the oculomotor system as potential saccade targets, even though the decision could have been simply made by retrieving a stimulus-response association stored in memory (e.g., green fixation – look at the previously green location). This suggests that, rather than representing the chosen saccade goal, the oculomotor system represents the decision making process.

Our findings are compatible with previous neurophysiological results, which have shown that visuomotor brain areas simultaneously represent competing or sequential saccade goals (Basso & Wurtz, 1998; Kim & Basso, 2008; McPeck & Keller, 2002; Platt & Glimcher, 1997; Sugrue et al., 2004), or reach goals (Baldauf, Cui & Andersen, 2008; Cisek & Kalaska, 2005; Gallivan et al., 2015; Klaes et al., 2011; Scherberger & Andersen, 2007). Convergent evidence also comes from behavioral research, where parallel saccade programming has been observed in a number of contexts (Becker & Jürgens, 1979; Godijn & Theeuwes, 2002; Hodgson, Parris, Gregory, & Jarvis, 2009; Irwin et al., 2000; Massen, 2004; McPeck, Skavenski & Nakayama, 2000; Morrison, 1984; Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999; Walker & McSorley, 2006). We recently observed that parallel saccade programming in the antisaccade task was accompanied by the simultaneous attentional selection of both saccade goals and that the distribution of attention predicted erroneous prosaccades (Klapetek et al., 2016).

An equivalent association between perception and saccade direction was evident in the present study, as both correct and erroneous saccades were preceded by a discrimination benefit at the saccade goal. The fact that vision and saccades tend to select the same spatial locations suggests that they rely on shared decisional mechanisms.

### ***Errors follow late decisions***

The general pattern of attentional selection, by which attention was allocated in parallel to both saccade targets, though with a clear benefit at the chosen target, did not differ between trials with a correct and erroneous saccade. Nevertheless, visual sensitivity began to rise significantly earlier on correct trials, where it also reached a plateau shortly before the onset of the saccade. Sensitivity on error trials continued to rise until the moment of saccade initiation, which suggests that the competition was resolved at a very late point. Our results suggest that more than 30% of errors in the rule-based condition resulted from a pre-selection during the delay period that was incongruent with the rule-defined target (see **Figure 5C**). The increased competition should take additional time to be resolved. However, the fact that saccadic latencies were shorter on error trials suggests that errors may partly be a consequence of participants prioritizing speed over accuracy, which could have modulated the accumulation rate of the evidence in favor of the erroneous target (Cisek, Puskas, & El-Murr, 2009; Hanks, Kiani, & Shadlen, 2014; Heitz & Schall, 2012). A faster accumulation of evidence for a target on the collicular motor map could be associated with less suppression of other locations via local inhibitory interactions (Sumner, 2011), which could explain why erroneous saccades tended to show less deviation away from the non-selected target than correct saccades (Van der Stigchel et al., 2006).

### ***Attention, decision making, or saccade programming?***

Although it is tempting to ask whether the modulatory effects that we observed on visual discrimination performance reflect attention, the emerging saccadic decision, or saccade programming, we cannot answer this question and we doubt that the three concepts can be clearly distinguished.



The mechanism behind the spatially-selective perceptual benefits that we measured has been traditionally called visuospatial attention. Current theories of attention are closely linked to the concept of priority maps (Fecteau & Munoz, 2006; Serences & Yantis, 2006), assuming that certain topographically organized brain areas integrate bottom-up and top-down signals into one or several online representations of the behavioral relevance or priority of spatial locations. In contrast to this type of theories, many decision-theoretic models of visual or saccadic choice posit that the same brain areas transform sensory evidence into saccade programs that compete against each other online. This assumption probably goes too far, as not every decision is automatically transformed into a saccade program (Gold & Shadlen, 2003), but it is in principle compatible with the priority map theory: Both frameworks describe the situation where multiple stimuli or spatial locations compete for further processing and both assume that the outcome of the competition is used to guide saccades. Their main difference lies in the degree of their focus on motor actions and in the terminology used to describe the competing neural representations: while the former speak of attentional or priority signals, the latter call them decision variables or saccade programs (not claiming that these signals directly drive eye movements). In agreement with this, attention has even been conceptualized as an outcome or byproduct of decisional processes (Fernandez-Duque & Johnson, 2002; Krauzlis, Bollimunta, Arcizet, & Wang, 2014).

The oculomotor system consists of a network of interconnected cortical and subcortical structures, most of which are known to participate in both visual and oculomotor selection. Neural correlates of decisions have been observed in all parts of the network, including the frontal eye field (e.g., Kim & Shadlen, 1999; Schall, 2003), the supplementary eye field (Coe, Tomihara, Matsuzawa, & Hikosaka, 2002), area LIP (e.g., Platt & Glimcher, 1999, Shadlen & Newsome, 2001), the superior colliculus (e.g., Horwitz & Newsome, 2001, Kim & Basso, 2008), the prefrontal cortex (Hasegawa, Sawaguchi, & Kubota, 1998; Watanabe & Funahashi, 2007) and the caudate nucleus (Ding & Gold, 2010; Isoda & Hikosaka, 2011). Most of these areas have also been proposed to accommodate a priority map. The final decision where a saccade will be executed is probably accomplished through a distributed consensus between the above mentioned brain areas, possibly involving a progressive amplification of the difference between target and non-target representations from the parietal to the frontal cortex and onto the superior colliculus (Paré & Dorris, 2011). This process involves a top-down modulation of neural activity in lower visual areas by higher visual areas as well as local neuronal interactions, which have important perceptual consequences and are typically summarized under the term attention (Carrasco, 2011; Maunsell, 2015).

In our view, this shows that it is not only impossible, but also unnecessary to make a distinction between the terms attention, saccade programming and saccadic decision making when referring to processes that are clearly related to the selection of the saccade goal. We mainly consider important that theories move away from the traditional view that attention or motor programming are guided by a winner-take-all mechanism, as this view is incompatible with existing results on parallel movement planning and simultaneous attention allocation to multiple locations. While a winner-take-all mechanism must be necessarily applied during the final selection of the upcoming saccade in motor neurons of the superior colliculus, covert processes, such as visual attention or saccade programming, seem to be guided by the momentary priority of the competing targets or response alternatives.

## CONCLUSIONS

In the present study, we investigated the allocation of visuospatial attention during decisions between two memorized saccade targets. Attention, as measured by visual discrimination performance, was allocated in parallel to the two competing saccade targets, both during the memory delay and in the pre-saccadic decision period, when the saccade was being programmed.

The distribution of attentional resources was influenced by task requirements, probe appearance and selection history and predicted the direction of future saccades. During saccade programming, discrimination performance increased gradually at the two potential saccade goals, consistent with a race of both saccade programs towards a decision threshold. Our results therefore indicate that saccade decisions take the form of a biased competition between potential saccade goals, which can begin by a pre-selection before the saccade cue.

What remains unclear is whether both motor programs are really accumulated in parallel until the last stage of oculomotor programming or whether the second motor program becomes suppressed at some earlier stage. The former strategy would increase the flexibility of saccade planning, for example when participants would want to change their decision or if they decided to carry out both alternative eye movements in sequence, while the latter could speed decisions and prevent errors. While our results seem to show that both locations competed until the beginning of the saccade, we cannot definitely rule out that one motor program was suppressed at some intermediate stage of oculomotor programming, as the suppression may not have affected visual perception any more.

In the same way, we cannot rule out that attentional selection close to saccade onset did not reflect the saccade decision, but rather some post-decisional processes related to decision commitment or to the evaluation of outcomes (Ding & Gold, 2012; Resulaj, Kiani, Wolpert, & Shadlen, 2009). These questions will hopefully be addressed by future studies.

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## **2.3 Study 3: TMS of the left frontal eye field biases endogenous visual attention independent of saccade programming**

### **Contributions:**

The author of this dissertation designed and programmed the experiment, collected and analyzed data, created plots, interpreted the results and wrote the manuscript.

Donatas Jonikaitis helped designing and programming the experiment and interpreting results.

Jasper Dezwaef participated in data collection, created a part of the plots and commented on the manuscript.

Heiner Deubel supervised the project, participated in designing the experiment and in interpreting results and commented on the manuscript.

Paul Taylor supervised the project, participated in designing the experiment and in interpreting results and commented on the manuscript.

Bas Neggens supervised the project, helped with experimental setup and data collection, participated in designing the experiment and in interpreting results and commented on the manuscript.

## **TMS of the left frontal eye field biases endogenous visual attention independent of saccade programming**

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### **Abstract**

The present study investigated the effects of TMS of the frontal eye fields on the coupling between visual attention and saccade programming. We employed a dual task paradigm, in which participants made saccades towards a location indicated by a central arrow cue (endogenous condition) or a peripheral onset cue (exogenous condition) and simultaneously discriminated the orientation of a visual probe shown at the saccade goal or at a neutral location 100 or 150 ms after the onset of the saccade cue. In each trial, we applied a single TMS pulse to the left FEF, right FEF or to the vertex of the scalp 30 ms prior to the onset of the discrimination probe. The results indicate that TMS of the left FEF enhanced endogenous attention to the right visual field, independent of saccade programming, which in turn reduced the well-known coupling of attention to saccade programming in the left visual field. The fact that we observed a right-sided facilitation of endogenous attention that was independent of saccade programming and that seemed to compete with attention at the saccade goal suggests that endogenous attention and visual selection as a part of saccade programming are separable within the frontal eye fields.

## INTRODUCTION

The relation between covert visual attention and saccadic eye movements (overt attention) has been a matter of longstanding scientific debate. Although there is abundant evidence that both processes are closely linked, the precise nature of this coupling remains controversial.

It is known that saccade programming and visual attention are controlled by a common network of frontal and parietal cortical areas (e.g., Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulam, 2000; Perry & Zeki, 2000; de Haan, Morgan & Rorden, 2008, Wardak, Olivier, & Duhamel, 2011). One of the central nodes of this network are the frontal eye fields (FEF), a structure in the left and right frontal lobes, where eye movement-related activity can be recorded in single units and electrical stimulation often elicits short latency saccades to the contralateral hemifield. In primates, the FEF is located in the rostral bank of the arcuate sulcus and its area has been defined rather functionally than anatomically, as the cortical area from which saccades can be elicited with currents of less than 50  $\mu$ A (Bruce & Goldberg, 1985). In humans, it is located in the rostral bank of the precentral sulcus, laterally to its intersection with the superior frontal sulcus (Amiez & Petrides, 2009; Neggers et al., 2012). The FEF is a suitable location for investigating the link between saccades and visual attention, as it is known to play a crucial role in the visual selection of goals for eye movements but also in the control of covert attentional shifts in the absence of eye movements (for reviews, see Schall, 2015; Vernet, Quentin, Chanes, Mitsumasu, & Valero-Cabré, 2014).

Behavioral studies in humans have demonstrated that during saccade planning attentional resources are automatically coupled to the saccade goal, which is reflected in enhanced visual perception at the saccade goal and poor visual perception at other spatial locations (e.g., Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Klapetek, Jonikaitis & Deubel, 2016; Kowler, Anderson, Doshier, & Blaser, 1995; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Jonikaitis & Theeuwes, 2013). A recent EEG study has shown that this saccade-related benefit may be achieved through a top-down modulation of visual activity in occipital areas by FEF activity (Gutteling, Van Ettinger-Veenstra, Kenemans, & Neggers, 2010).

A number of studies investigated saccade programming and/or visual attention in the human FEF with the help of transcranial magnetic stimulation (TMS), a method that can non-invasively influence cortical activity and thus allows to draw causal inferences about the function of specific brain areas. During TMS, very brief magnetic pulses are sent out through a coil held directly over a person's scalp, inducing an electric field in the underlying brain tissue, which eventually alters the transmembrane potentials of axons.

TMS can be applied in a single-pulse mode or as a series of pulses at rates between 1 and 50 Hz (repetitive TMS, or rTMS). When compared to rTMS, single-pulse TMS produces smaller outcomes, which is simply given by the fact that when several pulses are presented in close temporal succession; their effects add up in a non-linear fashion (Moliadze, Giannikopoulos, Eysel, & Funke, 2005). Due to the short duration of their consequences (in the order of milliseconds), single pulses or short pulse trains are always applied in an “on-line approach”, i.e., at previously defined time points during an experimental trial. The opportunity to affect neural activity with such a high temporal resolution makes TMS a very valuable tool for the study of the temporal dynamics of attentional and oculomotor processes.

Several investigators took advantage of the fact that TMS can create “virtual lesions” (Pascual-Leone, Bartres-Faz, & Keenan, 1999) and used it to transiently disrupt functioning in the targeted brain areas. TMS over the FEF was found to reduce spatial priming of pop-out (O’Shea, Muggleton, Cowey, & Walsh, 2007) and to impair visual search performance (Muggleton, Juan, Cowey, & Walsh, 2003; O’Shea, Muggleton, Cowey, & Walsh, 2004).

The results of another line of research, which studied the effects of TMS on oculomotor behavior, provided consistent evidence that FEF-TMS has inhibitory effects on saccadic performance. When delivered before the execution of a saccade, single TMS pulses over the FEF were shown to increase latencies of both prosaccades (Ro, Henik, Machado, & Rafal, 1997; Thickbroom, Stell, & Mastaglia, 1996), and of antisaccades (Müri, Hess, & Meienberg, 1991; Olk, Chang, Kingstone, & Ro, 2006; Terao et al., 1998).

Using exactly the same dual task paradigm as Deubel and Schneider (1996), but with a train of three TMS pulses over the FEF shortly before the presentation of the discrimination target, Neggers et al. (2007) demonstrated that the coupling between visual selection and saccade preparation is weakened by TMS contralateral to the saccade and discrimination goals. Van Ettinger-Veenstra et al. (2009), however, replicated their experiment with a single TMS pulse delivered at three possible times during the presentation of the discrimination target and found that early stimulation led to enhanced selection of contralateral saccade targets. A number of other studies also provided evidence that FEF-TMS can boost visual perception in the contralateral hemifield (Bosch, Neggers, & Van der Stigchel, 2012; Chanes, Chica, Quentin & Valero-Cabré, 2012; Grosbras & Paus, 2003) and that this enhancement might be achieved through top-down modulations of different visual cortical areas (Ruff et al., 2006, Silvanto, Lavie, & Walsh, 2006; Taylor, Nobre, & Rushworth, 2007).



The results of previous research indicate that TMS of the FEF can either enhance or disrupt visual processing, possibly depending on timing and intensity of the stimulation, coil type and orientation, and the activation state of the targeted cortical area (Nyffeler et al., 2004; Siebner, Hartwigsen, Kassuba, & Rothwell, 2009). Another critical factor could be stimulation frequency: while the majority of studies that found performance-reducing effects administered trains of several pulses, studies that found attention-boosting effects mostly used only a single pulse per trial. This could also explain why Neggers et al. (2007) and Van Ettinger-Veenstra et al. (2009) observed opposing effects in the same behavioral task.

The goal of the present study was to replicate the results of Van Ettinger-Veenstra et al. (2009), using a similar dual-task paradigm. Additionally, we aimed to compare the effects of TMS on exogenously and endogenously cued pre-saccadic attention shifts and to measure the time course of those shifts. The original version of Deubel and Schneider's (1996) dual-task, which was also used by Neggers et al. (2007) and Van Ettinger-Veenstra et al. (2009), contained a 500-1000 ms interval between the cue that defined the saccade goal and the go-signal for the saccade, which ensured that the saccade could be fully prepared by the time of the go signal. In our paradigm, saccades were cued by the onset of a central arrow (endogenous cue) or by a peripheral color change (exogenous cue), without a separate go-signal. The preparation of the saccade thus happened in the same interval where we measured attention allocation by probing perceptual performance and where we applied the single TMS pulse. In order to be able to sample discrimination performance at different times during saccade preparation, we used a Gabor patch as a discrimination probe that could be shown for a much shorter time than the perceptually more complex stimuli used in the previous studies. The reason why we chose to compare the effects of endogenous and exogenous cues is that it has been suggested that the FEF are less active during the programming of exogenously triggered saccades compared to endogenous saccades (Mort et al., 2003) and may be less needed for their generation (Dias & Segraves, 1999; Guitton, Buchtel, & Douglas, 1985; Henik, Rafal, & Rhodes, 1994; Rivaud, Müri, Gaymard, Vermersch, & Pierrot-Deseilligny, 1994; Sommer & Tehovnik, 1997). We thus expected to find smaller effects of TMS in trials with exogenous cues.

The goal of our purely behavioral Experiment 1 was to measure probe discrimination performance during the whole saccade programming process in order to obtain a performance baseline before employing TMS. Moreover, we wanted to make sure that all participants could perform the dual task satisfactorily, meaning that they would perform fast and accurate saccades and discriminate probes at the cued location above chance level.

Experiment 2 aimed to test the effects of single pulse TMS of the left and right FEF and of the vertex (as a control) on visual attention and on saccade programming. We measured discrimination performance and delivered TMS at two possible SOAs, assuming that TMS at the first SOA could have stronger effects in trials with exogenous saccade cues, while TMS at the second SOA could affect performance more in trials with endogenous cues. The rationale behind this assumption was that exogenous cues typically elicit faster attention shifts (Müller & Rabbit, 1989; Nakayama & Mackeben, 1989) and saccades with shorter latencies (Forbes & Klein, 1996; Henik et al., 1994; Mort et al., 2003; Rafal, Egly, & Rhodes, 1994; Walker, Walker, Husain, & Kennard, 2000) compared to endogenous cues. We wanted to stimulate the FEF shortly before the onset of the discrimination probe, as this would ensure that potentially modulated top-down signals from the FEF would reach the visual cortex simultaneously with probe-related signals from the retina. According to Neggers et al. (2007) the optimal moment to stimulate is around 30 ms before the onset of the target, which is the difference between the neural transmission time from FEF to visual cortex – estimated to be around 100 ms based on animal models (Super et al., 2004; Thompson et al., 2005) – and the transmission time from retina to cortex (66 ms, Leonard et al., 2011). Van Ettinger-Veenstra (2009) compared three different TMS times and found the largest effects 20 ms before the onset of the discrimination target. In agreement with these two studies, we decided to deliver the TMS pulse 30 ms before the onset of the discrimination probe.

## METHODS

### *Participants*

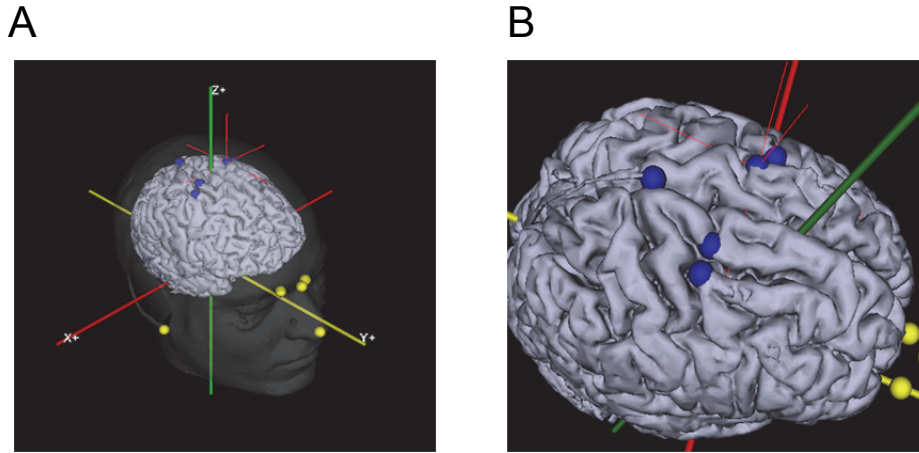
Sixteen volunteers participated in the study after giving informed written consent. Two participants were excluded due to poor quality of the eye-tracking data and bad task performance (i.e. 40% of the saccades were not directed to the target). The data of the other 14 participants (age: 20-33 years,  $M = 26$  years, 5 females) were included in the analysis. All participants had normal or corrected-to-normal vision, no history of mental or neurological illness and were naïve to the purposes of the study (except for one of the authors). They were screened for metal implants and general MRI compliance (UMC Utrecht internal guidelines), as well as for TMS compliance (Keel, Smith, & Wassermann, 2001). The experiments were approved by the Medical Ethical Committee of the University Medical Center Utrecht and the TMS protocol remained within the internationally accepted safety limits (Wassermann, 1998).

## *Apparatus*

The participants were seated in a quiet and dimly illuminated room in front of a 24-in LCD monitor (BenQ-XL2420T, spatial resolution: 1024 x 768 pixels, 100 Hz refresh rate), positioned at a viewing distance of 75 cm. Right-eye gaze position was recorded with an EyeLink 1000 desktop mounted eye tracker (SR Research, Canada) at a sampling rate of 1000 Hz while the head was supported by a chin and forehead rest and additionally restricted from movement by an elastic rubber band. The eye tracker was calibrated before each new block and whenever it was necessary. Trials in which no target-directed eye movement could be recorded were automatically repeated. Stimulus presentation and response collection were controlled by a Pentium PC using MATLAB software (MathWorks, Natick, MA) and the Psychophysics and Eyelink toolboxes (Brainard, 1997; Cornelissen, Peters, & Palmer, 2002; Kleiner, Brainard, & Pelli, 2007; Pelli, 1997; see <http://psychtoolbox.org>). Manual responses were collected via an external response pad (containing four standard arrow keys) placed at the participant's right hand.

TMS pulses were administered by a Magstim Rapid2 stimulator with a figure-of-8 TMS coil held by a mechanical arm. The coil was triggered by TTL pulses sent out through the parallel port of the stimulus PC. The placement of the TMS coil was stereotactically guided with the help of the Neural Navigator (by Brain Science Tools BV, the Netherlands, also see Neggers, 2004 and [www.neuralnavigator.com](http://www.neuralnavigator.com)). For stereotactic guidance, T1-weighted MRI scans were acquired for all participants in a separate session on a 3.0T Philips Achieva MRI scanner. Scanning parameters: whole-brain three-dimensional fast-field echo T1-weighted scan; 200 slices; TR = 10 ms; TE = 4.6 ms; flip angle = 8°; field of view, 240 x 240 x 160 mm; voxel size: 0.75 x 0.8 x 0.75 mm. The Neural Navigator renders the skin of each participant individually and creates a cortical surface through a grey matter map from that same T1-weighted scan. Once the skin and the brain map were loaded in the graphical user interface, the positions of eight anatomical landmarks on the head of the participant (tip and bridge of the nose, the inner and outer meeting points of the upper and lower eye lids, and the upper adherence of the left and right ear; see **Figure 1A**) were measured with a 3-D digitizer and mapped to corresponding locations on the image of the skin rendering on the computer screen. In the next step, the FEFs and the vertex were located on the cortical surface map and labeled with target markers (see **Figure 1B**). Each FEF was labeled with two markers: one at the medial and one at the lateral side of the superior frontal sulcus, where it connects to the precentral sulcus (the likely location of human FEF according to Amiez & Petrides, 2009 and Neggers et al., 2012). The center of the coil was placed over the medial marker and the coil handle was aligned with the lateral marker.

This ensures that TMS pulses generate currents perpendicularly to the sulcal walls of the superior frontal sulcus, optimizing induced neuronal activation (Kammer, Vorwerg, & Herrnberger, 2007). The spatial locations of the targets were then marked on a swim cap the participants were wearing. The position of the coil was checked after every block and was corrected, if necessary. In order to reduce the TMS-related noise disturbance, we asked participants to wear earplugs.



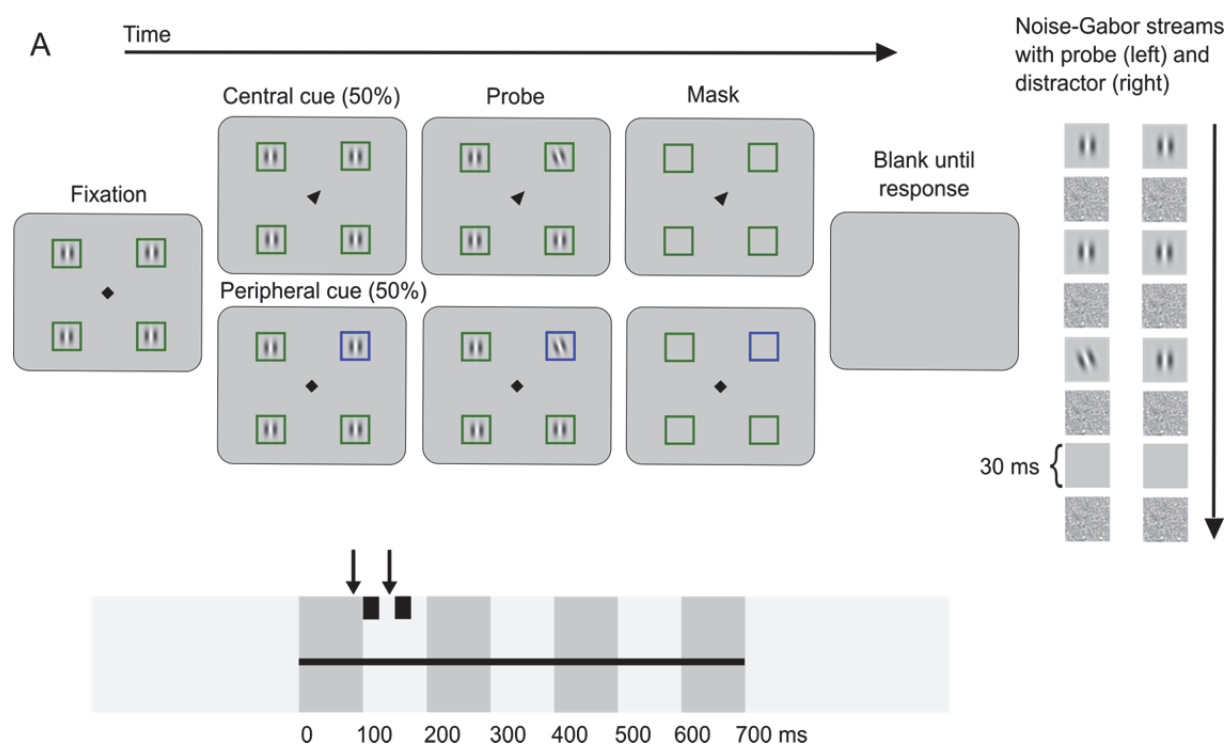
**Figure 1. (A)** Facial landmarks used to calibrate the Neural Navigator. **(B)** Individually determined markers for the FEFs and the vertex site.

### *Procedure*

Each trial started with the presentation of a central black fixation dot (diameter: 0.5 degrees of visual angle) and four green frames (edge length: 2°) on a gray background (see **Figure 2**). The frames were positioned on the outline of an imaginary circle (radius: 7°) around the fixation dot at angular positions of 45°, 135°, 225° and 315°. Each square contained a flickering stream of vertically oriented Gabor patches (spatial frequency: 2.5 cpd, 100% contrast, random phase) and noise masks (pixel gray values randomly drawn from a Gaussian distribution with  $M = 128$  (RGB),  $SD = 128$  and cut-offs at 0-black and 255-white), alternating every 3 frames (30 ms).

After a random fixation period of 700 to 1300 ms, the fixation dot was either replaced by an arrow (central cue) or one of the object frames changed from green to a more luminant blue (exogenous cue), indicating that a saccade was to be made to the cued square as quickly as possible. The probe, consisting of a 30-ms leftward or rightward tilt of the Gabor patch, was shown in one of the four objects (selected randomly with equal probability) following a variable SOA relative to saccade cue onset.

In Experiment 1, where we wanted to measure the time course of covert attention deployment without applying TMS, the SOA was randomly drawn from 36 time points between -100 and 250 ms. In Experiment 2, where the focus was mainly on TMS effects, the SOA only varied between 100 and 150 ms. The orientation of the tilted Gabor pattern (left or right) was also selected randomly and the tilt angle was chosen for each observer individually in a threshold procedure at the beginning of each experimental session (see **Pretests**). In Experiment 2, the probe was preceded (by 30 ms) by a TMS pulse to the left or right frontal eye field or to the vertex. Immediately after probe presentation, the probe- and distractor streams in all four squares were replaced by identical masking streams (noise masks alternating with blank sequences) and the display turned black 700 ms after the onset of the saccade cue. Participants responded to the perceived probe orientation by pressing the left arrow key for a leftward tilt or the right arrow key for a rightward tilt. They were instructed to focus on making fast and accurate saccades and to simply guess the orientation of the probe whenever they could not discriminate it well. A new trial started automatically 200 ms after the response.



**Figure 2. (A)** Schematic representation of the stimulus sequence and the probe and distractor streams (to the right). **(B)** Sequence of events with the two possible probe and TMS timings.

Participants first completed Experiment 1 in a single session (400 trials divided into eight blocks of 50 trials) and then proceeded with Experiment 2 (comprising three sessions, each consisting of 400 trials, divided as in Experiment 1). In each of these three sessions, TMS was applied to a different scalp location (left FEF, right FEF, vertex), the order of TMS conditions being carefully counterbalanced over participants. In both experiments, the saccade cue type (endogenous or exogenous) was alternated blockwise in a randomized order.

Before the experiment, the motor threshold (MT) of the right hemisphere was determined for each participant as the minimal output intensity of the TMS device at which 5 of 10 TMS pulses over the cortical motor area for the thumb evoked a visible twitch in the contralateral thumb. The TMS output intensity during the experiment was then set to 110% of the right hemisphere motor threshold.

### ***Pretests***

The pretests consisted of 60 trials, divided into two blocks of 30 trials with identical visual stimuli as in the main experiment, except that the probe was always presented at the cued location 150 ms after cue onset. Endogenous and exogenous cues were presented in separate blocks. Participants were instructed to covertly attend to the cued square while maintaining central fixation and to discriminate the orientation of the probe at the end of the trial. A modified version of the QUEST procedure (King-Smith et al., 1994; Watson & Pelli, 1983) was used to determine the tilt angles at which observers reached 82% correct probe discrimination in the endogenous and exogenous cueing conditions. Tilt angles ranged between 5 and 20 degrees in the endogenous ( $M = 10.6$ ,  $SD = 5.4$ ) and between 3 and 18 degrees in the exogenous condition ( $M = 7.8$ ,  $SD = 3.6$ ). The pretests were also used to train participants on the behavioral task in a separate practice session (a threshold of 20° or less had to be reached before the experiment).

### ***Data analyses***

We analyzed all behavioral and eye movement data using Matlab software (MathWorks, USA) and the Psychophysics and Eyelink toolboxes (Brainard, 1997; Cornelissen et al., 2002; Kleiner et al., 2007; Pelli, 1997; see <http://psychtoolbox.org>). Eye movements were evaluated offline using Eyelink's in-built saccade detection algorithm. Trials with primary saccade latencies (time from cue onset to saccade onset) below 80 ms or above 500 ms and those where the saccade started more than 2° away from the fixation point or did not

land within a  $3^\circ$  window around the target center were removed from analysis. In total, we excluded 4% of all trials of Experiment 1 and 11% of all trials of Experiment 2 due to blinks, missing data or inadequate saccade responses.

In order to optimally test for our hypothesized lateralized effects, we chose to exclude the uncued location ipsilateral to the saccade goal whenever we analyzed cueing effects (i.e., whenever we compared attention at or saccades towards the cued location and uncued locations). The “uncued” condition hence consisted of the average of the two locations contralateral to the saccade goal.

Statistical analyses contained repeated-measures analyses of variance (ANOVA) and post-hoc comparisons by t-tests with a Bonferroni correction. The Greenhouse-Geisser correction was employed whenever the assumption of sphericity was not met.

## RESULTS

### Experiment 1

#### *Saccade latency and amplitude*

Individual latency and amplitude means were subjected to repeated measures ANOVAs with the factors SACCADÉ DIRECTION (leftward, rightward), SOA (-100-0, 0-100, 100-200), CUE TYPE (endogenous, exogenous), and PROBE LOCATION (cued, uncued).

The analysis of saccade latencies revealed a significant main effect of CUE TYPE [ $F(1,11) = 16.83, p = .002$ ], as saccade latencies (Mean  $\pm$  SE) were longer in the endogenous cueing condition ( $247 \pm 9$  ms) than in the exogenous cueing condition ( $235 \pm 10$  ms), and a main effect of SOA [ $F(2,22) = 3.76, p = .039$ ]. Saccade latencies tended to be a little slower when the probe was shown between 100 and 200 ms after the saccade cue ( $244 \pm 9$  ms), than when it was shown before the saccade cue ( $242 \pm 10$  ms), or within 100 ms after the cue ( $241 \pm 10$  ms), but none of the differences reached significance.

Finally, the analysis showed a significant interaction between CUE TYPE and PROBE LOCATION [ $F(1,11) = 12.47, p = .005$ ], resulting from the fact that in the endogenous cueing condition saccades to the cued location ( $256 \pm 9$  ms) were slower than saccades to contralateral uncued locations ( $235 \pm 10$  ms), while in the exogenous condition saccades to the cued location ( $229 \pm 12$  ms) were faster compared to saccades to uncued locations ( $250 \pm 8$  ms).

The analysis of the amplitude did not reveal any significant main effects nor interactions. Saccades tended to slightly undershoot the distance to the target center, (mean gain = 0.97) but their amplitude was not modulated by any experimental variables.

### ***Discrimination performance***

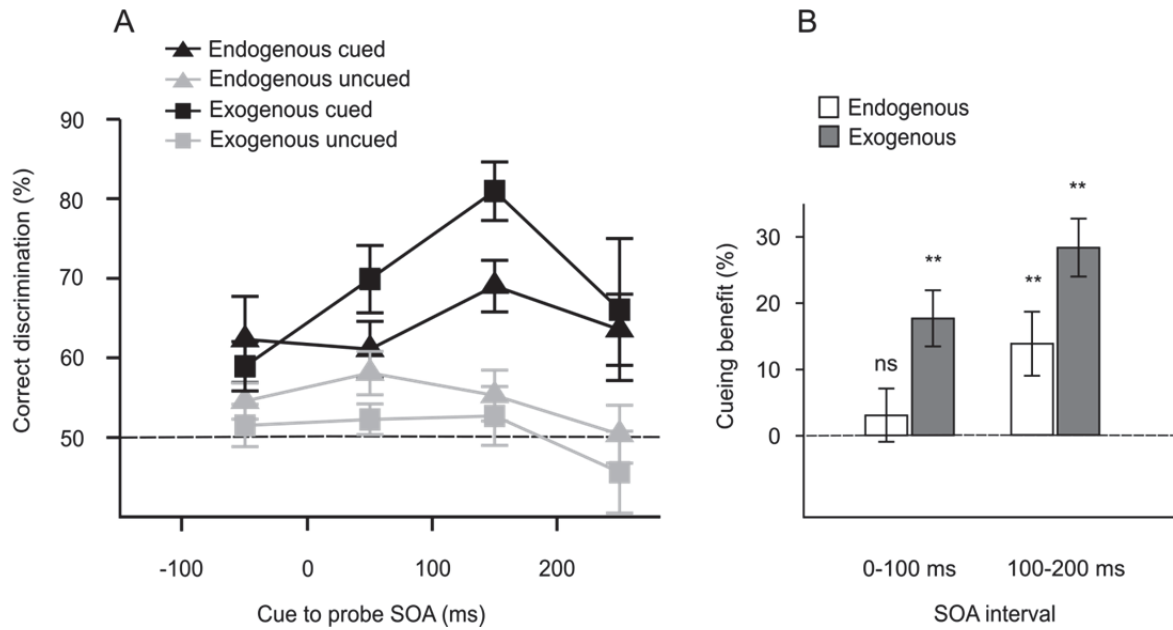
As the probe was presented at various SOAs relative to the onset of the saccade cue, we could determine the time courses of the covert attention shifts to the probed locations. For this purpose, we sorted all SOAs into bins of 100 ms and calculated the proportion of correct probe discriminations at the cued location (future saccade goal) and at contralateral uncued locations.

An ANOVA of the data with the factors CUE TYPE (endogenous, exogenous), PROBE LOCATION (cued, uncued) and SOA (-100-0, 0-100, 100-200) revealed significant main effects of PROBE LOCATION [ $F(1,13) = 38.21, p < .001$ ] and SOA [ $F(2,26) = 4.99, p = .015$ ], as well as a significant interaction between the two factors [ $F(2,26) = 4.56, p < .002$ ]. Probe discrimination ( $M \pm SE$ ) was better at cued locations ( $67 \pm 2$ ) than at uncued locations ( $54 \pm 1$ ), but it only grew over time at the cued location, where discrimination 100-200 ms after the cue was significantly better than in the earlier two time bins. Additionally, there was an interaction between CUE TYPE and PROBE LOCATION [ $F(1,13) = 6.61, p < .023$ ], reflecting the larger cueing effect with exogenous compared to endogenous cues.

While probe discrimination at uncued locations remained close to chance throughout the whole trial, performance at the saccade goal began to increase from the moment of cue appearance, peaking shortly before the onset of the saccade (see **Figure 3A**): In the endogenous cueing condition, cueing effects only emerged between 100 and 200 ms after cue onset, where there was a significant difference between cued and uncued locations [ $t(13) = 2.84, p = .014$ ]. This was later than with exogenous cues, where cueing effects were present both between 0 and 100 ms [ $t(13) = 4.16, p = .001$ ] and between 100 and 200 ms after cue onset [ $t(13) = 6.46, p < .001$ ]. This is consistent with previous reports of faster attention shifts following exogenous as compared to endogenous cues (Müller & Rabbit, 1989; Nakayama & Mackeben, 1989).

The small cueing effects before the onset of the saccade cue most likely reflect retro-active attention (see Sergent et al., 2013; Thibault, Cavanagh, & Sergent, 2015), but they were not statistically significant. **Figure 3B** summarizes the influences of cueing condition and SOA on the cueing effect.





**Figure 3.** (A) Probe discrimination performance in Experiment 1 at various time intervals relative to saccade cue onset. Correct discrimination (in %) is plotted as a function of probe location (cued location or contralateral visual field) and cue type (endogenous or exogenous). Error bars represent standard errors of the mean. The dashed line denotes the chance performance level. (B) Cueing benefit as a function of SOA interval, saccade latency (fast, slow) and cue type (endogenous, exogenous). Error bars represent standard errors of the mean.

## Experiment 2

### *Saccade latency and amplitude*

Individual latency and amplitude means were subjected to repeated measures ANOVAs with the factors SACCADIC DIRECTION (leftward, rightward), TMS (FEF-L, FEF-R, vertex), SOA (100,150), CUE TYPE (endogenous, exogenous), and PROBE LOCATION (cued, uncued).

Saccade latencies ( $M \pm SE$ ) in the endogenous cueing condition ( $249 \pm 7$  ms) were substantially longer than in the exogenous cueing condition ( $217 \pm 7$  ms), [CUE TYPE:  $F(1,9) = 28.64$ ,  $p < .001$ ]. This was an expected finding, consistent with the results of Experiment 1 and with previous studies (e.g., Forbes & Klein, 1996; Henik et al., 1994; Mort et al., 2003; Rafal et al., 1994; Walker et al., 2000).

Moreover, there was a significant effect of SOA [ $F(1,9) = 72.43$ ,  $p < .001$ ] and an interaction of SOA and CUE TYPE [ $F(1,9) = 12.56$ ,  $p = .006$ ], resulting from the fact that latencies in the exogenous condition were substantially shorter when the probe appeared 100 ms after saccade cue onset ( $208 \pm 7$  ms) than when it appeared 150 ms after cue onset ( $226 \pm 8$  ms), while there was no significant difference between the two SOAs in the endogenous condition ( $247 \pm 7$  ms vs.  $251 \pm 7$  ms). It thus seems that reflexive but not voluntary saccade programming was to some degree contingent on probe appearance.

Importantly, saccade latency was not influenced by TMS [ $F(2,18) = 0.09$ ,  $p = .91$ ] and there were no meaningful interactions between TMS site and any of the other factors. Latencies for the different stimulation sites, cue types and SOAs are summarized in **Table 1**.

The ANOVA of the amplitude data revealed no significant main effects nor interactions. As in Experiment 1, the mean amplitude of saccades ( $6.72 \pm 0.8$  deg) was slightly shorter than the target distance (mean gain = 0.96), but it was not influenced by any experimental factors.

**Table 1. Saccade latencies (means and standard deviations in milliseconds)**

	Left FEF		Right FEF		Vertex	
	Endogenous	Exogenous	Endogenous	Exogenous	Endogenous	Exogenous
<b>SOA 100</b>	249 (64)	211 (59)	243 (53)	210 (56)	246 (49)	208 (54)
<b>SOA 150</b>	254 (66)	228 (60)	249 (54)	228 (61)	249 (55)	226 (58)

### ***Discrimination performance***

We calculated the mean correct discrimination performance for each subject and experimental condition and subjected the data to a repeated measures ANOVA with the factors SACCADE DIRECTION (leftward, rightward), TMS (FEF-L, FEF-R, vertex), SOA (100, 150), CUE TYPE (endogenous, exogenous), and PROBE LOCATION (cued, uncued). To ensure that the discrimination probe could not have been viewed foveally, we excluded all trials where the eye moved away from fixation before the onset of the probe.

The analysis revealed that discrimination performance ( $M \pm SE$ ) was significantly better at the saccade goal ( $77 \pm 4\%$ ) than at uncued locations ( $55 \pm 3\%$ ), [PROBE LOCATION:  $F(1,7) = 152.90, p < .001$ ]. Moreover, performance at the saccade goal was better when the saccade was cued exogenously ( $82 \pm 5\%$ ) than with endogenous cues ( $75 \pm 8\%$ ), [CUE TYPE x PROBE LOCATION:  $F(1,7) = 12.84, p = .009$ ]. TMS had no significant effects [ $F(2,14) = 0.14, p = .87$ ].

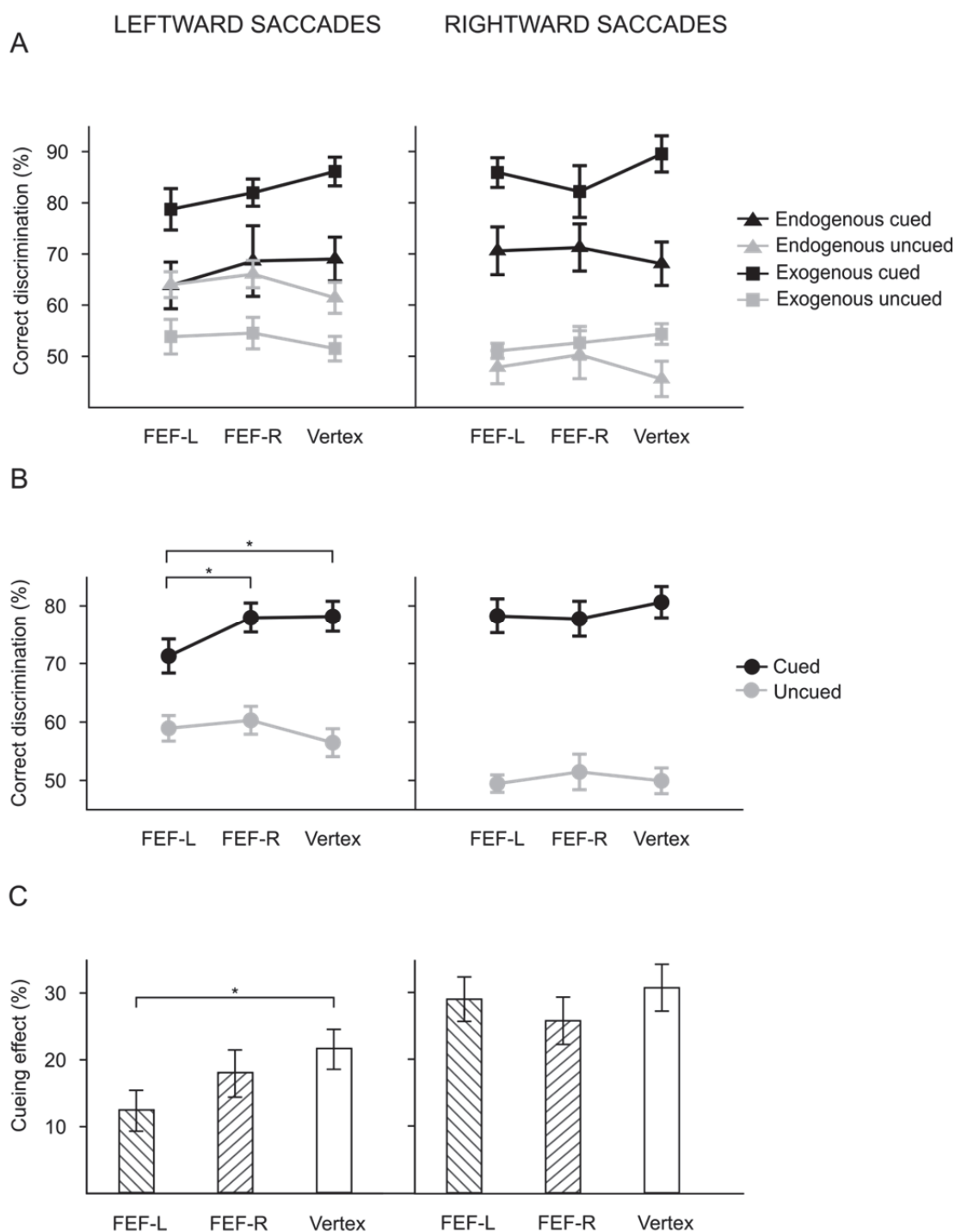
Since there also was a three-way interaction between SACCADIC DIRECTION, SOA and CUE TYPE [ $F(1,7) = 8.53, p = .022$ ], we decided to run a separate ANOVA with the factors TMS, CUE TYPE and PROBE LOCATION for each of the four combinations of SACCADIC DIRECTION and SOA. All four analyses revealed significant effects of PROBE LOCATION and CUE TYPE (better performance at the saccade goal than at uncued locations and with exogenous cues compared to endogenous cues), but only the ANOVA that combined saccades to the left visual field and probes shown at the first SOA (100 ms) disclosed an effect of TMS (see **Figure 4**).

More precisely, there was an interaction between PROBE LOCATION and TMS [ $F(2,14) = 4.05, p = .031$ ], because probe discrimination at the saccade goal was reduced with TMS of the left (ipsilateral) FEF ( $71 \pm 11\%$ ) compared to TMS of the right FEF ( $78 \pm 9\%$ ) or vertex ( $78 \pm 10\%$ ). As can be seen in **Figure 4A** (left panel), this impairment was present both in the endogenous and exogenous cueing conditions, so there was no significant interaction between all three factors. Discrimination performance at the uncued contralateral locations did not vary depending on stimulation site (see **Figure 4B** – left panel).

When we compared discrimination performance at uncued locations before saccades to the left and right visual hemifields (left vs. right panel of **Figure 4A**), it became evident that performance was markedly better before leftward saccades, particularly in the endogenous cueing condition. To confirm this statistically, we ran an ANOVA (on discrimination performance at the SOA of 100 ms) with the factors SACCADIC DIRECTION (leftward, rightward), TMS (FEF-L, FEF-R, vertex), CUE TYPE (endogenous, exogenous) and PROBE LOCATION (cued, uncued), which showed a significant interaction between SACCADIC DIRECTION and PROBE LOCATION [ $F(1,10) = 6.32, p = .031$ ], as there was a significant difference in the discrimination of uncued probes before leftward and rightward saccades. We also performed the same analysis for discrimination performance shortly before saccade onset (at the SOA of 150 ms) and found a completely different pattern of results.

This time, there were no differences for uncued probes, but a striking asymmetry in the opposite direction for cued probes: In the endogenous cueing condition, discrimination at the saccade goal was significantly better before rightward saccades than before leftward saccades [SACCADE DIRECTION x CUE TYPE x PROBE LOCATION:  $F(1,7) = 7.73$ ,  $p = .027$ ]. In our view, these finding must reflect hemispheric asymmetries in the control of endogenous visuospatial attention and we will examine them in more detail in the **Discussion**.

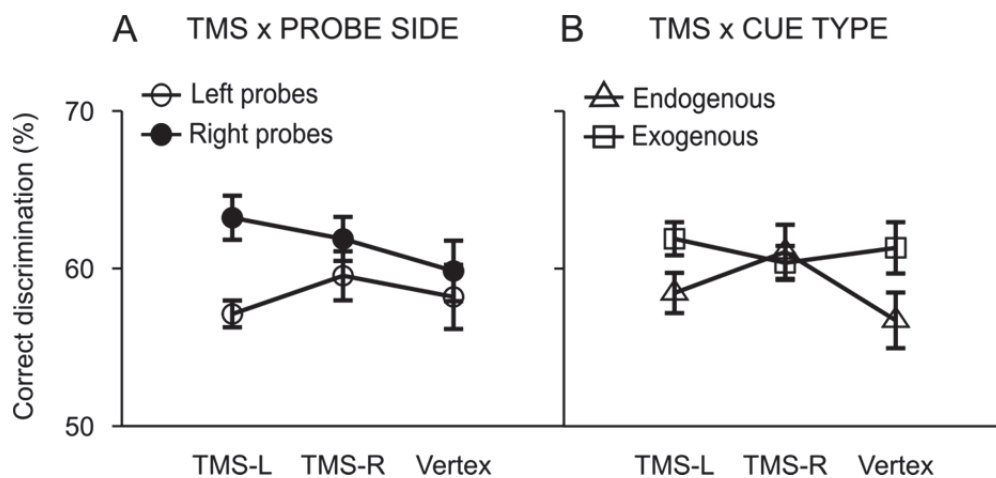
**Figure 4C** shows the results of two separate ANOVAs (for leftward saccades and for rightward saccades, only at the first SOA) of the cueing effect (the absolute discrimination benefit at the saccade goal compared to contralateral control locations) as a function of TMS (FEF-L, FEF-R, vertex) and SACCADE DIRECTION (leftward, rightward). The ANOVA for leftward saccades revealed a significant main effect of TMS [ $F(2,24) = 4.05$ ,  $p = .031$ ]. The cueing effect was significantly smaller for left FEF stimulation ( $12 \pm 11$  %) compared to vertex ( $22 \pm 11$  %), while right FEF stimulation ( $18 \pm 13$  %) did not differ from left FEF or vertex stimulation. For rightward saccades, the main effect of TMS was not significant [ $F(2,20) = 1.02$ ,  $p = .378$ ], as cueing effects for left FEF ( $29 \pm 12$  %), right FEF ( $26 \pm 13\%$ ) and vertex ( $31 \pm 13$  %) did not differ substantially. Overall, the cueing effect (especially at the 100 ms SOA) was much higher with exogenous cues ( $29 \pm 12$  % for leftward saccades at SOA 100) than with endogenous cues ( $4 \pm 10$  % for leftward saccades at SOA 100), [CUE TYPE:  $F(1,12) = 49.17$ ,  $p < .001$ ]. The differences between the endogenous and exogenous conditions are visible in **Figure 4A**.



**Figure 4.** Probe discrimination performance and cueing effect (100 ms after saccade cue onset) as a function of TMS site for saccades to the left and right visual field (left and right panels respectively). Error bars represent the standard error of the mean. **(A)** Discrimination performance as a function of cue type (endogenous, exogenous) and probe location (cued, uncued). **(B)** Discrimination performance (both cue types combined) as a function of probe location (cued, uncued). **(C)** Absolute cueing effect (difference between cued and uncued locations) for both cue types combined.

A possible reason for the reduction of the cueing effect in the left hemifield after ipsilateral stimulation is that TMS of the left FEF may have biased attention towards the right visual hemifield, independent of the saccade cues. Such a bias would lead to better discrimination of probes at both cued and uncued locations and less attention in the ipsilateral visual hemifield. To test this hypothesis, we ran another ANOVA with the factors SACCADIC DIRECTION (leftward, rightward), TMS (left FEF, right FEF, vertex), SOA (100, 150), CUE TYPE (endogenous, exogenous), and PROBE SIDE (left, right), focusing on potential interactions between TMS and other factors (see **Figure 5**).

The analysis revealed a significant interaction between TMS and PROBE SIDE [ $F(1.38,16.25) = 5.09, p = .029$ ], reflecting the fact that TMS of the left FEF led to significantly better discrimination of contralateral probes ( $63 \pm 6\%$ ) compared to ipsilateral probes ( $57 \pm 3\%$ ), while there was no such difference with TMS of the right FEF or vertex (see **Figure 5A**). It thus seems that TMS of the left FEF indeed biased visual processing towards the right side of space, which facilitated discrimination of right-sided probes and impaired discrimination of left-sided (ipsilateral) probes.



**Figure 5.** (A) Probe discrimination performance in the left and right visual hemifields as a function of TMS site. (B) Probe discrimination performance in the endogenous and exogenous cueing conditions as a function of TMS site

TMS also interacted with CUE TYPE [ $F(2,24) = 6.24, p = .007$ ], as right FEF stimulation increased discrimination performance (bilaterally) in the endogenous cueing condition, while there was no such increase (or rather a decrease) in exogenously cued trials (see **Figure 5B**). This finding is difficult to interpret, as the effect is based on a mixture of cued and non-cued probes, which could not be distinguished.

We therefore checked the results of our first ANOVA (with all experimental factors), and found exactly the same pattern of results, both for cued and for uncued probes. However, since the differences between TMS of the right FEF and the other two sites did not reach significance in any of the analyses, we cannot rule out that the performance increase after right FEF stimulation was only due to random variation.

## DISCUSSION

In the present study, TMS delivered to the left FEF between an endogenous or exogenous saccade cue and a visual target facilitated discrimination performance in the right visual field and reduced discrimination performance at saccade goals in the left visual field. TMS of the right FEF led to a tendency for better discrimination performance in both visual hemifields in the endogenous cueing condition that was independent of saccade programming, but the difference to the other two stimulation sites did not reach statistical significance.

The main goal of this study was to investigate how TMS of the frontal eye fields influences the coupling between visual attention and saccade programming. We used a dual-task setting, in which participants prepared saccades to an endogenously or exogenously cued location and simultaneously discriminated a visual probe that could be presented at the saccade goal or at one of three other possible locations. We replicated the well-established finding that attention during saccade preparation is coupled to the saccade goal (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Klapetek et al., 2016; Kowler et al., 1995; Neggers et al., 2007; Rolfs et al., 2011; Jonikaitis & Theeuwes, 2013; Van Ettinger-Veenstra et al., 2009), and found this coupling to emerge earlier and to be stronger for exogenously cued saccades. Additionally, we found that TMS of the left FEF biased attention towards the contralateral visual hemifield, enhancing visual perception in the right hemifield and reducing the coupling of attention to the saccade goal in the left hemifield.

Two previous studies (Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009) examined the same question using a behavioral task originally employed by Deubel and Schneider (1996). Both reported contralateral effects of FEF-TMS on attentional performance, but Neggers observed that FEF-TMS compromised saccade-related attention, while Van Ettinger-Veenstra found that it enhanced attention at the saccade goal.

The contradictory results are most likely a consequence of the different TMS protocols (the first study used trains of three pulses while the second used single pulses), and if we disregard them, the common conclusion of both studies is that both the left and the right FEF play a crucial role in the control of attention in the contralateral visual hemifield.

The results of the present study are difficult to reconcile with these previous findings. Although we also found that TMS of the left FEF biased visual attention towards the right hemifield, this effect was not coupled to saccade programming, as in the above mentioned studies. In contrary, there was a reduction of the saccade-related benefit for leftwards saccades. For the interpretation of these differences it is crucial to realize that the paradigm used in the preceding studies (Deubel & Schneider, 1996) and our dual task differ in a very important aspect: In the former, discrimination probes always appeared in the same visual hemifield as the saccade target and this hemifield was cued with 100% validity, which means that participants could simply ignore the other side of the display. In the present study, the cue was not predictive of the laterality of the discrimination probe (25% validity), so the optimal strategy participants could adopt was to split endogenous attention over both sides of the visual display, prioritizing the cued location just enough to maintain good oculomotor performance. The finding that saccade execution was contingent on probe appearance supports this view, as it shows that participants tended to prioritize the discrimination task over the saccade task. As a consequence, there was always some endogenous attention directed to uncued locations, which could also be enhanced by TMS. The enhancement of contralateral probe discrimination after left FEF stimulation could thus have been mediated by top-down attentional control, even though it was not coupled to the saccade goal. Consequently, the bias towards the contralateral visual field may have caused the ipsilateral impairment of probe discrimination through some kind of interhemispheric inhibition. Our results may therefore indirectly support the same conclusion as Neggers et al. (2007) and Van Ettinger-Veenstra et al. (2009) that the left FEF exerts top-down control over contralateral visual space.

In contrast to Van Ettinger-Veenstra et al. (2009), we did not find evidence for a contralateral attentional benefit following TMS of the right FEF, but we found a tendency towards a bilateral enhancement of attention that was also independent of saccade programming. This enhancement was specific for the endogenous cueing condition, most likely because attention in the exogenous cueing condition was so quickly and automatically summoned by the sudden onset cues that there was no room left for any modulation. (which also explains why the cueing effect was generally larger with exogenous cues). Alternatively, the FEF may be less active during the programming of exogenously cued saccades.



Although the tendency in our data cannot be taken as a reliable effect, it is consistent with previous reports that single pulse TMS of the right FEF leads to a bilateral enhancement of endogenous spatial attention (e.g., Chanes et al., 2012; Grosbras & Paus, 2002, 2003). We therefore believe that further studies on a larger data set could come to this same conclusion, reaching statistical significance.

Besides this asymmetrical pattern of TMS effects, the present study revealed significant attentional asymmetries that were independent of TMS. At the earlier SOA, participants were better at discriminating uncued probes when they were planning a saccade to the left, while at the later SOA they were better at discriminating probes at the saccade goal when planning a saccade to the right. We think that these effects may be a consequence of the relative dominance of the right cerebral hemisphere in the control of spatial attention.

It has been proposed that the right hemisphere mediates attention shifts to both visual hemifields, while the left hemisphere only mediates attention shifts to the right hemifield (Heilman & Abell, 1980; Heilman & Valenstein, 1979, Mesulam, 1981). Based on a careful review of empirical evidence for and against this “hemispacial theory”, Duecker and Sack (2015) proposed that the right hemisphere dominance applies to frontal but not to the posterior parts of the brain’s attention network (also see Szczepanski, Konen, & Kastner, 2010). A substantial part of the evidence comes from TMS studies that found a right hemisphere dominance at the level of the FEF, with bilateral effects on covert or overt attention after TMS of the right FEF and only unilateral effects (affecting contralateral visual space) after TMS of the left FEF (Cazzoli et al., 2015; Chanes et al., 2012; Duecker, Formisano, & Sack, 2013; Hung, Driver, & Walsh, 2011; Grosbras & Paus, 2002, 2003; Ruff et al., 2009; Silvanto et al., 2006; Walker, Techawachirakul, & Haggard, 2009).

The experimental design in the present study, where the saccade cue did not predict the location of the discrimination probe, encouraged participants to distribute attention over both visual hemifields. However, during saccade planning attentional resources become increasingly engaged at the saccade goal (Castet, Jeanjean, Montagnini, Laugier, & Masson, 2006; Deubel, 2008; Doré-Mazars, Pouget, & Beauvillain, 2004; Jonikaitis & Deubel, 2011; Montagnini & Castet, 2007) and can only be allocated elsewhere at the very beginning of the saccade programming process (Doré-Mazars et al., 2004; Montagnini & Castet, 2007). This may explain why the pattern of asymmetries was different at the early and later SOAs. It seems that 100 ms after the cue participants could still split attention over both hemifields and they were better at it before leftward than before rightward saccades.

The reason may have been that the programming of leftward saccades predominantly recruited the right FEF, which modulates visual performance in both visual hemifields, while rightward saccades predominantly recruited the left FEF, which only modulates visual performance in the right hemifield. At 150 ms, when nearly all attentional resources were engaged by saccade programming, the coupling of attention to the saccade goal was stronger before rightward saccades, which could be due to the previously weaker competition by contralateral attention. This difference was absent in the exogenous cueing condition, probably because exogenous cues quickly summoned most attentional resources, leaving less room for competition.

The effects of TMS that we observed are also consistent with the suggested asymmetry in attention control by the FEFs and with many previous TMS studies (Cazzoli et al., 2015; Chanes et al., 2012; Duecker et al., 2013; Hung et al., 2011; Grosbras & Paus, 2002, 2003; Ruff et al., 2009; Silvanto et al., 2006; Walker et al., 2009), as TMS of the left FEF only facilitated contralateral probe discrimination, whereas probe discrimination after right FEF did not differ on both sides and was slightly better than with left or vertex stimulation.

So why do some authors find bilateral effects after TMS of the right FEF, while others (e.g. Bosch et al., 2012; Neggers et al., 2007; Van Ettinger-Veenstra et al., 2009) only find contralateral effects? We believe that the controversy can be explained by differences in experimental designs. Even if the right FEF can orient attention bilaterally, it will only do so when there is a need for it. When the probed hemifield is fully predicted by the saccade cue, as in the task used by Neggers et al. (2007) and Van Ettinger-Veenstra et al. (2009), the right FEF only has to orient attention to the left, so it would not be logical to find any ipsilateral effects of TMS. The same is true for the oculomotor paradigm employed by Bosch et al. (2012), where good performance required the allocation of all attentional resources to a single target.

In contrast to previous studies which found TMS to increase the latency of prosaccades (e.g., Ro et al., 1997; Thickbroom et al., 1996) we did not find any effect of TMS on the latency of saccades. This is most likely due to the timing of the pulses that were delivered 180 or 130 ms before average saccade onset in the endogenous cueing condition, which is later than in Ro et al.'s (1997) study and earlier than in the study of Thickbroom et al. (1996). A study by Nyffeler et al. (2004) revealed that, depending on the time of stimulation and the exact saccade paradigm, TMS of the FEF can either facilitate or inhibit saccade execution or not affect it at all. Moreover, neither Neggers et al. (2007) nor Van Ettinger-Veenstra et al. (2009), who used a similar paradigm as we did, observed any modulation of saccade latencies.

In conclusion, the present study revealed that TMS of the left FEF modulates endogenous visual attention independently of saccade programming, even in a paradigm where endogenous attention is strongly coupled to the saccade goal. Our results thus support the notion that attention and saccade programming are separate functions that are dissociable at the level of FEF neurons (Juan et al., 2008; Juan, Shorter-Jacobi, & Schall, 2004; Sato & Schall, 2003; Wardak et al., 2011). Since the attentional modulation was independent of cueing, we could not determine to what extent the FEF is involved in the programming of exogenously cued saccades or in the shifts of attention that precede them. Future studies will hopefully reveal more about the role of the FEF in exogenous attention and uncover the exact mechanisms and pathways by which TMS affects the activity of the FEF and of downstream visual areas.

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### 3 General Discussion

The present thesis investigated how visual attention is linked to saccade programming and saccadic decision making. I will briefly summarize the results of the three studies and discuss how they have helped to clarify the relationship between attention, saccade decisions and saccade programming.

#### 3.1 Summary of findings

The first study (**Chapter 2.1**) examined the coupling between oculomotor selection and perceptual selection in an antisaccade paradigm. Previous studies provided evidence that antisaccade programming involves a competition between exogenous and endogenous influences, but none of them assessed the allocation of spatial attention by measuring perceptual performance at the competing locations. Our results have filled this gap by showing that attention is allocated in parallel to both the visual cue and the antisaccade goal and that pre-saccadic attention at the antisaccade goal is predictive of initial saccade direction. Besides this, we replicated previous findings on parallel saccade programming of pro- and antisaccades and the relationship between the awareness of prosaccade errors and their correction. Our study found no relationship between attention allocation and awareness of saccade errors and thus disproves a previous hypothesis by Deubel & Mokler (2000) that erroneous, unperceived prosaccades may occur without attentional involvement.

The second study (**Chapter 2.2**) investigated oculomotor and attentional measures in rule-based or free decisions between two memorized saccade goals. The main finding was that attentional selection evolved in parallel at the final saccade goal and the competing target, with a bias towards the saccade goal both before correct and before erroneous rule-based choices. Moreover, we found that decisions emerged from the competition of several types of biases and that they tended to form at a very early point in time, before task-relevant information was made available. While several neurophysiological studies provided evidence for such parallel competitive processes in the monkey brain, our study was the first to show that the competition is also reflected in visual perception and that saccade decisions can be predicted from the spatial distribution of attention.

The third study (**Chapter 2.3**) tested whether interfering with activity of the frontal eye fields (FEF), a brain region crucially involved in both visual and oculomotor selection, can modulate the coupling between saccades and visual selection.

Previous studies have demonstrated that transcranial magnetic stimulation (TMS) of the left or right FEF can either weaken (Neggers et al., 2007) or enhance (Van Ettinger-Veenstra et al., 2009) the obligatory coupling of attention to a future saccade goal in the contralateral visual hemifield, depending on the stimulation protocol. These studies used the behavioral task introduced by Deubel and Schneider (1996), in which participants have to saccade to one of three horizontally aligned locations in the left or right visual hemifield and discriminate a target at one of these locations. Our study employed a novel dual-task paradigm, in which the saccade cue was not predictive of the probe location and saccade programming occurred in parallel to the attentional task. We therefore increased the degree of attentional competition between both tasks and introduced an additional component of interhemispheric rivalry. The results showed that TMS of the left FEF enhanced endogenous attention to the contralateral visual field, independent of saccade programming. Contrary to our expectations, the results could not help to discern the role of the FEF in the control of exogenous attention, but they still contributed to the understanding of the relationship between exogenous and endogenous attention by providing evidence that they compete through interhemispheric connections.

### 3.2 Parallel saccade programming

In most situations, average fixation durations between two subsequent saccades lie between 180 and 330 ms (Rayner & Castelhana, 2007). Sometimes, however, intervals between subsequent saccades are so short that their programming must have overlapped in time (e.g., Becker & Jürgens, 1979; Godijn & Theeuwes, 2002; Hodgson, Parris, Gregory, & Jarvis, 2009; Irwin et al., 2000; Massen, 2004; McPeck, Skavenski & Nakayama, 2000; Mokler & Fischer, 1999; Morrison, 1984; Theeuwes et al., 1998, 1999; Walker & McSorley, 2006).

Amongst other examples, parallel saccade programming occurs when erroneous prosaccades in the antisaccade task are followed by corrective antisaccades (Massen, 2004; Mokler & Fischer, 1999). The first study of this dissertation (**Chapter 2.1**) replicated this finding and extended it by showing that the parallel saccade programming is associated with parallel attention allocation to both saccade goals. Moreover, we observed mutual inhibitory interactions between the two parallel saccade programs and thus provided behavioral evidence that reflexive and endogenous saccade programs in the antisaccade task compete within the same neural structures.

The second study (**Chapter 2.2**) revealed that saccadic decisions between two memorized visual targets leads to a parallel increase in attention at both alternative saccade goals, with a benefit at the chosen target. This is consistent with previous neurophysiological results that visuomotor brain areas simultaneously represent competing goals for saccades (Basso & Wurtz, 1998; Kim & Basso, 2008; McPeck & Keller, 2002; Platt & Glimcher, 1997; Sugrue et al., 2004) or reaching movements (Baldauf, Cui & Andersen, 2008; Cisek & Kalaska, 2005; Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015; Klaes et al., 2011; Scherberger & Andersen, 2007), even in the absence of visual input. Our results complement these findings by showing that competitions between motor alternatives have direct perceptual consequences and that these consequences can be used to track the process of decision making without the need to measure brain activity.

Taken together, our results on parallel saccade programming suggest that the covert decisional processes that lead to the final selection of a saccade goal are inherently parallel. Compared to sequential action planning, the parallel preparation of several movement plans increases an organism's capacity to flexibly react to changes in the environment and reduces idle time after responses. It therefore seems to be advantageous for the brain to have multiple response possibilities available until very late processing stages, even at the expense of a higher rate of erroneous actions.

While the competition between oculomotor plans needs to be resolved by a winner-take-all mechanism, the results of the present thesis suggest that attention can remain allocated to both oculomotor goals. Consistent with this, a recent study showed that the spatial averaging that occurs when saccades are planned towards one of two close peripheral locations – known as the *global effect* (Coren & Hoenig, 1972; Findlay, 1982) – does not apply to attention, which rather remains allocated to both potential saccade goals (Van der Stigchel & de Vries, 2015).

### 3.3 Attention, decision making and saccade programming

While there is no doubt that spatial attention and saccade programming are intimately related, the exact nature of their link and its neural underpinnings still remain to be determined. A major problem is that attention is a vague theoretical concept that has substantially changed over the years, depending on the metaphors used to describe it and the growing amount of evidence on the functioning of the brain. While long-established metaphors of attention, such as the *attentional spotlight* or the *limited resource pool* view attention as a direct cause of some executive processing, an alternative view is that attention emerges from competitive processes in sensory or sensorimotor brain areas,

without the need for any particular agent (Fernandez-Duque & Johnson, 2002). This idea can be traced back to the work of Desimone and Duncan (1995), who first described attention as a biased competition between objects in the visual field.

The results of the present thesis support the latter view, as they indicate that spatial attention is not a consequence of oculomotor or perceptual decisions, but rather something that is indistinguishable from such decisional processes. In the first study (**Chapter 2.1**), spatial attention predicted the direction of saccades in the antisaccade task, which suggests that the distribution of attention reflects saccadic decision processes. The second study (**Chapter 2.2**) investigated the relationship between oculomotor decisions and covert attention in detail and revealed that attention predicted saccadic choices long before the saccades were executed, which means that participants tended to preselect one of the two locations. The preselection was mainly driven by the secondary discrimination task and led to many saccade errors, which renders an explanation in terms of a voluntary strategy unlikely. This shows that oculomotor decisions are biased at the same time and by the same influences as visual selection and that a distinction between covert attention and the saccadic decision process is futile in this context.

I would like to emphasize that this does not mean that covert attention is always accompanied by saccade programming, as has been proposed by the premotor theory of attention (see **Chapter 1.1.1**). Contrary to this, I assume that the link between saccade programming and covert attention may vary substantially across different situations, as it depends on the relative importance of perception and of saccade programming at a given moment in time (i.e., the urgency of perception or saccade programming) as well as on various characteristics of the perceptual and oculomotor goals. In real life situations saccades tend to be directed to locations that are either perceptually salient or need to be further explored, so there is often little competition between covert and overt attention. Nevertheless, when goals for saccades and for perception are artificially separated by instructions, the conflicting attentional demands of the two processes (i.e., the sums of biases in favor of each spatial location) compete against each other, each weighed by the relative urgency of the process.

The dual task experiments employed in this thesis were designed to pose such conflicting demands on visual attention, but to prevent that participants would delay saccade programming, we always asked them to prioritize the saccade task over the visual discrimination task. The saccade task therefore biased attention more than the discrimination task, which explains why no attention could be allocated to saccade-irrelevant locations, except in the third study (**Chapter 2.3**), where participants managed to split off some endogenous attention at the expense of saccade latency.

Belopolsky and Theeuwes (2009, 2012) proposed an updated version of the premotor theory, suggesting that shifting covert attention to a location always involves a saccade program to that location, whereas maintaining attention can lead to both activation or suppression of saccades to the attended location. The first part of this claim is corroborated by the results of our first study, which showed that shifting attention to the antisaccade cue often led to involuntary prosaccades towards it. The second claim can be reconciled with the results of our second study, where we found some evidence for the suppression of saccade programming to the non-chosen target while it was selected by attention. The finding that discrimination performance at the non-chosen target was worse than at the chosen target, but still kept improving towards saccade onset could mean that attentional representations of the non-chosen target were simultaneously downweighed by top-down information about the task rule (Dhawan et al., 2013) and upweighed due to their relevance for the decision task.

The third study (**Chapter 2.3**) demonstrated that the frontal eye fields (FEF), which are crucially involved in the control of eye movements, also participate in endogenous attention shifts that are independent of saccade programming. This indicates that the role of the FEF in attentional control is separable from its role in saccade planning, as has already been shown by other authors (Juan et al., 2008; Juan et al., 2004; Sato & Schall, 2003; Wardak et al., 2011). The finding that attention at saccade-irrelevant locations competed with attention at the saccade goal is compatible with the view that saccade preparation constitutes an independent attentional bias that competes with other types of biases (Desimone & Duncan, 1995). Consistent with this, a recent study in monkeys provided evidence that saccade preparation in the FEF modulates activity in area V4 at least as much as covert attention (Steinmetz & Moore, 2014).

Taken together, the results of this thesis support the view that covert attention, saccadic decision making and saccade programming are consequences of a common competitive process that aims to prioritize certain spatial locations over others. Several theories of selective attention have suggested that visual selection and eye movements may be guided by the output of a “priority map”, which represents the behavioral relevance of locations in visual space based on a combination of their bottom-up visual saliency as well as top-down biases reflecting task demands (e.g., Fecteau & Munoz, 2006; Serences & Yantis, 2006). This concept is compatible with accumulator models of decision making (see **Chapter 1.1.3**) and it has been proposed that the activity on the map could also represent the evolution of parallel motor plans towards the represented locations (Cisek, 2007), which is congruent with the premotor theory of attention.

In search for the neural substrate of the priority map, researchers have proposed several candidate areas, including the FEF (Thompson & Bichot, 2005), SC (Bayguinov, Ghitani, Jackson, & Basso, 2015; Krauzlis, Bollimunta, Arcizet, & Wang, 2014) and LIP (Bisley & Goldberg, 2010; Bisley et al., 2009; Ipata et al., 2009; Goldberg et al., 2006). While these areas fulfill the criteria (i.e., they are topographically organized, integrate bottom-up and top-down signals and represent priority independent of task), it is likely that they represent intermediate maps and that the final priority map emerges from the interaction of several areas (Mirpour & Bisley, 2015).

The results of this doctoral thesis do not allow to conclude where the signals that concurrently drive saccade preparation to selected locations and facilitate visual perception at these locations originate and whether it is more appropriate to view them as attentional or as premotor activity. They mainly show that the influence between attention and saccade programming is mutual: On one hand, attentional selection of a location increases the likelihood of saccades to that location, and on the other hand, saccade programming automatically biases attention towards locations in space.

And what are the implications of the present results for the premotor theory of attention? The premotor theory of attention was undoubtedly useful, as it challenged the formerly prevalent view that attention constitutes an independent cognitive domain and opened up a whole new field of research. Since then, many studies, including the ones that comprise this thesis, have confirmed that visual and oculomotor selection tend to be linked, but can also be dissociated. Consistent with this, single cell recordings have shown that both processes tend to be carried out by the same neural structures, where they show crosstalk but also partial independence (see **Chapter 1.1.4**). In the light of these findings, the question whether attention and saccade programming are linked or independent has become a philosophical one, as the answer mainly depends on how the two terms are defined.

### 3.4 Endogenous and exogenous attention

One of the goals of this doctoral thesis was to examine the relationship between endogenous and exogenous attention, particularly in relation to saccade programming, as it has recently been suggested that endogenous attention is more independent from the oculomotor system than exogenous attention (Smith et al., 2012, 2014; Smith & Schenk, 2012). Both the first and the third study (**Chapters 2.1 and 2.3**) employed experimental designs that promoted the competition between endogenous and exogenous orienting, and the third study contrasted the effects of endogenous and exogenous saccade cues.



Besides confirming the well-known finding that exogenous cues tend to summon attention faster and more automatically than endogenous cues (Müller & Rabbit, 1989), both studies provided evidence that exogenous and endogenous attentional components can be simultaneously allocated to spatially disparate targets. Moreover, the results on discrimination performance suggest that spatially opposed endogenous and exogenous components inhibit each other, which indicates that they compete within the same neural structures. This is consistent with previous reports that both types of orienting can act independently when attentional demands are low, while they are likely to compete when attentional resources become scarce (Berger et al., 2005; Müller & Humphreys, 1991).

The first study of this thesis (**Chapter 2.1**) extended previous results by showing that the outcomes of this competitive process in the visual and oculomotor systems are correlated, which suggests that the outcome of the biased competition is used to guide both perception and saccades. The second study (**Chapter 2.2**) did not directly compare exogenous and endogenous biases, but the results also support the view that attention results from the competitive interactions of various types of biases. We observed an interaction between endogenous attention at the two memorized locations and exogenous attention attracted by the appearance of the visual probe that was additionally modulated by the progression of saccade preparation. This shows that the influence of exogenous biases on visual performance and on saccade programming depends on the currently active endogenous biases, which in turn depend on momentary task demands. Such interactions between endogenous and exogenous attention have been reported in previous studies (Anderson & Folk, 2010; Eimer & Kiss, 2008; Folk, Remington, & Johnston, 1992), but our results extend their findings by showing that these interactions may change depending on whether saccade programming or visual perception is prioritized, while their outcome (i.e., the resulting priority signal) affects performance on both tasks similarly. Another interesting finding was that visual and oculomotor performance were also influenced by selection history, which can neither be considered an exogenous nor a purely endogenous bias (Awh, Belopolsky, & Theeuwes, 2012). The results of our second study thus support the view that the traditional dichotomy between endogenous and exogenous attention needs to be revised (Awh et al., 2012; Macaluso & Doricci, 2013). Particularly the “endogenous” category is very fuzzy and may contain potentially conflicting biases. An endogenous cue, for instance, can compete with expectations regarding the target appearance and with a voluntary saccade plan and each of these biases can be weighted differently at different moments in time, depending on further “endogenous” factors, such as the reward associated with spatial locations or the relative urgency of responses.

A more elaborate taxonomy that would distinguish between implicit and voluntary biases as well as between cognitive, perceptual and motor demands would already make it much easier to evaluate the relationship between overt and covert attention.

The results of this dissertation neither clearly support nor refute the view that exogenous but not endogenous attention depends on saccade programming (Smith et al., 2012, 2014; Smith & Schenk, 2012), which is mainly based on evidence that exogenous attention cannot be allocated to locations outside the oculomotor range. We observed that exogenous cues elicited faster attention shifts than endogenous cues (**Chapter 2.3**) and tended to be followed by involuntary saccades (**Chapter 2.1**). This is consistent with a bulk of neurophysiological evidence that salient visual information quickly activates saccade-related motor neurons, for example in the superior colliculus (see **Chapter 1.1.4**). However, there is also evidence that less salient visual information is represented within the same spatial maps (at least up to the intermediate layers of the superior colliculus), where it can either be outcompeted by the more salient information or override it and win the competition, depending on the modulatory influences of endogenous biases. In consequence, perception and behavior are never based exclusively on endogenous or exogenous biases, but always on a weighted combination of both. I therefore disagree with the view that only exogenous attention depends on the oculomotor system.

### 3.5 Conclusion and Future Perspectives

The present doctoral thesis investigated the relationship between covert attention, saccade decisions and saccade programming. Our results are consistent with a model in which saccade programming and visual perception are guided by a common attentional priority map resulting from the weighted combination of multiple different biases. While saccade execution is guided by the most prominent peak of the map, saccade programming and visual processing occur at several locations in parallel, as they are biased by the map as a whole. This explains why visual processing is always superior at an upcoming saccade goal, but can still be allocated to other locations.

Further evidence is needed, however, to prove that this model is correct. Hopefully, the experiments reported here will inspire further studies, which will address some of the questions that we could not answer. Methodological approaches that would combine a thorough assessment of the behavioral effects of attention with spatially and temporally sensitive measures of brain activity could be particularly fruitful, as they could reveal potential correlations between behavioral effects and brain activity in areas that purportedly contain priority maps.

The second study (**Chapter 2.2**), for instance, demonstrated that temporal dynamics of spatial attention reflect ongoing oculomotor decisions and that the perceptual consequences of this attentional selection can serve as a window into the otherwise hidden decision process. Future studies could strengthen our claims by showing that saccadic decision processes are associated with ERP components that have been repeatedly related to attention and saccade programming (e.g., Eimer, Van Velzen, Gherri, & Press, 2007; Van der Lubbe, Neggers, Verleger, & Kenemans, 2006; Van der Stigchel, Heslenfeld, & Theeuwes, 2006).

More research is also needed to uncover the functional differences between spatial maps in different parts of the brain. The current status of knowledge indicates that attentional selection is achieved through some sort of distributed consensus between multiple priority maps, but very little is known about the interactions that actually take place. The same is true for the neural mechanisms that transform sensory information into saccadic commands.

The experiments reported in this thesis also demonstrated that distinctions between endogenous and exogenous attention are not always straightforward, for example because the influence of exogenous biases may be contingent on endogenous attention, or because different endogenous biases can compete within the same task. I am therefore convinced that the traditional distinction between endogenous and exogenous attention should be replaced by a new taxonomy that will include a distinction between different kinds of voluntary biases and additional categories for implicit biases. Future studies should continue to systematically test interactions between different types of attentional biases, trying to isolate them as much as possible in order to avoid confounds by related biases.

Finally, it would be of interest to see whether some of our findings also apply to other types of movements, particularly to reaching, or if they are unique to the oculomotor system.



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## Curriculum Vitae

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### Education

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1999-2002	BcA. in Sound Design/Engineering Film and TV Faculty (FAMU), Academy of the Performing Arts in Prague, Czech Republic
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## List of Publications

### Journal articles

**Klapetek, A.**, Jonikaitis, D., & Deubel, H. (2016). Attention allocation before antisaccades. *Journal of Vision*, 16(1):11, doi: 10.1167/16.1.11.

**Klapetek, A.**, Ngo, M. K., & Spence, C. (2012). Does crossmodal correspondence modulate the facilitatory effect of auditory cues on visual search? *Attention, Perception, & Psychophysics*, 74(6), 1154–1167.

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### Conference abstracts

**Klapetek, A.**, & Deubel, H. (2015). Distribution of attention and parallel saccade programming in antisaccades (meeting abstract). *Journal of Vision*, 15(12):71. doi: 10.1167/15.12.71.

**Klapetek, A.**, & Deubel, H. (2013). Parallel attentional allocation in antisaccades (meeting abstract). *Journal of Vision*, 13(9):1228, doi: 10.1167/13.9.1228.

Chladová, H., Tesařová, T., Hodková, P., Weiss, P., **Klapetek, A.**, & DeMartini, A., Fila, L., Zemkova, D., Smolikova, L., & Lekes, M. (2008). Sexuality in CF patients in Czech Republic. *Journal of Cystic Fibrosis*, 7(2), 109.





## **Eidesstattliche Versicherung/Affidavit**

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation „The link between visual and oculomotor selection: Evidence from competitive tasks“ selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation “The link between visual and oculomotor selection: Evidence from competitive tasks” is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München, den

Munich, date

Unterschrift/Signature



## Author Contributions

### Chapter 2.1

A version of this chapter has been published as Klapetek, A., Jonikaitis, D., & Deubel, H. (2016). Attention allocation before antisaccades. *Journal of Vision*, 16(1):11.

The author of this dissertation participated in designing the experiments, programmed the experiments, collected and analyzed the data, created plots, interpreted the results and wrote the journal article.

Donatas Jonikaitis participated in designing the experiments, in analyzing and interpreting the results, and he commented on and helped revising the manuscript.

Heiner Deubel conceived and supervised the project, participated in designing the experiments and interpreting the results, and commented on the manuscript.

### Chapter 2.2

The author of this dissertation participated in data collection and analysis, interpreted the results and wrote the manuscript.

Donatas Jonikaitis designed and programmed the experiment, collected and analyzed data, created plots, interpreted the results and participated in writing the manuscript.

Heiner Deubel supervised the project, interpreted results and commented on the manuscript.

### Chapter 2.3

The author of this dissertation designed and programmed the experiment, collected and analyzed data, created plots, interpreted the results and wrote the manuscript.

Donatas Jonikaitis helped designing and programming the experiment and interpreting results.

Jasper Dezwaef participated in data collection, created a part of the plots and commented on the manuscript.

Heiner Deubel supervised the project, participated in designing the experiment and in interpreting results and commented on the manuscript.

Paul Taylor supervised the project, participated in designing the experiment and in interpreting results and commented on the manuscript.

Bas Neggers supervised the project, helped with experimental setup and data collection, participated in designing the experiment and in interpreting results and commented on the manuscript.

The above contributions to the doctoral thesis of Anna Klapetek-Dünnweber are all correct as stated above.