Visual attention and visually guided actions:

Psychophysical investigations on the role of visual attention for visuomotor control

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Summary

Our visual perception does not reflect an accurate representation of the environment. Among the huge flood of sensory information projected onto our eyes at any given moment, only a small fraction is being processed thoroughly in the brain as to be perceived at a high resolution and enter consciousness. Thus, as a consequence of the limited processing capacities of the brain, visual perception emerges from a continuous selection process which operates upon the retinal image of the external world. The key to this selection process is visual attention. By attending we can selectively focus the available cognitive resources of the brain onto the currently most relevant aspects of the environment, which can thereby be processed in detail and precisely perceived. Importantly, apart from establishing a fundamental means for efficient visual perception, attentional mechanisms have been found to be tightly linked – both spatially and temporally – to motor action. This link is well illustrated, for instance, by the observation that both eye and hand movements are typically preceded by so-called premotor shifts of visual attention (i.e., spatially selective shifts of visual attention to the upcoming movement target which occur during movement preparation).

The present thesis aimed at investigating the role of visual attention for the control of visually guided actions in a series of psychophysical dual-task studies involving human participants. Each study combined a specific motor task (requiring the preparation and execution of eye, hand, or concurrent eye-hand movements) with a visual discrimination task (which allowed to assess the spatio-temporal dynamics of visual attention during movement preparation). The central insights of these studies are briefly summarized below.

The first study *(Chapter 2.1)* examined the coupling between visuospatial attention and the endpoint of saccadic eye movements. Crucially, the presentation of two nearby, competing saccade targets (rather than single one) induced a broad distribution of saccade endpoints. This allowed to evaluate the deployment of visual attention depending on whether subsequent saccades landed accurately at either one of the two saccade targets (target saccades) or erroneously in between them (so-called

averaging saccades). The results revealed a striking dissociation between the locus of visual attention and the endpoint of averaging saccades, clearly demonstrating that presaccadic attentional shifts are not obligatorily coupled to the saccade endpoint. Moreover, contrary to target saccades, attentional resources were found to be equally distributed across the two neighboring saccade targets prior to the execution of averaging saccades, suggesting that precise eye movement control is tightly linked to successful attentional selection.

The second study *(Chapter 2.2)* investigated the effects of spatial predictability and increased movement preparation time on both the efficiency of attentional selection and the accuracy of saccadic eye movements during episodes of competition between a saccade target and a nearby, task-irrelevant distractor. It was observed that spatial predictability of both the saccade target and the distractor location largely improved the accuracy of short-latency saccades. Moreover, already a short prolongation of movement preparation time substantially enhanced saccade accuracy even under spatial uncertainty. Interestingly, the presaccadic deployment of visual attention was not systematically affected by spatial predictability, but predominantly modulated as a function of movement preparation time. The appearance of the saccade target and distractor objects likewise captured attention in a rapid and automatic fashion, leading to pronounced attentional competition early on during movement preparation. However, this initial competition was resolved over time: While attentional resources were allocated to the designated target object in a sustained fashion, attentional facilitation at the distractor progressively decayed and eventually vanished completely. In sum, these results provided several novel insights concerning the link between goal-directed eye movement control and the spatio-temporal dynamics of visual attention.

The third study *(Chapter 2.3)* explored the interaction among premotor attentional mechanisms and voluntary attentional control. While the assessment of visual discrimination performance during concurrent eye-hand movement preparation allowed to resolve whether corresponding effectors exploit shared or separate attentional resources/mechanisms, the use of a spatial cueing manipulation made it possible to additionally evaluate how premotor attentional shifts affect the ability to voluntarily attend at movement-irrelevant locations. The results demonstrated that attention can be successfully allocated in parallel to spatially distinct eye and hand movement targets, implying that movement target selection is achieved through independent, effector-specific attentional resources/mechanisms. Strikingly, however, movement preparation in both effector systems similarly impaired voluntary attentional control. This finding argues for the idea that visual attention predominantly subserves the selection of targets for upcoming actions.

Apart from the three original studies described above, an additional methodologically oriented manuscript *(Chapter 2.4)* was compiled as a part of this thesis. Aiming to facilitate replicability in the spirit of *“Open Science“*, this manuscript (published together with a video) presents a thorough description of the experimental procedure underlying the psychophysical assessment of visuospatial attention during movement preparation (using the example of the dual-task employed in the first study).

Zusammenfassung

Unsere visuelle Wahrnehmung entspricht keinem realitätsgetreuen Abbild der Umwelt. Von der überwältigenden Flut sensorischer Information die auf unsere Augen einströmt verarbeitet unser Gehirn jeden Moment lediglich einen Bruchteil, welcher in Folge dessen akkurat wahrgenommen werden kann und in unser Bewusstsein vordringt. Dementsprechend ist visuelle Wahrnehmung vielmehr als das Ergebnis eines kontinuierlichen Selektionsprozesses anzusehen, der eine Anpassung an die begrenzte Verarbeitungskapazität unseres Gehirns darstellt. Dieser Selektionsprozess wird maßgeblich durch Mechanismen der visuellen Aufmerksamkeit bestimmt. Durch die zielorientierte Ausrichtung visueller Aufmerksamkeit können wir die kognitiven Ressourcen des Gehirns selektiv auf die aktuell relevanten Umweltreize konzentrieren um diese wirksam zu verarbeiten und präzise wahrzunehmen. In den letzten Jahrzehnten hat sich gezeigt, dass visuelle Aufmerksamkeitsmechanismen jedoch nicht nur eine entscheidende Rolle im Kontext eines effizienten Wahrnehmungsvorgangs spielen, sondern darüber hinaus ebenfalls - räumlich sowie zeitlich - eng an unsere motorischen Handlungen gekoppelt sind. Diese Kopplung manifestiert sich beispielsweise in der prä-motorischen (d.h. während der Bewegungsvorbereitung auftretenden) Verschiebung des Aufmerksamkeitsfokus zum Zielort bevorstehender Augen- und Handbewegungen.

Die vorliegende Dissertation befasst sich mit eben jener Kopplung und der Frage nach der Funktion visueller Aufmerksamkeitsmechanismen bei der Steuerung von zielgerichteten motorischen Handlungen. Vor diesem Hintergrund wurden diverse experimentelle, psychophysikalische Studien an menschlichen Probanden durchgeführt. Jede dieser Studien kombinierte eine spezifische motorische Aufgabe (welche die Vorbereitung und Ausführung von Augen-, Hand-, oder gleichzeitigen Augen-Hand-Bewegungen erforderte) mit einer visuellen Diskriminierungsaufgabe (welche es ermöglichte räumliche und zeitliche Aspekte visueller Aufmerksamkeit während der Bewegungsplanung zu erfassen). Die folgenden Abschnitte beinhalten eine kurze Zusammenfassung der zentralen Ergebnisse dieser Studien.

Die erste Studie *(Kapitel 2.1)* untersuchte den räumlichen Zusammenhang zwischen der Verteilung visueller Aufmerksamkeitsressourcen und dem Endpunkt sakkadischer Augenbewegungen. Ein zentrales Merkmal dieser Studie war die Darbietung von zwei nahegelegenen, konkurrierenden sakkadischen Zielreizen (anstatt nur einem einzelnen Zielreiz). Dadurch konnte eine breite Streuung sakkadischer Endpunkte hervorgerufen werden. In der Folge war es möglich, die prä-sakkadische, räumliche Verteilung der Aufmerksamkeitsressourcen getrennt für Sakkaden auszuwerten, welche entweder präzise an einem der beiden sakkadischen Zielreize landeten (Ziel-Sakkaden) oder fehlerhafterweise zwischen diesen beiden Zielreizen landeten (sogenannte Schwerpunkt-Sakkaden). Die Ergebnisse offenbarten eine ausgeprägte räumliche Dissoziation zwischen dem visuellen Aufmerksamkeitsfokus und dem Endpunkt von Schwerpunkt-Sakkaden – ein Befund, der klar zeigt, dass prä-sakkadische Aufmerksamkeitsverschiebungen nicht obligatorisch an den Sakkadenendpunkt gekoppelt sind. Darüber hinaus zeigte sich, dass die verfügbaren visuellen Aufmerksamkeitsressourcen, anders als bei Ziel-Sakkaden, vor der Ausführung von Schwerpunkt-Sakkaden gleichmäßig über die beiden nahegelegenen Zielreize verteilt waren. Dies impliziert, dass präzise okulomotorische Kontrolle eng an eine erfolgreiche, prä-sakkadische Aufmerksamkeitsselektion geknüpft ist.

Die zweite Studie *(Kapitel 2.2)* erforschte, inwiefern sich räumliche Vorhersagbarkeit und zunehmende Bewegungsvorbereitungszeit auf die Effizienz der prä-sakkadischen Aufmerksamkeitsselektion und die Präzision von sakkadischen Augenbewegungen auswirken, wenn ein ablenkender Reiz (ein sogenannter Distraktor) in der Nähe eines sakkadischen Zielreizes erscheint. Hierbei wurde beobachtet, dass die Vorhersagbarkeit des Darbietungsortes von Sakkadenzielen und Distraktoren gleichermaßen die Präzision von Sakkaden mit kurzer Latenz erhöht. Des Weiteren konnte gezeigt werden, dass bereits eine geringe Verlängerung der Bewegungsvorbereitungszeit (d.h. der Sakkadenlatenz) selbst ohne derartiges räumliches Vorwissen zu einer deutlichen Verbesserung der sakkadischen Präzision führt. Interessanterweise hatte die räumliche Vorhersagbarkeit aber keinen systematischen Einfluss auf die prä-sakkadische Verteilung der Aufmerksamkeitsressourcen, welche sich hauptsächlich über die Zeit hinweg veränderte (d.h. mit zunehmender Bewegungsvorbereitungszeit). Die Darbietung von Sakkadenziel und Distraktor löste rasche und automatische Verschiebungen der Aufmerksamkeit aus, sodass entsprechende Reize in einem frühen Stadium der Bewegungsvorbereitung maßgeblich um die verfügbaren Aufmerksamkeitsressourcen konkurrierten. Dieser initiale Aufmerksamkeitskonflikt wurde jedoch im Verlauf der Zeit aufgelöst: Die Aufmerksamkeitsressourcen konnten über einen längeren Zeitraum lediglich auf das Sakkadenziel fokussiert werden, wohingegen die Aufmerksamkeitsausrichtung hin zum Distraktor zunehmend abnahm und letztendlich verschwand. Zusammenfassend konnten in dieser Studie diverse neue Einblicke hinsichtlich des Zusammenhangs zwischen zielgerichteter okulomotorischer Kontrolle und der räumlich-zeitlichen Dynamik visueller Aufmerksamkeitprozesse erlangt werden.

Die dritte Studie *(Kapitel 2.3)* widmete sich der Frage nach der Wechselwirkung zwischen prä-motorischen Aufmerksamkeitsverschiebungen und willentlicher Aufmerksamkeitskontrolle. Zum einen erlaubte die Auswertung visueller Diskriminierungsleistung während der Vorbereitung gleichzeitiger Augen-Hand-Bewegungen zu klären, ob die beteiligten Effektoren auf gemeinsame oder eigenständige Aufmerksamkeitsressourcen zurückgreifen. Zum anderen konnte mittels eines zusätzlichen *„Spatial Cueing“* Paradigmas ermittelt werden, wie sich prä-motorische Aufmerksamkeitsverschiebungen auf die Fähigkeit auswirken, Aufmerksamkeitsressourcen willentlich auf bewegungs-irrelevante Reize zu fokussieren. In dieser Studie konnte eine parallele Verschiebung visueller Aufmerksamkeit zu zwei räumlich diskreten Zielorten für Augen- und Handbewegungen festgestellt werden. Dieser Befund deutet stark darauf hin, dass prä-motorische Zielort-Selektion mittels unabhängiger, effektoren-spezifischer Aufmerksamkeitsressourcen realisiert wird. Im Gegensatz zu dieser Flexibilität zeigte sich allerdings auch, dass die willentliche Aufmerksamkeitsausrichtung deutlich negativ durch die Vorbereitung von Augen- als auch Handbewegungen beeinträchtigt wird. Dementsprechend scheint der prä-motorischen Zielort-Selektion eine zentrale und übergeordnete Rolle im Kontext der Kontrolle visueller Aufmerksamkeit zuzukommen.

Neben den drei experimentellen Studien beinhaltet diese Dissertation auch ein methodisch orientiertes Manuskript *(Kapitel 2.4)*. Dieses beschreibt (anhand des Beispiels der Doppelaufgabe aus der ersten Studie und einer zugehörigen Videodemonstration) detailliert das experimentelle Vorgehen im Rahmen der psychophysikalischen Erhebung visuell-räumlicher Aufmerksamkeitseffekte während der Bewegungsvorbereitung. Somit wurde im Sinne des *„Open Science“* Gedankens eine Grundlage für die Replikation des hier angewendeten experimentellen Vorgehens und der erlangten Ergebnisse geschaffen.

Table of Contents

List of Figures

List of Abbreviations

Frequently used abbreviations:

FEF	Frontal Eye Fields
LIP	Lateral Intraparietal Area
PRR	Parietal Reach Region
SC	Superior Colliculus

1 General Introduction

1.1 Visual attention as a fundamental mechanism for selection

Our visual experience unfolds in a seemingly effortless flow of conscious visual perception. Yet, visual perception does not simply emerge passively, but rather reflects the result of our brains actively engaging with the visual information contained within the environment. In fact, the vast amount of visual information projected onto our eyes by far exceeds the limited processing resources of our brains (Lennie, 2003; Carrasco, 2011). At any moment, only a small fraction of the available visual information can be thoroughly processed as to enter conscious experience and reach behavioral relevance (Desimone & Duncan, 1995; Schneider 2013). Thus, efficient visual perception and goal-directed behavior fundamentally depend on a selection process (Treue, 2003), which is accomplished via the mechanism of *visual attention*.

1.1.1 The perceptual and neuronal correlates of visual attention

Visual attention is commonly defined as a mechanism by which we can selectively bias information processing in order to focus on relevant aspects in the surrounding environment and conversely ignore irrelevant aspects (Duncan, Humphreys, & Ward, 1997; Carrasco, 2011). Visual attention therefore allows us to assign perceptual and behavioral priority among the continuous flood of visual input entering our eyes. This intriguing cognitive capacity has stimulated a large body of research dedicated to the investigation of both the perceptual and neuronal correlates of attentional mechanisms.

Classical evidence for the perceptual ramifications of visual attention was obtained via the assessment of manual reaction times. For instance, spatial cueing paradigms, which allow to systematically manipulate the deployment of visual attention despite fixation of the eyes, revealed that a peripheral stimulus can be detected faster (slower) when appearing at an attended (unattended) location in the visual field (Posner, 1980; Posner, Snyder, & Davidson, 1980). Moreover, the influence of visual attention on perception has been inferred from the results of visual search tasks in which participants are required to rapidly report the presence of a variably conspicuous target object among several distractor objects (Wolfe, 1998; Verghese, 2001). These experiments demonstrated that manual reaction times systematically increase with the number of distractors when participants have to search for an inconspicuous target (i.e., for a stimulus sharing one or more visual features with the distractors; so-called *conjunction search*), but not when searching for a conspicuous one (i.e., for a stimulus defined in a unique feature dimension; so-called *feature search*) (Treisman & Gelade, 1980; Treisman, 1982). To account for this effect, it has been originally suggested that a conspicuous target can be detected efficiently via pre-attentive parallel processing, whereas the detection of an inconspicuous target requires serial processing via selective visual attention (Treisman & Gelade, 1980; Wolfe, 1994). This dichotomy of parallel and serial processes has however been challenged by some authors (Duncan & Humphreys, 1989; Palmer, Verghese, & Pavel, 2000).

Accounting for the notion that reaction times confound measures of sensory and motor components (Nakayama & Mackeben, 1989), other authors set out to reveal the sensory signatures of visual attention more directly via visual discrimination tasks. These tasks typically do not require speeded manual responses, but assess the ability of participants to correctly report particular features of a briefly presented target object (e.g., a clockwise rotated object vs. a counterclockwise rotated object). Based on this approach, it was shown that objects which appear at attended locations in the visual field can be discriminated better and processed faster (Carrasco & McElree, 2001; Giordano, McElree, & Carrasco, 2009). Similarly, several studies demonstrated that the selective deployment of visual attention enhances contrast sensitivity (Lee, Itti, Koch, & Braun, 1999; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Cameron, Tai, & Carrasco, 2002) and spatial resolution (Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2000; Carrasco, Williams, & Yeshurun, 2002). Alike the psychophysical approach adopted in these latter studies, the experiments contained in this thesis investigated the perceptual correlates of visual attention by means of a visual discrimination task.

The commonly observed attention-induced perceptual benefits have been explained in different ways in the literature. Several authors have suggested that attentional effects arise from an amplification of the signal within the locus of attention (Cameron et al., 2002; Carrasco et al., 2002), whereas others have argued that attention effectively reduces external noise (Dosher & Lu, 2000; Lu, Lesmes, & Dosher, 2002). However, it has also been proposed that the deployment of visual attention may lead to changes in decision criteria rather than a modulation of perceptual processing per se (Shiu & Pashler, 1995).

Beyond the insights obtained in psychophysical studies, neurophysiological experiments allowed to elucidate some of the neuronal correlates of visual attention. Various methods — such as functional magnetic resonance imaging (fMRI; Brefczynski & DeYoe, 1999; Gandhi, Heeger, & Boynton, 1999), electroencephalography (EEG; Hillyard & Anllo-Vento, 1998; Sauseng et al., 2005), and single-cell recordings in the monkey brain (Moran & Desimone, 1985; Reynolds, Chelazzi, & Desimone, 1999; Reynolds, Pasternak, & Desimone, 2000) — have been used to record neuronal activity depending on the attentional state of the observer. Such protocols consistently demonstrated that visual attention selectively modulates the activity of neuronal populations distributed along the visual processing stream. The selective deployment of visual attention enhances the activity of visually responsive neurons encoding attended aspects of the visual input and can conversely reduce activity within neuronal populations dedicated to the processing of unattended aspects (Treue, 2001). Interestingly, attention-induced neuronal effects can already emerge in V1 of the primary visual cortex (Motter, 1993; Brefczynski & DeYoe, 1999), suggesting that attention fundamentally affects sensory processing, and thus perception. Despite this observation, attentional control mechanisms are commonly believed to originate from higher-level cognitive processing within a network including frontal and parietal brain areas (Kastner & Ungerleider, 2000; Ptak, 2012). More generally, it has been suggested that the neuronal effects of visual attention accumulate throughout the visual processing hierarchy (Treue, 2001), which hints towards the notion that visual perception is in fact highly selective and biased towards the current behavioral goals of the observer.

1.1.2 The properties of visual attention

Owing to a growing scholarly interest (Carrasco, 2011), our understanding of visual attention has been constantly refined over the last decades. The following sections provide a brief overview of the literature on visual attention as to highlight central properties of (and common distinctions among) attentional phenomena.

Metaphors of visual attention. A seminal framework for the study of attention in cognitive psychology was introduced by Broadbent (1958). Conceptualizing cognition in analogy to computerized information processing and accounting for the limited processing capacities of the brain, he proposed that attention acts like a filter which extracts only a fraction of the available information based on its physical properties (Driver, 2001). As research focused on the spatial characteristics of attention in the visual domain, attention was next conceptualized as a steerable *spotlight* which selectively accentuates certain regions or aspects within the visual scene (Posner et al., 1980). Only some years later, a *zoom lens* metaphor of attention emerged based on the observation that the size of the attentional locus can be rather flexibly adjusted, with an inverse relationship between processing resolution and the size of the attentional locus (Eriksen & James, 1986). Moreover, given that processing resolution was found to decrease as a function of the distance from the center of the attentional locus, the common understanding of attentional mechanisms was further refined with reference to a *gradient* metaphor (Shulman, Wilson, & Sheehy, 1985). Amongst the rise of attentional metaphors (for a review see: Fernandez-Duque & Johnson, 1999), a central debate developed around the question whether or not visual attention can be allocated to multiple locations in parallel. While early research suggested that visual attention is confined to a single locus (Posner et al., 1980; Eriksen & Yeh, 1985), later studies consistently demonstrated that attention can in fact be deployed to multiple noncontiguous locations (Driver & Baylis, 1989; Castiello & Umiltà, 1992).

The control of visual attention. The control of visual attention is typically accounted for within a two-component framework which distinguishes between bottom-up (stimulus-driven) and top-down (goal-driven) mechanisms (Wolfe, 1994; Itti & Koch, 2001). While salient aspects (i.e., conspicuous relative to their surrounding) of the visual input can attract visual attention automatically via bottom-up visual processing (often referred to as *attentional capture*; Theeuwes, 1991; Theeuwes, 1992), top-down processes can effectively bias the deployment of visual attention according to the current behavioral goals and expectancies of the observer (which can be established based on certain task instructions, prior knowledge, or reward contingencies). It has been proposed that salient aspects of the visual input are encoded within a central, topographically organized *saliency map* (Itti, Koch, & Niebur, 1998; Itti & Koch, 2001). This map is thought to integrate the output from several *feature maps* in early visual cortices which are characterized by competition among neurons tuned to specific visual features within a given dimension (e.g., color, orientation, motion, etc.). Subsequently, attention acts upon this bottom-up representation via selecting the location of highest activity (i.e., the most salient location across all feature dimensions) on the saliency map. Though it has been acknowledged that top-down mechanisms can bias processing at most stages of this influential bottom-up model of visual attention, other authors have introduced the concept of a *priority map* (which is to be discussed in detail in the next chapter) to emphasize the influence of top-down (i.e., goal-directed) mechanisms on attentional phenomena (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010). Another general distinction between bottom-up and top-down attentional mechanisms concerns their temporal properties. Bottom-up attentional effects have been shown to occur fast and transiently, whereas top-down attentional modulations emerge only slower and in a more sustained fashion (Nakayama & Mackeben, 1989; Theeuwes, 2010; Carrasco, 2011). Moreover, to account for the duality of attentional control, so-called *exogenous* attentional orienting responses elicited rather automatically by salient events in the visual environment are commonly distinguished from so-called *endogenous* attentional orienting responses which underlie voluntary control and reflect the intention of the observer (Theeuwes, 1991; Berger, Henik, & Rafal, 2005). This well-established theoretical dichotomy between bottom-up (exogenous) and top-down (endogenous) attentional control mechanisms has, however, been challenged more recently (see for instance: Awh, Belopolsky, & Theeuwes, 2012).

Different types of visual attention. While visual attention generally facilitates selective processing of certain aspects in the visual scene at the cost of other aspects, various types of visual attention have been distinguished in the literature (Duncan et al., 1997; Carrasco, 2011). First, visual attention can be selectively allocated to a given region in space (*spatial attention*; Martínez et al., 1999). Second, visual attention can target a specific object (*object-based attention*; Arrington, Carr, Mayer, & Rao, 2000).

Third, attentional mechanisms can enhance processing of a specific feature dimension (e.g., color, shape, orientation; so-called *dimensional weighting*; Müller, Heller, & Ziegler, 1995; Found & Müller, 1996) or a particular feature within a given dimension (e.g., red, rectangular, or vertical; so-called *feature-based attention*; Maunsell & Treue, 2006). However, despite their specificity, it has been suggested that the different types of attentional phenomena may recruit a common neuronal substrate within parietal brain areas (Wojciulik & Kanwisher, 1999).

Covert and overt orienting of attention. Another central distinction in the context of visual attention relates to the role of eye movements. Even though visual attention can improve processing of peripheral visual information without concurrent movement of the eyes, we can also exploit eye movements to relocate the locus of visual attention (Posner, 1980). The former mode is commonly referred to as *covert attention* (conveying the notion of attentional agency without observable motor action), whereas the latter mode which comprises the execution of eye movements is commonly referred to as *overt attention* – see **Figure 1** for a schematic illustration of both mechanisms and their neuronal and perceptual effects. In fact, we continuously explore our visual environment in such an overt fashion via rapid, ballistic movements of the eyes – so-called *saccades* – which are executed about three times every second (Rayner, 1998; Henderson & Hollingworth, 1999; Ross, Morrone, Goldberg, & Burr, 2001). This likely reflects an adaptation inherently related to a fundamental bias towards the central part of the retina – the *fovea* – manifesting in the architecture of the human visual system (Liversedge & Findlay, 2000). Throughout the visual processing stream this bias is reflected by a distinctively high density of cone cells in the fovea (Curcio, Sloan, Kalina, & Hendrickson, 1990), oversampling of foveal cone cells by midget retinal ganglion cells (Dacey & Petersen, 1992), and smaller foveal receptive field size (Smith, Singh, Williams, & Greenlee, 2001). In sum, this leads to a cortical overrepresentation of the fovea relative to the retinal periphery (Sereno et al., 1995). Indeed, psychophysical measures of visual acuity have been found to scale with these properties (Weymouth, 1958; Anstis, 1974; Virsu & Rovamo, 1979). Visual acuity is highest in the fovea and markedly decreases as a function of eccentricity. Thus, saccadic eye movements provide an attentional mechanism per se as they allow us to redirect our gaze onto novel, relevant aspects in the visual environment and process their content at high foveal resolution during intermittent periods of fixation. Interestingly, as to be discussed in detail in the next chapter, covert and overt attentional mechanisms are tightly coupled to each other – a phenomenon which poses the main subject of this thesis.

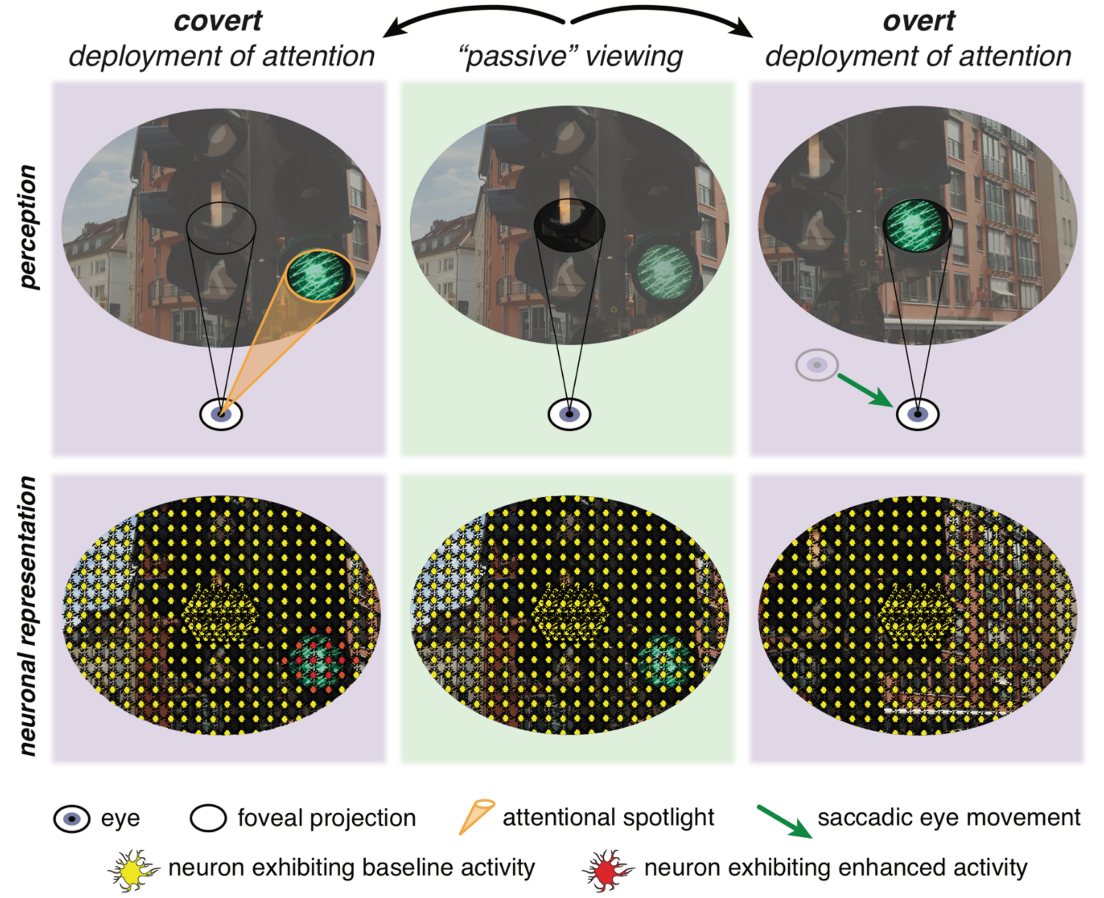

Figure 1. Covert and overt deployment of visual attention.
Schematic illustration depicting the effects of visual attention at the perceptual (*perception*) and neuronal (*neuronal representation*) level. Without the operation of selective attentional mechanisms (*passive viewing*; middle panel highlighted in light green) visual resolution is distinctly enhanced at the central part of the visual field which is projected onto the fovea, and thus receives preferential neuronal processing throughout the visual system (represented here by the high density of neurons encoding foveal information). However, the perceptual and neuronal representation of the visual scene can be systematically modulated via the operation of spatial, object-based, or feature-based attentional mechanisms. The covert deployment of visual attention (left panel highlighted in light purple) selectively enhances the activity of neurons encoding a designated object (i.e., the green light) which can therefore be perceived at a higher resolution. Yet, this is achieved without concurrent movement of the eyes, i.e., without effectively changing the retinal input. In contrast, the overt deployment of visual attention (right panel highlighted in light purple) comprises the execution of eye movements which effectively change the retinal input. By moving the eyes, a designated object (i.e., the green light previously located in the visual periphery) can be brought into foveal vision such that it receives enhanced neuronal processing (owing to the high density of neurons encoding foveal information) and is consequently perceived at a higher resolution. Note: The *perception* and *neuronal representation* visualizations are highly simplified for the sake of illustration.

1.2 The coupling between visual attention and saccadic eye movements

As described, attentional mechanisms can operate covertly in the absence of oculomotor action or overtly via concurrent movement of the eyes. The relationship between these two mechanisms has been thoroughly investigated at various levels, and it is now well established that covert attention is tightly coupled to saccadic eye movement programming. Yet, the exact nature of this coupling has remained a matter of debate to this date.

1.2.1 Psychophysical evidence

The functional interdependence between visual attention and oculomotor control has been addressed in a variety of psychophysical experiments. Early evidence for this interdependence was reported in a study combining a spatial cueing paradigm with a saccade task (Shepherd, Findlay, & Hockey, 1986). Saccade preparation was found to systematically accelerate reaction times towards a peripheral target stimulus. Moreover, it was observed that target detection was fastest at the location of the saccade goal even when the target stimulus was most likely to appear at an opposite location in the display, suggesting that eye movement programming entails obligatory, corresponding shifts of visual attention. Only one year later, similar evidence was observed in a spatial cueing task, leading to the formulation of the influential *premotor theory of attention* (Rizzolatti, Riggio, Dascola, & Umiltà, 1987) – to be discussed in more detail in *Chapter 1.2.3*. In this task, target detection time was found to slow down as the distance between the attended location (i.e., the location likely to contain the target stimulus) and the location at which the target stimulus actually appeared increased. Further, for a given distance, an additional detection time cost was observed when corresponding locations were contained in opposite hemifields separated either by the horizontal or vertical meridian. The authors concluded that covert orienting of attention depends on an underlying motor computation. Accordingly, they argued that reorienting attention towards more distant locations requires more time because it involves larger modifications of the underlying motor program.

Another classical line of evidence comes from dual-task paradigms which allow to assess the deployment of visual attention during saccade preparation via the combination of a saccade task with a visual-perceptual task. Importantly, this approach was employed throughout all experiments contained in this thesis *(Chapters 2.1 - 2.3)* and further covered in detail in a methodological manuscript *(Chapter 2.4)*. Several dual-task studies demonstrated that saccade preparation selectively enhances visual processing at the impending saccade target (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995; Hoffman & Subramaniam, 1995) – a phenomenon commonly known as *presaccadic shift of attention*. For instance, Deubel and Schneider (1996) asked participants to saccade towards locations within lateralized horizontal letter strings upon the offset of a central arrow cue. During movement preparation a discrimination target (E vs. Ǝ) was briefly presented at one of the locations within the letter strings, and participants had to report its identity at trial end. Visual discrimination performance was found to be selectively enhanced at the saccade target location, but remained around chance level at the neighboring locations in the letter string. This benefit was observed irrespective of the actual saccade endpoint. A second experiment revealed that participants were unable to allocate attention towards a location which did not coincide with the saccade target location. Consequently, it was proposed that visual attention and saccade programming are obligatorily coupled, with a single attentional mechanism facilitating both perceptual and motor target selection. Later studies suggested that the deployment of attention is particularly restricted to the saccade target shortly before saccade onset (i.e., when the motor plan is sufficiently elaborated), but not necessarily during early stages of oculomotor preparation (Doré-Mazars, Pouget, & Beauvillain, 2004; Deubel, 2008). Moreover, it was shown that visual attention can be deployed in parallel towards multiple saccadic targets during the preparation of a fast sequence of saccades (Godijn & Theeuwes, 2003; Baldauf & Deubel, 2008).

Apart from the vast amount of behavioral evidence arguing for an intriguingly tight link between attentional and oculomotor processes, a number of behavioral studies challenged the idea of an obligatory coupling between visual attention and saccade preparation (Hunt & Kingstone, 2003; Smith, Schenk, & Rorden, 2012; Belopolsky & Theeuwes, 2012; Born, Mottet, & Kerzel, 2014; Hanning, Szinte, &

Deubel, 2019). For instance, it was demonstrated that visual attention does not shift to the saccade target when saccade execution is successfully inhibited by a stop-signal (Born et al., 2014), and that visual attention can be effectively deployed to locations which are beyond the effective oculomotor range (Hanning et al., 2019). Moreover, the exact properties characterizing the commonly observed coupling between visual attention and saccades have been debated. Some studies found that visual attention shifts to the intended saccade target irrespective of the saccade endpoint (Deubel & Schneider, 1996; Ditterich, Eggert, & Straube, 2000), whereas other studies suggested that the presaccadic shift of attention is systematically modulated by the saccade endpoint (Doré-Mazars et al., 2004; Doré-Mazars & Collins, 2005; Collins & Doré-Mazars, 2006).

A central goal of the current thesis was to revisit this controversy and investigate whether or not visual attention obligatorily shifts to the endpoint of subsequent saccades. To this end, the first study *(Chapter 2.1)* exploited the so-called *saccade averaging* phenomenon – to be discussed in detail in *Chapter 1.4* – to assess how attentional resources are deployed prior to the execution of saccades for which the endpoint is largely dissociated from the location of an intended saccade target.

1.2.2 Neurophysiological evidence

A large body of neurophysiological studies have fostered our understanding of the neuronal mechanisms of both visual attention and saccadic eye movements. Additionally, a variety of neurophysiological techniques have been employed to specifically examine the coupling between visual attention and saccadic eye movements at the neuronal level.

Functional magnetic resonance imaging (fMRI) studies revealed that covert and overt attentional mechanisms recruit overlapping neuronal circuitries which comprise frontal and parietal brain areas (Corbetta et al., 1998; Beauchamp, Petit, Ellmore, Ingeholm, & Haxby, 2001; De Haan, Morgan, & Rorden, 2008). The idea that the control of visual attention and saccadic eye movements are subserved by common neuronal substrates was further supported by the effects of electrical microstimulation within oculomotor key structures of the monkey brain. For instance, it was observed that stimulating neurons within the midbrain superior colliculus (SC) (Müller, Philiastides, & Newsome, 2005) and the frontal eye fields (FEF) (Moore & Fallah, 2004) below the threshold required to systematically elicit saccadic eye movements selectively enhances visual sensitivity at corresponding locations in the visual field. Similarly, subtreshold microstimulation of FEF neurons was found to amplify visual responses of retinotopically corresponding neurons in area V4 of the extrastriate cortex (Moore & Armstrong, 2003; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008). Finally, it was also demonstrated that systematic saccadic inaccuracies can be induced via focal inactivation of neurons in the SC (McPeek & Keller, 2004). Taken together, the neurophysiological evidence obtained in microstimulation studies clearly highlights that central cortical and subcortical oculomotor structures play a crucial role for the deployment of visual attention.

Various authors (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Ptak, 2012; Zelinsky, & Bisley, 2015; Bisley & Mirpour, 2019) have suggested that the areas associated with a functional overlap between saccadic eye movements and visual attention – such as the SC, FEF, and the lateral intraparietal area (LIP) – form the basis of so-called *priority maps* (see **Figure 2** for a schematic illustration). These maps integrate bottom-up signals from early visual areas (conveying visual saliency) and top-down signals from frontal brain areas (conveying the goals of the observer) into a retinotopic representation of visual space. Accordingly, neuronal activity within the maps is thought to be closely related to the behavioral relevance of objects in the visual field. This means that behaviorally relevant objects are represented by local peaks of activity at corresponding locations in the priority maps. Importantly, in addition to controlling saccadic eye movements via connections to downstream oculomotor structures (Fecteau & Munoz, 2006), neuronal activity in the priority maps is thought to modulate early sensory processing in a top-down fashion via feedback connections to feature-selective areas of the visual cortex (Moore & Armstrong, 2003; Ekstrom et al., 2008; Rolfs & Szinte, 2016). As such, the instantiation of a priority map characterized by the described properties provides a plausible framework which can account for the coupling between visual attention and oculomotor programming at the neuronal level. Within this framework, attention is allocated on a moment-to-moment basis to objects or locations in the visual field which are associated with enhanced activity in the map (Bisley & Goldberg, 2010). Similarly, saccades are typically executed to the object or location which reaches peak activity in the map at the moment of movement onset.

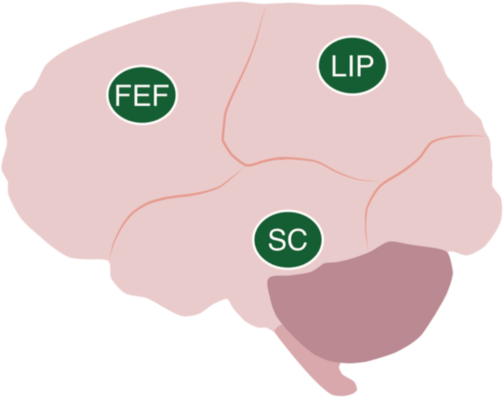

Figure 2. The priority map network.
Schematic illustration depicting the substrates of so-called priority maps in the human brain (lateral view). Brain areas such as the subcortical superior colliculus (SC) in the midbrain, the frontal eye fields (FEF) in the frontal lobe, and the lateral intraparietal area (LIP) in the parietal lobe are thought to encode the behavioral relevance of objects in retinotopic coordinates. They establish major visuomotor integration nodes and play a crucial role for the guidance of visual attention and the control of saccadic eye movements.

However, despite the evidence for a coupling between visual attention and oculomotor programming at the neuronal level, some studies demonstrated that attentional and motor signals can be dissociated within central priority map substrates. For instance, different classes of neurons in the FEF (Thompson, Biscoe, & Sato, 2005; Gregoriou, Gotts, & Desimone, 2012) and SC (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004) of the monkey brain could be distinguished based on their response properties. More specifically, some neurons in these areas responded to visual stimulation within their receptive field (visual neurons), whereas other neurons were found to predictively encode the execution of a saccade into their respective movement field (motor neurons) or exhibit both visual and motor related activity (visuomotor neurons). Based on this distinction it was demonstrated that the activity of motor neurons in the FEF and SC is not enhanced during covert shifts of visual attention (Ignashchenkova et al., 2004; Thompson et al., 2005), which suggests that the deployment of visual attention is not necessarily accompanied by motor-specific activity. Accordingly, neurons within the priority maps appear to reside along a continuum regarding their potential to influence the spatial parameters of visual attention and saccadic eye movements.

1.2.3 Theoretical frameworks

The wealth of empirical evidence linking visual attention and oculomotor programming has led to the proposal of different theoretical frameworks. Arguably the most influential theory on the coupling between attention and motor programming is the *premotor theory of attention* (Rizzolatti et al., 1987; Sheliga, Riggio, & Rizzolatti, 1994; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999), which suggests a very strict dependence of attentional orienting on oculomotor programming. It postulates that the neuronal signals underlying the guidance of visual attention arise from activity within the motor system, and that a shift of visual attention requires the programming of a motor command towards a corresponding location. In other words, visual attention is considered merely an epiphenomenon of motor programming, with shifts of attention being equivalent to motor programming without subsequent movement execution. Despite being supported by a variety of experimental findings, several studies revealing behavioral (Smith et al., 2012; Belopolsky & Theeuwes, 2012; Hanning et al., 2019) and neuronal (Ignashchenkova et al., 2004; Thompson et al., 2005; Gregoriou et al., 2012) dissociations between attentional and oculomotor mechanisms have challenged the premotor theory of attention. Consequently, some authors have proposed modified, less rigorous accounts of the premotor theory of attention as to reconcile an emerging controversy over the idea that visual attention is strictly contingent on motor processing (Smith et al., 2012; Belopolsky & Theeuwes, 2012).

A different account regarding the interplay between attention and motor programming has been proposed in the *visual attention model* (Schneider, 1995), which considers visual attention as a fundamental mechanism for both perception and action. As such, it builds on a classical functional dichotomization of the primate visual system into a ventral stream specialized for perceptual processing and a dorsal stream primarily involved in spatial computations for motor actions (Goodale & Milner, 1992; Milner & Goodale, 1993). Importantly, the visual attention model suggests that attention operates at an early level, that is before the division of the ventral and dorsal processing streams. This means that, once an object is attended, it can be thoroughly analyzed perceptually via enhanced ventral stream processing and its spatial parameters can be efficiently extracted in the dorsal stream as to program an appropriate motor action. Thus, according to the visual attention model, perceptual processes play a fundamental role for guiding attention and selecting the targets for upcoming movements.

Even though both the premotor theory of attention and the visual attention model suggest a tight coupling between perception and action, they imply a different causal structure. While the former considers visual attention a consequence of motor programming, the latter frames visual attention as a precursor of motor programming (Schneider & Deubel, 2002).

1.3 The interplay between visual attention, eye movements, and hand movements

So far, the coupling between visual attention and motor action has been discussed within the context of saccadic eye movements. However, attentional mechanisms have also been investigated with respect to the programming of more complex motor actions such as hand movements.

Psychophysical studies combining a manual movement task with a visual discrimination task consistently revealed that selective perceptual facilitation during movement preparation is not exclusive to the oculomotor system. Similar to saccades, visual processing was found to be selectively enhanced at the target of an upcoming reaching (Deubel, Schneider, & Paprotta, 1998; Deubel & Schneider, 2003; Rolfs, Lawrence, & Carrasco, 2013) or grasping movement (Schiegg, Deubel, & Schneider, 2003). Such attentional selection of manual movement targets was further confirmed in an electrophysiological study assessing event-related potentials (Baldauf & Deubel, 2009). The communality among the attentional dynamics preceding movements of the eye and the hand highlights the general role of visual attention for goal-directed motor action. Moreover, several studies argued for a fine-tuned coordination of eye and hand movements (Land, Mennie, & Rusted, 1999; Neggers & Bekkering, 2000; Johansson, Westling, Bäckström, & Flanagan, 2001; Land & Hayhoe, 2001; Neggers & Bekkering, 2001; Mennie, Hayhoe, & Sullivan, 2007). These studies demonstrated, for instance, that hand movements are typically preceded by spatially coinciding shifts of the gaze, which suggests that eye movements guide manual actions. Further, it was observed that the eyes typically fixate parts of objects which are currently being manipulated, implying that the oculomotor system facilitates efficient monitoring of manual actions.

Despite this apparent functional coupling between eye and hand movements at the behavioral level, the neuronal substrates underlying movement target selection in the two effectors can at least be partially dissociated in the macaque brain (Snyder, Batista, & Andersen, 1997; Snyder, Batista, & Andersen, 2000; Andersen & Buneo, 2002; Calton, Dickinson, & Snyder, 2002). While the SC, FEF, and LIP have been consistently linked to visual attention and saccadic eye movements (Bruce & Goldberg, 1985; Gnadt & Andersen, 1988; Schall & Hanes, 1993; Mazzoni, Bracewell, Barash, & Andersen, 1996; Dorris, Paré, & Munoz, 1997; McPeek & Keller, 2002; Bisley & Goldberg, 2003), the so-called *parietal reach region* (PRR) and the *anterior intraparietal area* (AIP) are known to establish specialized visuomotor transformation substrates for reaching and grasping movements of the hand (Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Batista & Andersen, 2001; Castiello, 2005; Scherberger & Andersen, 2007; Baldauf, Cui, & Andersen, 2008). A schematic depiction of this effector-specific functional division in the macaque brain is provided in **Figure 3**.

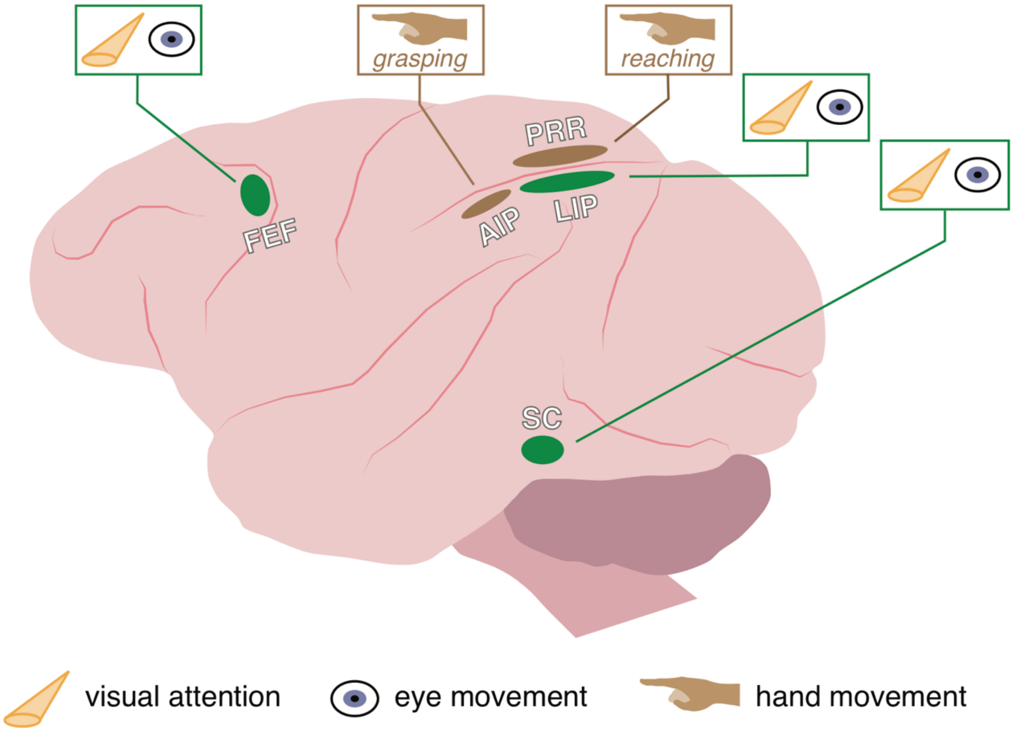

Figure 3. The functional division of eye and hand movement control.
Schematic illustration depicting central substrates underlying the control of eye and hand movements in the macaque brain (lateral view). Brain areas such as the subcortical superior colliculus (SC), the frontal eye fields (FEF), and the lateral intraparietal area (LIP) play an important role for saccadic eye movement programming and likewise guide visual attention. The parietal reach region (PRR) and the anterior intraparietal area (AIP) provide unique signals for the programming of reaching and grasping movements of the hand, respectively.

Recent psychophysical studies have addressed the question whether different effectors draw upon shared attentional resources for movement target selection (Khan, Song, & McPeek, 2011; Jonikaitis & Deubel, 2011; Hanning, Aagten-Murphy, & Deubel, 2018). However, despite similarly contrasting conditions requiring either a single eye or hand movement with conditions comprising the concurrent execution of eye and hand movements, these studies yielded contradictory results. Khan et al. (2011) reported that both effectors recruit a common attentional resource to which the oculomotor system has prioritized access when effector-specific movement targets are spatially dissociated. In contrast, Jonikaitis and Deubel (2011) as well as Hanning et al. (2018) found evidence in favor of independent, effector-unspecific attentional resources.

To resolve this controversy, a similar dual-task approach which allowed to assess the deployment of visual attention during the preparation of concurrent eye and hand movements was employed in the third study of this thesis *(Chapter 2.3)*. Importantly, as it has been demonstrated that saccade preparation interferes with the capacity to attend at locations other than the intended saccade target (Deubel & Schneider, 1996; Kowler et al., 1995; Hoffman & Subramaniam, 1995), this study further introduced a spatial cueing manipulation to systematically investigate the interaction between premotor attentional mechanisms in both effectors and the ability to exert voluntary attentional control.

1.4 Oculomotor competition and saccade averaging

So far, saccadic eye movements have been discussed as a central selection mechanism for the sake of efficient visual perception and goal-directed behavior. Each saccade, however, does not only provide a gateway to visual selection (via foveation), but also reflects the outcome of a selection process. In fact, as our visual environment typically entails a multitude of objects and thereby provides a wealth of potential saccade targets, efficient eye movement control appears to be inherently contingent upon selection (Deubel & Schneider, 1996). Despite the general capacity to exert voluntary control over saccadic eye movements, the oculomotor system is susceptible to systematic errors under certain circumstances. For instance, the execution of saccades towards an instructed target can be systematically delayed by the simultaneous occurrence of a salient visual event (distractor) in the opposite visual hemifield (the so-called *remote distractor effect*; Walker, Kentridge, & Findlay, 1995; Walker, Deubel, Schneider, & Findlay, 1997). Moreover, salient visual events which interfere with the current movement intention of the observer can even trigger reflexive saccades (commonly referred to as *oculomotor capture*; Theeuwes, Kramer, Hahn, & Irwin, 1998; Irwin, Colcombe, Kramer, & Hahn, 2000). While both of these phenomena generally highlight the influence of automatic bottom-up processes on oculomotor control, the following section focuses on another prominent phenomenon arising from oculomotor competition: *saccade averaging*.

The term saccade averaging – also known as *the global effect* or *center of gravity effect* – refers to the observation of systematic saccade endpoint deviations towards an intermediate location within a stimulus configuration consisting of multiple nearby objects (Findlay, 1982; Findlay & Walker, 1999; Vitu, 2008; Van der Stigchel & Nijboer, 2011). Corresponding saccades landing in between neighboring, competing objects (rather than precisely at a circumscribed target object) are called *averaging saccades*.

Early empirical evidence for saccade averaging was obtained in a study asking participants to move their eyes along the horizontal meridian towards a peripheral target which could either appear alone or together with nearby, irrelevant distractors

(Coren & Hoenig, 1972). The presence of distractors in the same hemifield as the target was found to systematically influence saccade amplitudes such that the eyes tended to land at the center of gravity of the overall stimulus configuration. Importantly, saccade endpoint deviations away from the target were found to decrease as the distance between a single distractor and the target was increased. Some years later, Findlay (1982) reported similar averaging tendencies of the eyes in response to the presentation of two peripheral stimuli. Furthermore, he observed that this effect was most pronounced at short latencies. These early studies already revealed two central properties associated with saccade averaging, namely stimulus competition within narrow space and speeded saccade execution. Note however, that, even though these studies used stimulus configurations in which the competing objects appeared at different eccentricities along the same angular axis, saccade averaging can also be observed for stimulus configurations in which equally eccentric objects are presented at different angles relative to eye fixation. In this case saccades tend to land at a location which corresponds to an intermediate angle relative to the angles of the competing objects (e.g., Ottes, Van Gisbergen, & Eggermont, 1984). Later studies consistently confirmed that saccade averaging is indeed rather specific to competition between objects within a restricted area. The spatial extent of this area, however, varied across different experiments reporting saccade averaging for an angular distance between competing objects ranging from 20° (Walker et al., 1997) to 30° (Ottes et al., 1984), or even somewhat beyond this range (Van der Stigchel, Heeman, & Nijboer, 2012; Van der Stigchel & Nijboer, 2013). Similarly, the latency dependence of saccade averaging was confirmed in later studies which demonstrated that averaging saccades occur most frequently at short saccade latencies (Ottes, Van Gisbergen, & Eggermont, 1985; Coëffé & O'Regan 1987; Edelman & Keller, 1998; Chou, Sommer, & Schiller, 1999). In addition to these spatial and temporal constraints, it was shown that saccade endpoints systematically vary as a function of the relative size (Findlay, 1982), intensity (Deubel, Wolf, & Hauske, 1984), and background dissimilarity (Deubel, Findlay, Jacobs, & Brogan, 1988) of nearby, competing stimuli. Consequently, accounting for the majority of the described properties, the saccade averaging phenomenon has been originally considered a rather automatic oculomotor response (Ottes et al., 1985) arising from a global visual integration process (Findlay, 1982). While this conception emphasizes the role of low-level visual properties and bottom-up processing, other authors demonstrated that spatial predictability of the saccade target reduces the occurrence of averaging saccades (Coëffé & O'Regan 1987; He & Kowler, 1989). This highlights that saccade averaging is not inevitable under conditions in which higher-level cognitive processes can effectively counteract bottom-up visual competition.

Importantly, despite the notion of a tight coupling between visual attention and saccadic eye movements, little is known about the perceptual correlates of saccade averaging. The first study of this thesis *(Chapter 2.1)* aimed to fill this gap via assessing the deployment of visual attention prior to the execution of averaging saccades (induced via the presentation of two nearby, potential saccade targets), and thereby gain novel insights into the relationship between visual attention and oculomotor control. Moreover, the second study *(Chapter 2.2)* elucidated how higher-level (i.e., top-down) processes affect both the spatio-temporal dynamics of visual attention and the accuracy of saccadic eye movements during episodes of competition between a saccade target and a nearby distractor (i.e., conditions which typically give rise to saccade averaging).

The neuronal correlates of saccade averaging have been most prominently investigated at the level of the SC. Early electrophysiological work showed that averaging saccades can be evoked via simultaneous microstimulation of two collicular sites in the monkey brain (Robinson, 1972; Schiller & Sandell, 1983). In line with these observations, various theoretical and computational models on the generation of saccadic eye movements have linked saccade averaging to the neuronal dynamics within a retinotopically organized priority map contained in the intermediate layers of the SC (Kopecz & Schöner, 1995; Findlay & Walker, 1999; Trappenberg, Dorris, Munoz, & Klein, 2001; Godijn & Theeuwes, 2002; Meeter, Van der Stigchel, & Theeuwes, 2010; Marino, Trappenberg, Dorris, & Munoz, 2012). These models typically propose that the collicular map integrates bottom-up and top-down signals from a distributed network of brain areas (Godijn & Theeuwes, 2002; Meeter et al., 2010; Marino et al., 2012). Neurons in the map have large and overlapping movement fields and encode possible target locations for upcoming eye movements (Sparks, Holland, & Guthrie, 1976; Findlay & Walker, 1999). A given saccade target object is therefore represented by a population of active collicular neurons, which can be thought of as a local activity peak at a retinotopically corresponding site in the map (Van der Stigchel & Nijboer, 2011). Accordingly, the appearance of multiple potential saccade targets (i.e., conspicuous objects in the visual field) will elicit several distinct activity peaks in the collicular map. This can, however, interfere with efficient saccade target selection because saccadic vectors are encoded in a collicular population code (Sparks et al., 1976; Van Gisbergen, Van Opstal, & Tax, 1987; Lee, Rohrer, & Sparks, 1988). While it is generally agreed upon that each collicular neuron contributes – proportional to its activity level – a fixed vectorial component (determined by its location in the map) to the subsequent saccade (Katnani, Van Opstal, & Gandhi, 2012), it has been discussed whether oculomotor structures decode activity in the SC via vector summation (Van Gisbergen et al., 1987; Goossens & Van Opstal, 2006) or vector averaging (Lee et al., 1988; Walton, Sparks, & Gandhi, 2005). Despite making slightly different predictions for the spatial metrics of saccades, both of these decoding schemes imply that efficient saccade target selection (i.e., precise saccadic control) requires that there is only one distinct, local activity peak in the collicular map at saccade onset. It has been suggested that competitive interactions among neuronal populations in the SC can account for this requirement (Godijn & Theeuwes, 2002; Meeter et al., 2010). Inhibitory connections among neuronal populations in the SC are thought to establish an effective winner-take-all mechanism which ensures the emergence of a single activity peak in the collicular map over time (Findlay & Walker, 1999; Marino et al., 2012) – see left panel of **Figure 4** for a schematic illustration. This means that competition among multiple potential saccade targets can typically be resolved efficiently such that the eyes will precisely move towards the designated target object encoded as the only remaining activity peak in the map. Crucially, these winner-take-all dynamics may only operate across distant locations in the map (i.e., long-range inhibition), rendering saccade target selection efficient when potential saccade targets appear at sufficiently remote locations, but not when occupying nearby locations in the visual field. In fact, adjacent neuronal populations are thought to mutually excite each other (i.e., local excitation) (Munoz & Istvan, 1998; Trappenberg et al., 2001; Marino et al., 2012). As a consequence, competition among neighboring potential saccade targets can remain unresolved because multiple peaks reside in the collicular map until the moment the saccade is executed (Port & Wurtz, 2003; Meeter et al., 2010; Van der Stigchel & Nijboer, 2011). The subsequent saccade vector will therefore roughly correspond to the vector obtained from a single peak located at an intermediate collicular site. Alternatively, some authors have suggested that two adjacent collicular activity peaks may in fact merge into a single, intermediate peak (Godijn & Theeuwes, 2002; Marino et al., 2012; Vokoun, Huang, Jackson, & Basso, 2014). Yet, in both cases saccade averaging will occur: The eyes will land at an intermediate location between the competing objects – see right panel of **Figure 4** for a schematic illustration. Indeed, both of these theoretical accounts (multiple adjacent peaks vs. emergent intermediate peak) are supported by empirical evidence obtained in electrophysiological studies which assessed collicular activity before visually guided averaging saccades. While Glimcher and Sparks (1993) reported evidence for a single peak of activity located in between the collicular sites encoding two nearby objects, Edelman and Keller (1998) observed that averaging saccades were preceded by two separate collicular activity peaks representing corresponding objects. Thus, it has remained a matter of debate whether the visuomotor transformation underlying the generation of averaging saccades (i.e., the transformation of two competing sensory representations into a single “corrupted“ motor command) occurs already at the level of the SC or in downstream oculomotor structures of the brainstem.

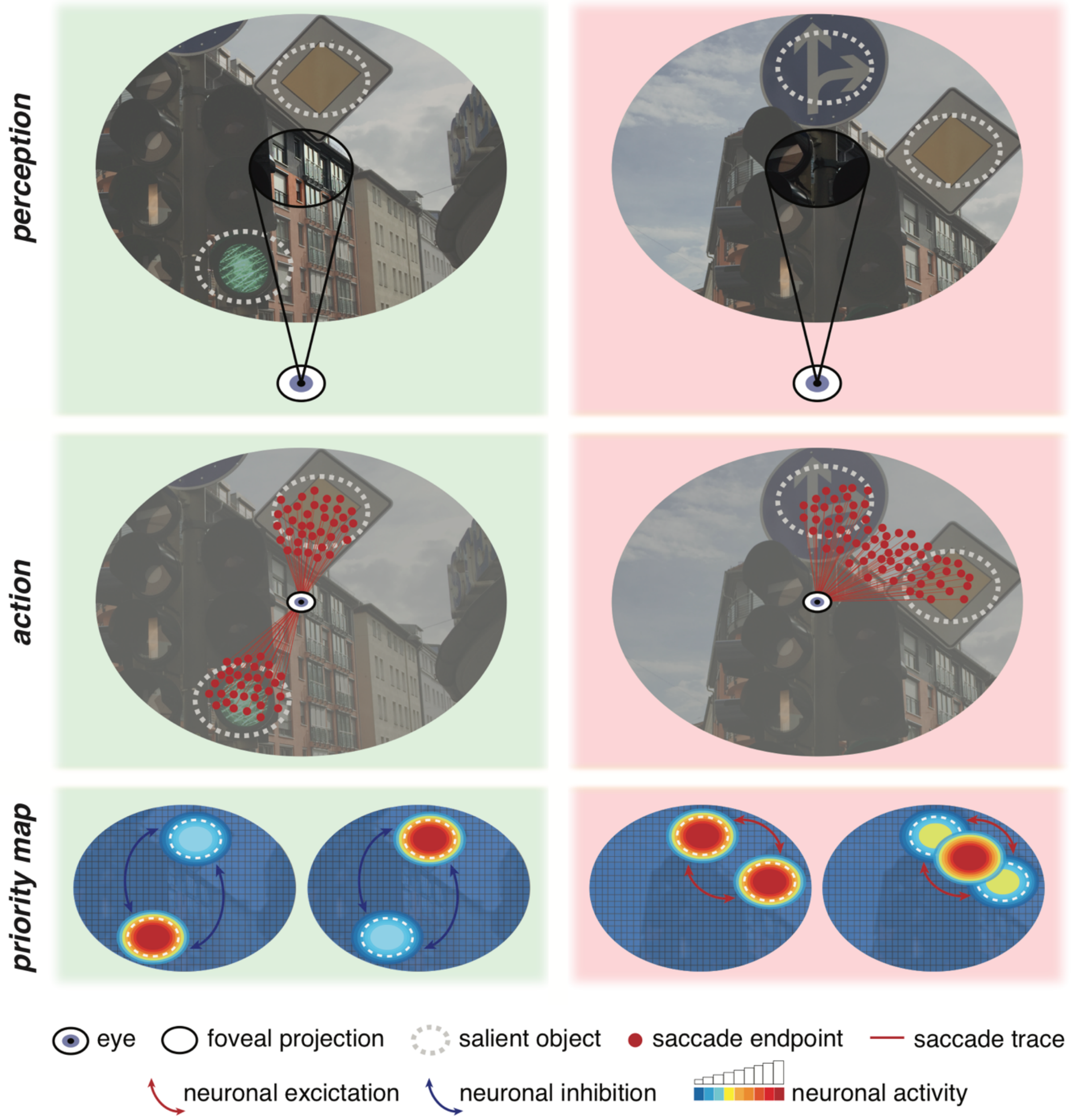

Figure 4. Oculomotor competition and the occurrence of averaging saccades.
Schematic illustration depicting the oculomotor (*action*) and neuronal (*priority map*) consequences arising from the presence of multiple (in this example two) salient objects which compete for saccade target selection in the visual field (*perception*). When two potential saccade targets (green light and yellow street sign) appear at distant locations in the visual field (left panel highlighted in light green), competition among neuronal populations encoding corresponding objects can be efficiently resolved – presumably via long-range inhibition – such that a single peak of activity emerges within the priority map. Thus, saccades typically land precisely at either one of the objects. However, when two objects (blue and yellow street signs) appear at nearby locations (right panel highlighted in light pink), competition among corresponding neuronal populations may not be efficiently resolved prior to movement onset – presumably owing to local excitation – such that the priority map either contains two distinct activity peaks or a merged, intermediate peak at the moment of movement onset. Consequently, the eyes will frequently land at and intermediate location between the two objects, i.e., saccade averaging. Note: The *perception* and *priority map* visualizations are highly simplified for the sake of illustration.

1.5 Thesis objectives

The following paragraphs briefly summarize the central objectives of the experimental studies conducted over the course of the present thesis.

The first study *(Chapter 2.1)* aimed at resolving whether presaccadic shifts of visual attention are obligatorily coupled to the saccade endpoint. A second main objective of this study was to understand how the spatial distribution of attentional resources prior to saccade onset relates to systematic variability in saccade endpoints. Both of these questions were addressed by means of a dual-task which allowed to assess localized visual sensitivity measures during the preparation of saccades which subsequently landed either accurately at one of two nearby saccade targets or erroneously in between these targets (i.e., averaging saccades).

The second study *(Chapter 2.2)* was designed to extend the insights of the first study by elucidating the influence of top-down control on the efficiency of attentional selection and the accuracy of saccadic eye movements. To this end, it was investigated how manipulations of spatial predictability and movement preparation time affect both the presaccadic deployment of visual attention and the distribution of saccade endpoints during episodes of competition between a saccade target and a nearby, task-irrelevant distractor.

The third study *(Chapter 2.3)* combined – within the same dual-task framework employed in the first two studies – variable motor tasks (requiring the execution of eye, hand, or combined eye and hand movements) with a spatial cueing paradigm. The main objective of this study was to examine how attentional mechanisms related to the preparation of visually guided actions interact with voluntary attentional control. Importantly, this study furthermore allowed to resolve whether targets for upcoming eye and hand movements are selected by a common attentional system or separate, effector-specific ones.

Finally, a methodologically oriented manuscript *(Chapter 2.4)* was compiled with the goal of providing a detailed guideline for psychophysical investigations concerning the link between visual attention and saccadic eye movement control (using the example of the dual-task employed in the first study).

2 Cumulative Thesis

The following section contains three peer-reviewed, published manuscripts *(Chapters 2.1, 2.2, and 2.4)* and one manuscript submitted for publication *(Chapter 2.3)*.

2.1 Visual attention is not deployed at the endpoint of averaging saccades

This manuscript has been published as:

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Author contributions:

Luca Wollenberg designed the study, co-programmed the experiment, collected, analyzed, interpreted, and visualized the data, and wrote the manuscript.

Heiner Deubel contributed to the study design, participated in interpreting the results, and commented on the manuscript.

Martin Szinte contributed to the study design, co-programmed the experiment, participated in interpreting and visualizing the data, and commented on the manuscript.

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SHORT REPORTS

Visual attention is not deployed at the endpoint of averaging saccades

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Abstract

The premotor theory of attention postulates that spatial attention arises from the activation of saccade areas and that the deployment of attention is the consequence of motor programming. Yet attentional and oculomotor processes have been shown to be dissociable at the neuronal level in covert attention tasks. To investigate a potential dissociation at the behavioral level, we instructed human participants to move their eyes (saccade) towards 1 of 2 nearby, competing saccade targets. The spatial distribution of visual attention was determined using oriented visual stimuli presented either at the target locations, between them, or at several other equidistant locations. Results demonstrate that accurate saccades towards one of the targets were associated with presaccadic enhancement of visual sensitivity at the respective saccade endpoint compared to the nonsaccaded target location. In contrast, averaging saccades, landing between the 2 targets, were not associated with attentional facilitation at the saccade endpoint. Rather, attention before averaging saccades was equally deployed at the 2 target locations. Taken together, our results reveal that visual attention is not obligatorily coupled to the endpoint of a subsequent saccade. Rather, our results suggest that the oculomotor program depends on the state of attentional selection before saccade onset and that saccade averaging arises from unresolved attentional selection.

Author summary

The premotor theory of attention postulates that spatial visual attention is a consequence of the brain activity that controls eye movement. Indeed, attention and eye movement share overlapping brain networks, and attention is deployed at the target of an eye movement (saccade) even before the eyes start to move. But is attention always deployed at the endpoint of saccades? Here, we measured visual attention before accurate saccades and before saccades that landed in between 2 targets (averaging saccades). While accurate saccades were associated with a selective enhancement of visual sensitivity at their endpoint, no such enhancement was found at the endpoint of averaging saccades. Rather, visual sensitivity was evenly distributed across the 2 saccade targets, suggesting that saccade

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Abbreviations: BTW, position in between the saccade targets; CTRL, control position; FEF, Frontal Eye Field; fMRI, functional magnetic resonance imaging; LIP, Lateral Intraparietal Cortex; MT, Middle Temporal Visual Area; SC, Superior Colliculus; ST_1, saccade target 1; ST_2, saccade target 2; V, Visual Area.

averaging arises from unresolved attentional selection. Overall, our results reveal that attention is not always coupled to the endpoint of saccades, arguing against a simplistic view of the premotor theory of attention at the behavioral level. Instead, we propose that saccadic responses depend on the state of attentional selection at saccade onset.

Introduction

To process information from our rich visual environment, we evolved with attentional mechanisms allowing us to discriminate which flow to account for and which to ignore [1,2]. For example, we can extract salient saccade targets from a cluttered visual scene to later examine their contents with precise foveal vision [3–6]. This link between attention and saccadic eye movements led researchers to propose that spatial visual attention is directly dependent on the oculomotor system [7,8], introducing what they called the “premotor theory of attention.”

This influential theory relies on 2 main hypotheses. The first hypothesis states that visual attention is operated by the oculomotor system itself. Indeed, overlapping neuronal activations have been observed in visual attention tasks involving the deployment of attention with (overt) or without (covert) eye movements in functional magnetic resonance imaging (fMRI) [9]. These activations include cortical and subcortical areas such as the Frontal Eye Field (FEF), the parietal cortex, and the Superior Colliculus (SC).

At the behavioral level, there is indeed evidence for a concurrent encoding of spatial attention and saccade programming [10]. For example, various studies demonstrated that visual attention, measured as a local improvement in visual sensitivity, is allocated to the saccade target before the eyes start to move [11,12]. Nevertheless, some other studies suggested that saccade preparation does not necessarily entail a shift of attention towards the saccade goal, casting some doubt in regard of the coupling between attention and oculomotor control [13–16].

The second hypothesis of the premotor theory of attention implies that the deployment of visual attention is always preceded by an activation of the oculomotor system. Under this hypothesis, covert attention involves the preparation of a saccade that is canceled before the eyes move. In line with this hypothesis, subthreshold microstimulation of the FEF or the SC, which did not systematically lead to a saccade, resulted in attentional benefits measured both behaviorally and electrophysiologically at the stimulated movement field position [17–20]. However, because microstimulation effects cannot be solely restricted to the motor cells within the stimulated areas, these results did not demonstrate that the deployment of visual attention is preceded by a premotor activation alone. Instead, it was shown that motor cells within FEF or SC stayed completely silent during a covert attention task [21–23], while visual and visuomotor cells displayed sustained attentional effects. In other words, attention is not always preceded by motor activity, at least not within these recorded oculomotor centers.

To shed light on this controversy and to test this second hypothesis at the behavioral level, one can imagine measuring visual sensitivity at the intended saccade goal and at the endpoint of the saccade. Under such conditions, measured sensitivity should correlate with the activity of both the visual and motor cells within oculomotor centers. Taking advantage of the fact that saccades tend to undershoot the target, Deubel and Schneider [12] found that attention was restricted to the intended saccade goal rather than to the saccade endpoint. However, using saccadic adaptation to decrease the saccadic gain, some authors found the exact opposite effect, with attention allocated to the adapted saccade endpoint rather than to the intended saccade goal [24,25]. Knowing that oculomotor centers have several overlapping large receptive fields within the range of these effects [26,27], it is hard to link these contradictory behavioral findings to the neurophysiology described above.

Here, we thus propose to use a paradigm leading to a larger spatial dissociation between the intended saccade goal and the saccade endpoint, such as the global effect [28–31]. Indeed, the global effect is associated with systematic and large saccade endpoint deviations towards the center of gravity of 2 saccade targets [28,32,33], or of a saccade target and a distractor [34,35], shown at 2 positions separated by up to 60° of rotation [34]. Although the global effect was originally described as reflecting a low-level averaging of neuronal activity (and therefore respective saccades are often called averaging saccades) within the oculomotor centers [28,36,37], different behavioral observations later suggested a dependency on higher-level attentional processes. First, it was shown that averaging saccades can be elicited by second- and third-order saccade targets [38,39], suggesting that the global effect cannot merely reflect low-level oculomotor processes. Next, it was shown that specifying the location [40,41], the identity [42,43], or the probability of a saccade target to appear at a certain location relative to a distractor [44] systematically reduced the occurrence of averaging saccades. Monkeys make averaging saccades when the FEF or the SC are simultaneously microstimulated at 2 sites [45–48] and when 2 targets are shown in close proximity [49,50]. At the neuronal level, it was first proposed that a single peak of motor cell activity associated with saccades ending in between 2 targets precedes an averaging saccade [51,52]. Later work suggested instead that averaging saccades follow 2 peaks of activity associated with saccades directed towards the 2 saccade targets [53,54]. Recently, Vokoun and colleagues [55] used voltage imaging of slices of rat SC to record population dynamics in response to dual-site electrical stimulation. They observed that the simultaneous stimulation of 2 nearby sites in the intermediate layers led to a merged peak centered in between them in the superficial layers. Moreover, they proposed that such merged activation feeds back into the visual system, leading to the perception of a target at the averaging saccade endpoint.

If this proposal of a feedback of merged activation from the superficial layers of the SC into the visual system was true, we would expect to find a presaccadic enhancement of attention at the endpoint of averaging saccades, a result that would be in line with the premotor theory of attention. Van der Stigchel and de Vries [56] directly tested this proposal, instructing participants to move their eyes towards a saccade target presented simultaneously with a distractor and measuring presaccadic attention at these positions as well as in between them. They observed both averaging saccades as well as saccades directed towards the target and the distractor, allowing them to compare the deployment of attention at the intended saccade goal and at the saccade endpoint. Unfortunately, they reported no main effect of the saccade landing direction as well as no interaction between the saccade landing direction and the position of their attention probes when analyzing visual discrimination performance as a function of the saccade endpoint. Therefore, contrary to many reports [11,12], the saccade landing position had no significant effect on the deployment of attention in their paradigm, preventing any conclusion about whether or not attention is deployed at the endpoint of averaging saccades.

Other studies suggested that attention is not necessarily allocated to the saccadic endpoint [11,44] or argued that saccades towards the center of gravity within extended target configurations are based on the computation of a central reference point via spatial pooling [57,58]. However, none of these studies measured visual attention at the averaging saccade endpoint to determine whether averaged oculomotor programs are associated with attentional averaging. Here, we measured visual attention at various locations in space, including the averaging saccade endpoint, in a free-choice saccade task that entailed the presentation of 2 nearby saccade targets. Our design therefore allowed us to investigate whether attention is allocated at the endpoint of averaging saccades. More specifically, given the spatial resolution of our design, we could distinguish the following 3 possible outcomes related to the deployment of visual attention before averaging saccades: (a) attention is deployed at the exact location of the saccade endpoint, (b) attention spreads across an extended area including the saccade endpoint, and (c) attention is deployed at 2 discrete saccade target areas flanking the saccade endpoint but not at the endpoint itself. We observed a presaccadic enhancement of visual sensitivity at the endpoint of accurate but not averaging saccades, ruling out an obligatory coupling of attention to the endpoint of a subsequently executed saccade (against [a]). Contrary to the idea of an extended spread of attention around the center of gravity, averaging saccades were associated with moderate enhancement of visual sensitivity at the 2 saccade targets (against [b]). Our results instead suggest that the oculomotor program depends on the state of attentional selection before saccade onset, with attention being deployed at the 2 discrete targets (favoring [c]) and saccade averaging resulting from uncompleted attentional selection.

Results

Our goal was to determine whether the presaccadic deployment of attention is obligatorily coupled to the saccade endpoint. To do so, we probed visual attention at various locations while participants prepared a saccade towards 1 of 2 potential saccade targets, presented either transiently or continuously and separated by an intertarget angular distance of either 90° or 30° (Fig 1A). Just before the saccade, a discrimination target was shown randomly across trials at 1 of the 2 potential saccade targets (ST_1 and ST_2), at the position in between the saccade targets (BTW), or at 1 of 21 equidistant control positions (CTRL).

Fig 1B shows the normalized frequency of saccade landing endpoints observed across participants within the 90° and 30° condition, irrespective of the duration of the saccade targets (i.e., transient and continuous combined). While saccades were equally distributed over the 2 saccade targets in the 90° condition (Fig 1B, top), a substantial proportion of saccades ended in between them in the 30° condition (Fig 1B, bottom). To further analyze our data, we looked

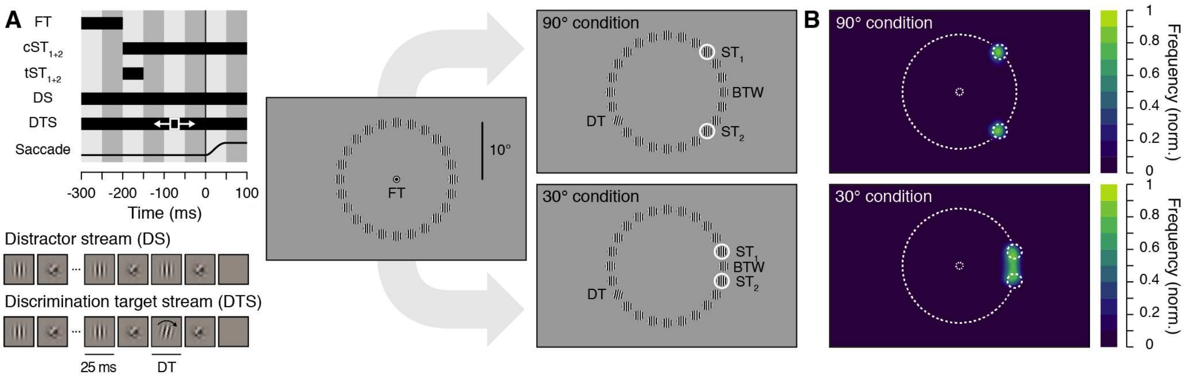

Fig 1. Experimental procedure and normalized saccade landing frequency maps. (A) Stimulus timing and display. Participants prepared a saccade from the fixation target to 1 of 2 potential saccade targets (ST_1 and ST_2), presented simultaneously at 2 randomly chosen stimulus streams with an intertarget angular distance of either 90° (top panels) or 30° (bottom panels). The saccade targets were either shown continuously (cST_{1+2}) or transiently (tST_{1+2}). Stimulus streams could either be distractor streams, composed of alternating vertical Gabors and masks (40 Hz), or discrimination target streams, which included the presentation of a brief discrimination target (25 ms)—a clockwise or counterclockwise tilted Gabor—shown between 75 and 175 ms after the saccade target onset. Participants saccaded towards 1 of the saccade targets and had to report the orientation of the discrimination target, appearing randomly at 1 of the 24 stimulus stream locations. Note that stimuli are sketched in order to increase their visibility. Actual stimuli match those shown in the stimulus streams depiction. (B) Normalized saccade landing frequency maps averaged across participants ($n = 10$) for the 90° (top) and 30° (bottom) conditions (collapsed across the transient and continuous saccade target presentation). BTW, position in between the saccade targets; cST_{1+2}, saccade targets continuously shown; DS, distractor stream; DT, discrimination target; DTS, discrimination target stream; FT, fixation target; ST_1, saccade target 1; ST_2, saccade target 2; tST_{1+2}, saccade targets transiently shown.

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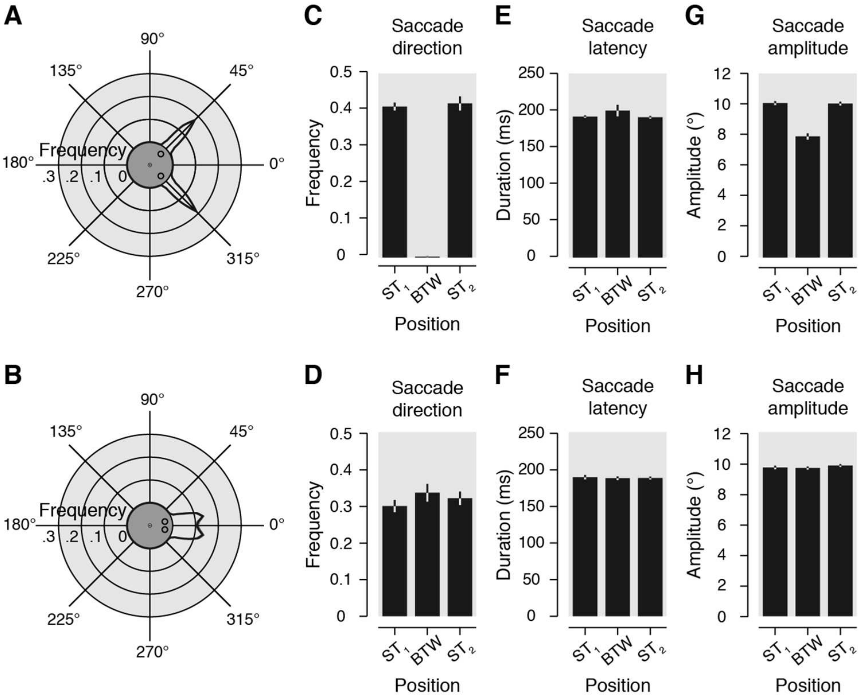

Fig 2. Saccade metrics. (A, B) Circular plots show the averaged frequency distribution of the saccade landing direction binned in evenly distributed angular sectors of 5˚, in the 90˚ (panel A) and 30˚ (panel B) conditions. Stimulus configuration is rotated as to align the 2 saccade targets symmetrically around the geometrical angle zero (see central insets). (C, D) Bar graphs illustrate averaged frequency of trials as a function of the saccade landing direction binned in 24 evenly distributed angular sectors of 15˚. Data are shown for the 3 positions of interest (ST_1, BTW, and ST_2) in the 90˚ (panel C) and 30˚ (panel D) conditions. (E–H) Averaged saccade latency (E, F) and amplitude (G, H) observed for the same 3 positions of interest in the 90˚ (panel E and G) and 30˚ conditions (panel F and H). All data are shown irrespective of the duration (continuously or transiently) of the saccade targets. Light gray areas and error bars represent SEM. Polar plot black lines and corresponding light gray areas show linear interpolation between data points. BTW, position in between the saccade targets; ST_1, saccade target 1; ST_2, saccade target 2.

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at the distribution of saccade landing directions either binned in evenly distributed angular sectors of 5˚ (Fig 2A and 2B) or 15˚ (centered on the 24 stimuli streams, Fig 2C and 2D). In the 90˚ condition (Fig 2C), 41.0% ± 1.0% of the saccades ended within the sector including ST_1 (most counterclockwise saccade target) and 41.8% ± 1.9% within the sector including ST_2 (most clockwise saccade target). Note that an average of 4.0% ± 0.9% of saccades ended within the sectors adjacent to the saccade targets. In the 30˚ condition (Fig 2D), 33.6% ± 2.4% of the saccades ended within the sector in between the 2 saccade targets (BTW), while 29.95 ± 1.6% of the saccades ended within the sector of ST_1 and 32.0% ± 1.8% within the sector of ST_2. Therefore, when participants had to select between 2 equidistant saccade targets separated by an angular distance of 30˚, they executed an averaging saccade (ending in the BTW sector) in about one-third of the trials. For further inspection, saccade endpoint distributions as a function of saccade latency are provided for each participant in S1 Fig. In order to determine potential differences between the 2 intertarget angular distance conditions (90˚ and 30˚), we first looked at saccade latencies and amplitudes. We found slightly longer saccade latencies (90˚: 192.2 ± 1.7 ms versus 30˚: 188.2 ± 2.2 ms; $p = 0.0012$) and larger amplitudes (90˚: 10.0 ± 0.1˚ versus 30˚: 9.7 ± 0.1˚; $p = 0.0002$) in the 90˚ as compared to the 30˚ condition.

Saccade latency did not differ as a function of the saccade landing position (ST_1, ST_2, or BTW) both in the 90˚ and 30˚ condition (all $p > 0.05$, Fig 2E and 2F). In the 90˚ condition, amplitudes of saccades towards ST_1 (10.1 ± 0.1˚) and ST_2 (10.0 ± 0.1˚) did not differ significantly from each other (ST_1 versus ST_2: $p = 0.7902$), whereas amplitudes of saccades towards BTW (7.9 ± 0.2˚) were significantly smaller than those of saccades towards ST_1 and ST_2 (both $p < 0.0001$) (see Fig 2G). In the 30˚ condition, amplitudes of saccades towards ST_1 (9.7 ± 0.1˚) and ST_2 (9.8 ± 0.1˚), as well as towards ST_1 and BTW (9.7 ± 0.1˚), did not differ significantly from each other (ST_1 versus ST_2: $p = 0.2216$; ST_1 versus BTW: $p = 0.5998$), whereas amplitudes of saccades towards ST_2 were significantly larger than those of saccades towards BTW (ST_2 versus BTW: $p = 0.0118$) (see Fig 2H). Note that the proportion of averaging saccades did not vary as a function of saccade latency. Comparing trials of the 30˚ condition separated in 2 equal groups of early (167.1 ± 1.8 ms) and late (209.3 ± 3.2 ms) saccade latencies, we found a comparable proportion of averaging saccades (early BTW: 35.1 ± 3.0% versus late BTW: 32.1 ± 2.2%; $p = 0.1632$). This effect is most likely the consequence of the instruction given to the participants to saccade as fast as possible, such that early and late averaging saccade latencies differed by less than 40 ms (early BTW: 168.2 ± 2.0 ms versus late BTW: 207.4 ± 3.1 ms; $p < 0.0001$). However, we found that the mean absolute saccade endpoint deviation relative to the BTW location slightly increased as a function of saccade latency (see A-B in S2 Fig and A-B in S2 Fig for individual participant data for both the 90˚ and 30˚ conditions). Thus, saccade averaging was more pronounced for short-latency saccades. Overall, for each intertarget angular distance, we observed either no differences or only some nonsystematic differences of a few milliseconds and a few minutes of arc. Although saccade latencies and amplitudes did not differ much between these conditions, the saccade landing-direction distributions reflect 2 distinct oculomotor modes as a function of the intertarget angular distance. Saccades were mostly accurate in the 90˚ condition, whereas we observed both accurate and averaging saccades in the 30˚ condition.

Our paradigm allowed us to measure both the oculomotor behavior and the presaccadic allocation of attention through the presentation of a discrimination target at 1 of 24 possible positions. We first verified that the presentation of the discrimination target itself did not systematically influence oculomotor behavior. We did not find any differences with respect to saccade latency and amplitude when comparing trials with and without the presentation of a discrimination target (3.5% of trials were without discrimination target, both $p > 0.05$). This result validates that the distractor streams and, in particular, the presentation of a discrimination target did not bias the deployment of attention. Fig 3A and 3B shows visual sensitivity as a function of the discrimination target position rotated as to align the 2 saccade targets around the geometrical angle zero in both the 90˚ (Fig 3A) and 30˚ (Fig 3B) condition. Irrespective of the duration of the saccade targets, we found higher sensitivity for discrimination targets shown at the saccade targets than at the control positions (corresponding to the average across all positions except for ST_1, ST_2, and BTW) in both the 90˚ (ST_1: d' = 2.2 ± 0.3 versus CTRL: d' = 0.3 ± 0.1, $p < 0.0001$; ST_2: d' = 2.2 ± 0.4 versus CTRL, $p < 0.0001$; ST_1 versus ST_2, $p = 0.8964$; Fig 3A) and the 30˚ (ST_1: d' = 2.2 ± 0.3 versus CTRL: d' = 0.3 ± 0.1, $p < 0.0001$; ST_2: d' = 2.1 ± 0.3 versus CTRL, $p < 0.0001$; ST_1 versus ST_2, $p = 0.6026$; Fig 3B) condition. These effects contrast with the low sensitivity observed for discrimination targets shown in between the saccade targets (BTW) in the 90˚ (BTW: d' = 0.2 ± 0.1 versus ST_1, $p < 0.0001$; BTW versus ST_2, $p < 0.0001$) and especially in the 30˚ (BTW: d' = 0.6 ± 0.2 versus ST_1, $p < 0.0001$; BTW versus ST_2, $p < 0.0001$) condition.

Thus, despite the fact that saccades landed in between the saccade targets in a third of the trials in the 30˚ condition, the overall sensitivity at this position stayed rather low. One should, however, note that sensitivity was still increased at this position compared to the control

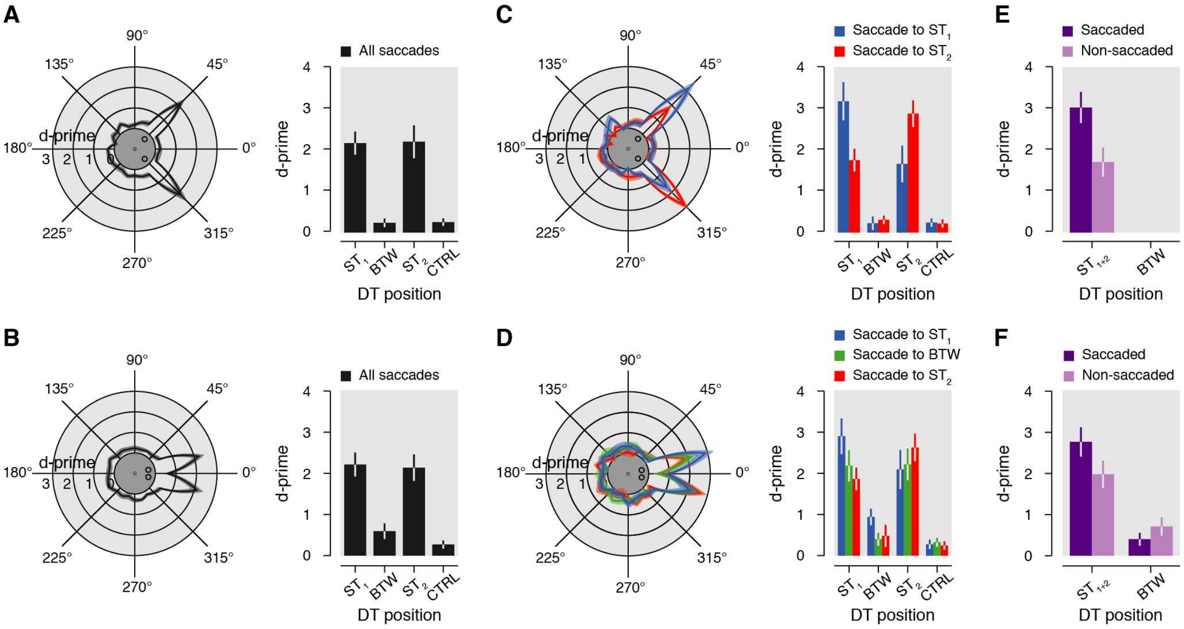

Fig 3. Visual sensitivity. (A, B) Circular plots show averaged visual sensitivity (d') as a function of the DT position in the 90° (panel A) and 30° (panel B) conditions, irrespective of the duration of the saccade targets and across all saccade directions observed. Bar graphs illustrate visual sensitivity for 4 positions of interest (ST_1, BTW, ST_2, CTRL). (C, D) Visual sensitivity as a function of the DT position relative to the saccade landing direction in the 90° (panel C) and 30° (panel D) conditions, irrespective of the duration of the saccade targets (blue: saccade to ST_1; green: saccade to BTW; red: saccade to ST_2). For each saccade direction, we took the average sensitivity for each discrimination target location. For example, the blue line plots visual sensitivity when saccades were made towards ST_1 and the discrimination target was either at ST_1 (+15° on the polar plot), BTW (15° counterclockwise to ST_1; 0° on the polar plot), or ST_2 (30° counterclockwise to ST_1; +345° on the polar plot), and so on. (E, F) Bar graphs illustrate sensitivity observed for DT shown at the saccaded (purple: e.g., DT at ST_1 and saccade to ST_1) and the nonsaccaded (light purple: e.g., DT at ST_1 and saccade to ST_2 or BTW) positions in the 90° (panel E) and the 30° (panel F) conditions. Conventions are as in Fig 2. BTW, position in between the saccade targets; CTRL, control position; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.

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positions in the 30° condition (30°: BTW versus CTRL, $p = 0.0010$), whereas this was not the case in the 90° condition (90°: BTW versus CTRL, $p = 0.7732$). On the other hand, such slight facilitation observed in between the saccade targets in the 30° condition relative to the control positions was only observed for trials in which the targets were shown transiently (BTW: d' = 0.8 ± 0.2 versus CTRL: d' = 0.3 ± 0.1, $p < 0.0001$) but not continuously (BTW: d' = 0.5 ± 0.2 versus CTRL: d' = 0.3 ± 0.0, $p = 0.10880$). It is important to note that the discrimination target temporally overlapped with the saccade targets in the continuous but never in the transient condition. The observed difference between the 2 conditions therefore suggests that the appearance of a discrimination target at BTW was masked by the continuous presentation of the saccade targets. Altogether, the results above demonstrate that presaccadic attention was mainly allocated towards the saccade targets, and to a much smaller extent towards the position in between. This last result, however, cannot be attributed to a large spread of attention extending to more than 1 of the tested directions because we did not observe a consistent benefit at the 2 other positions adjacent to the saccade targets in the 30° condition ($ST_1 + 15°$: d' = 0.4 ± 0.1 versus CTRL: d' = 0.3 ± 0.1, $p = 0.0914$; $ST_2 - 15°$: d' = 0.4 ± 0.1 versus CTRL, $p = 0.0336$; here, CTRL excludes $ST_1 + 15°$ and $ST_2 - 15°$, respectively, in addition to ST_1, ST_2, and BTW) nor at the 4 adjacent positions of the saccade targets in the 90° condition ($ST_1 \pm 15°$: d' = 0.3 ± 0.1 versus CTRL: d' = 0.2 ± 0.1, $p = 0.5742$; $ST_2 \pm 15°$: d' = 0.3 ± 0.1 versus

CTRL, $p = 0.3200$; here, CTRL excludes $ST_1 \pm 15^\circ$ and $ST_2 \pm 15^\circ$, respectively, in addition to ST_1, ST_2, and BTW).

At that stage, one cannot exclude the possibility that attention is always drawn towards the saccade endpoint before both accurate and averaging saccades because we found higher sensitivity for both the saccade targets—and, in the 30° condition, also for the position in between them—compared to the control locations. Although we found higher sensitivity at the saccade targets than in between them, this may just reflect the combined effect of the saccade preparation and the presence of visual cues (the saccade targets themselves). To estimate the effect of saccade preparation, we thus needed to specify our results depending on where the saccade ended within each trial. To do so, we redefined the position of the discrimination targets relative to the saccade direction. Fig 3C and 3D shows visual sensitivity as a function of the discrimination target position relative to the saccade direction. We found higher sensitivity for discrimination targets shown at the saccade targets when compared to the position in between them or to the control positions in both the 90° and 30° conditions, for trials in which accurate saccades were made towards ST_1 (all $p < 0.0001$) or ST_2 (all $p < 0.0001$). The same effects were found for averaging saccades in the 30° condition (all $p = 0.00010$). In addition to the facilitation effect of the saccade target presentation, we found that, irrespective of the intertarget distance (90° or 30°), sensitivity at ST_1 was improved when an accurate eye movement was made towards ST_1 (90°: ST_1: d' = 3.2 ± 0.5 versus ST_2: d' = 1.7 ± 0.4, $p < 0.0001$ [see blue lines and bars in Fig 3C and 3D]; note that in the 30° condition, sensitivity at ST_1: d' = 2.9 ± 0.4 was only marginally superior to those observed at ST_2: d' = 2.1 ± 0.5, $p = 0.0740$). The same selective improvement was observed at ST_2 before the execution of accurate saccades towards it (90°: ST_2 versus ST_1, $p < 0.0001$; 30°: ST_2 versus ST_1, $p = 0.0002$ [see red lines and bars in Fig 3C and 3D]). In particular, preparing an accurate eye movement towards 1 of the 2 saccade targets improved sensitivity when comparing trials in which the discrimination target was shown at the saccaded location (e.g., DT at ST_1 and saccade made towards ST_1) to trials in which the discrimination target was shown at the same position when it was not the saccaded position (e.g., DT at ST_1 and saccade landing at ST_2 or BTW) in both the 90° (Fig 3E; ST_{1+2} saccaded: d' = 3.0 ± 0.4 versus ST_{1+2} nonsaccaded: d' = 1.7 ± 0.4, $p < 0.0001$) and the 30° (Fig 3F; ST_{1+2} saccaded: d' = 2.7 ± 0.4 versus ST_{1+2} nonsaccaded: d' = 2.0 ± 0.3, $p = 0.0080$) condition. Crucially for averaging saccade trials, for which the intended saccade goal (ST_1 or ST_2) and the saccade endpoint (BTW) were dissociated (see green lines and bars in Fig 3D), we found a rather low sensitivity for discrimination targets shown in between the saccade targets (BTW: d' = 0.4 ± 0.2), highly reduced when compared to discrimination targets shown at the saccade targets (ST_1: d' = 2.2 ± 0.4 and ST_2: d' = 2.2 ± 0.4, both $p < 0.0001$). Furthermore, and contrary to above (Fig 3B), it was not different from the sensitivity gathered across the control locations (CTRL: d' = 0.3 ± 0.1, $p = 0.4026$), both when the saccade targets were shown transiently or continuously (both $p > 0.05$). Thus, contrary to accurate saccades, the execution of averaging saccades did not lead to any improvement at the saccade endpoint. Moreover, a visual inspection of sensitivity as a function of the saccade latency shows a relative independence of these measures, suggesting that, irrespective of the saccade latency, attention was not deployed at the averaging saccade endpoint (see C-D in S2 Fig and A-B in S4 Fig for individual participant data in the 90° and 30° conditions). Visual sensitivity was significantly reduced at the intermediate location (BTW) before averaging saccades compared to saccades that landed at 1 of the saccade targets (Fig 3F; BTW saccaded: d' = 0.4 ± 0.2 versus BTW nonsaccaded: d' = 0.7 ± 0.2, $p < 0.0001$). This sensitivity reduction can, however, be mainly attributed to a masking effect of the continuous presentation of the saccade targets (BTW saccaded: d' = 0.3 ± 0.3 versus BTW nonsaccaded: d' = 0.7 ± 0.2, $p = 0.0088$) because it was not found for saccade targets presented transiently (BTW saccaded: d' = 0.7 ± 0.2 versus BTW nonsaccaded: d' = 0.7 ± 0.3, $p = 0.9664$).

These findings demonstrate, contrary to what is predicted by the premotor theory of attention, that the preparation of averaging saccades does not lead to a deployment of attention at the corresponding saccade endpoint. Instead, we found that averaging saccades were associated with an equal distribution of attention towards the 2 saccade targets (ST_1: d' = 2.2 ± 0.4 versus ST_2: d' = 2.2 ± 0.4, $p = 0.8402$). One interpretation of these effects could be that averaging saccades result from an unsuccessful or at least uncompleted presaccadic attentional selection among the 2 saccade targets, with resources equally distributed between them. On the other hand, it is possible that, despite landing in between the targets, presaccadic attentional selection was successful before averaging saccades but directed half of the time towards the most clockwise saccade target and half of the time towards the most counterclockwise saccade target. If this were the case, across trials, one would also expect to find an equal and moderate enhancement of sensitivity for discrimination targets shown at the saccade targets.

To disentangle these 2 interpretations, we analyzed trials in which a corrective saccade followed the execution of an averaging saccade. We reasoned that if averaging saccades resulted from a successful trial-by-trial presaccadic attentional selection of 1 of the 2 saccade targets, they should be followed by corrective saccades directed equally often towards both targets. Moreover, they should be associated with an attentional benefit at the goal of the corrective saccades. Contrary to these predictions, we observed corrective saccades in only 48.1% ± 5.8% of the averaging saccade trials. Corrective saccades were not all clearly directed towards the saccade targets (see A-B in S5 Fig), ending either in the angular sector of the most counterclockwise saccade target (ST_1: 48.3% ± 3.1% of all the corrective saccades following an averaging saccade), the most clockwise saccade target (ST_2: 38.3% ± 2.5%), or in between them (BTW: 11.9% ± 2.8%). They were, moreover, not equally often directed towards each of the saccade targets (ST_1 versus ST_2, $p = 0.0288$), probably reflecting a bias of our participants. As shown in C in S5 Fig, we did not find any significant benefit at the endpoint of the corrective saccades following an averaging saccade, when comparing trials in which discrimination targets were shown at the endpoint of the corrective saccade (ST_{1+2} correctively saccaded: d' = 2.8 ± 0.5) to trials in which a discrimination target was shown at the same position when it was not the endpoint of the corrective saccade (ST_{1+2} correctively nonsaccaded: d' = 2.5 ± 0.8, $p = 0.68300$). Moreover, no significant benefit could be found when the corrective saccades following an averaging saccade ended still in between the saccade targets (BTW correctively saccaded: d' = 0.7 ± 1.1 versus BTW correctively nonsaccaded: d' = −0.1 ± 0.6, $p = 0.4698$). Taken together, these results suggest that averaging saccades result from an unsuccessful or uncompleted presaccadic attentional selection among the 2 saccade targets.

Finally, we wanted to exclude the possibility that the poor discrimination performance at the endpoint of averaging saccades was a result of the rather coarse saccade direction binning used in our analysis (±7.5° of rotation around ST_1, BTW, ST_2, and the distractor locations). We chose this binning procedure to end up with 24 equal saccade direction bins centered on the locations at which we measured visual sensitivity. Nevertheless, one might argue that we thereby classified a substantial proportion of saccades as averaging saccades (landing within the BTW bin) despite the possibility that they were actually biased towards 1 of the saccade targets and landed in the outer areas of the bin. To validate our analysis, we analyzed visual sensitivity as a function of the saccade direction using smaller bins (±2.5°). As evident in S6 Fig, in which we contrast the data for these 2 binning procedures, the smaller binning did not systematically alter our results. Crucially, we still found low visual sensitivity at BTW even for the proportion of saccades landing precisely at the most central bin (i.e., within ±2.5° around the center of BTW).

Discussion

We observed a clear oculomotor dissociation between trials in which 2 equidistant saccade targets were shown at 2 different angular distances from each other. While only accurate saccades were found for an intertarget angular distance of 90˚, we observed both accurate and averaging saccades when the same targets were separated by 30˚. Combined with a measure of presaccadic visual sensitivity, this dissociation allowed us to determine the influence of saccade preparation on the deployment of attention when the intended saccade goal and the saccade endpoint were spatially associated (accurate saccades) or clearly dissociated from each other (averaging saccades). Accurate saccades were associated with a strong and systematic presaccadic enhancement of visual sensitivity at the saccade endpoint when compared to the nonsaccaded locations for intertarget angular distances of both 90˚ and 30˚. In contrast, we did not observe a presaccadic enhancement of visual sensitivity at the endpoint of averaging saccades. Rather, averaging saccades were associated with an equal deployment of attention at the 2 saccade target locations. Our corrective saccade analysis indicated that this result cannot be explained by a trial-by-trial presaccadic attentional selection of 1 of the 2 saccade targets. Overall, these effects rule out the proposal that the deployment of attention is strictly derived from the upcoming oculomotor program. Rather, they reflect a spatial dissociation between the deployment of visual attention and the averaging saccade endpoint. More specifically, these results rule out an account in which attention is precisely allocated to the saccade endpoint (alternative [a] in Introduction) or spreads over an extended region including the saccade endpoint before averaging saccades (alternative [b] in Introduction). Our data instead favor an account in which attention is equally allocated at 2 discrete saccade target locations before averaging saccades (alternative [c] in Introduction). Contrary to the idea that the activation of the oculomotor system precedes spatial attention, we propose that the oculomotor program depends on the state of attentional selection before the saccade, with averaging saccades arising from an uncompleted attentional selection process.

Findlay [28] referred to the "global effect" as the phenomenon of directing the eyes towards the center of gravity of 2 presented targets [29]. To his view, this phenomenon reflects a coarse or global processing of a visual scene before rapidly generated eye movements. His account thus predicts that in our experiment, visual sensitivity should be coarsely distributed over the 2 saccade targets as well as over their adjacent locations before the execution of averaging saccades. Our precise measure of presaccadic visual sensitivity allowed us to determine the spatial specificity of attentional deployment during saccade preparation. Contrary to the notion of a global processing (including the locations at the saccade targets and in between) before averaging saccades, we observed a precise allocation of attention limited only to the saccade targets (limited to at least approximately 2.6˚, the distance between 2 of our adjacent stimuli). Therefore, before an averaging saccade, the visual system indeed seems to have precise access to the saccade target configuration, reflecting an enhancement of local rather than global visual information processing [59]. Such a discontinuous deployment of attention was also found in various tasks entailing the presentation of multiple targets [60–62]. Our results can also rule out other models of averaging saccades based solely on low-level oculomotor processing [36,37,63]. We report here that when an accurate saccade is prepared towards 1 of 2 identical saccade targets, the subsequent movement correlates with an attentional benefit at the saccade endpoint, whereas averaging saccades resulted in the absence of a selective attentional benefit at 1 of the 2 targets as well as in between them (i.e., at the saccade endpoint). In this regard, our results match with previous studies showing a reduction in the occurrence of averaging saccades when attentional selection of the saccade goal is made easier by specifying its location or its identity [40–44]. Similarly, a model relying on attentional selection could also explain why averaging saccades are less often observed in delayed saccade tasks [40,64], as they also give more time for the attentional selection to complete [43]. Early studies have often reported that averaging saccades are associated with faster saccade latencies as compared to accurate saccades [28,34]. Yet, recently, Weaver, Zoest, and Hickey [65] proposed that the spatial and temporal components of saccade programming are relatively independent from each other. They argued that attentional mechanisms can affect oculomotor behavior only when acting upon it before the onset of the movement. It might well be that our instructions to saccade as fast and as accurately as possible reduced the saccade latency range and thereby reduced potential differences between the latencies of accurate and averaging saccades. Furthermore, given that participants were engaged in a dual task, the attentional task might have slowed down saccade execution, leading to averaging saccades even at longer latencies. We propose that the type of saccade executed on a given trial was determined by the speed at which attentional selection was processed. Accordingly, accurate saccades were presumably executed whenever attentional selection of a target was readily resolved before saccade onset.

Another account of the global effect is that averaging saccades reflect a time-saving strategy [40], in which an averaging saccade followed by a correction movement allows for faster oculomotor action than a deliberately delayed accurate saccade. Given that participants saccaded accurately towards one of the targets with a similar latency as found for averaging saccades in two-thirds of the trials in our paradigm, our results speak against such a strategy. Although we observed some corrective saccades that ended nearby the saccade targets and therefore increased the accuracy of initial averaging saccades, they came with a cost of about 200 ms, rendering such strategy inefficient. Moreover, if participants would have strategically planned 2 successive saccades (an averaging saccade followed by a corrective saccade), we would expect to find attentional benefits at both saccade endpoints as reported in sequential saccade tasks [62,66]. Contrary to this prediction, we found neither an attentional enhancement at the endpoint of averaging saccades nor at the endpoint of corrective saccades compared to the positions not reached by corrective saccades.

Therefore, our results argue against earlier accounts of the global effect and propose that averaging saccades reflect a compromise between the dynamics of attentional selection and the instructions to move the eyes as fast as possible. Our proposal is based on the results of a combined measure of visual attention and averaging saccades. Similar to a previous report [56], we found an overall enhancement of visual sensitivity at the 2 saccade targets, when the data were not split depending on the saccade direction. In order to conclude on the deployment of attention before averaging saccades, however, one needs to specify visual sensitivity depending on the saccade direction. Crucially, and contrary to Van der Stigchel and de Vries [56], we indeed found an influence of the saccade direction (i.e., endpoint) on the allocation of attention when taking into account saccade direction. Within a paradigm producing both accurate and averaging saccades, we observed a presaccadic shift of attention [11,12], reflected by selectively enhanced sensitivity at the endpoint of accurate saccades. The replication of this presaccadic attention effect comes as a prerequisite to drawing conclusions on the effect of averaging saccades, for which, instead, we found no attentional benefit at the saccade endpoint. Van der Stigchel and de Vries [56] concluded that there is no attentional shift towards the endpoint of averaging saccades. However, they also reported no main effect of the saccade landing direction as well as no interaction between the saccade landing direction and the position of their attention probes when they analyzed their data as a function of the saccade endpoint. Their results are therefore inconclusive, or even speak in favor of an attentional global effect. Moreover, when we combined all trials irrespective of the saccade direction, we found a slight increase of sensitivity at the position in between the 2 potential saccade targets when they were presented transiently but not when they were presented continuously. Because Van der

Stigchel and de Vries [56] used a continuous presentation of a saccade target and a distractor, their results most likely reflect a masking effect of their stimuli on the discrimination target rather than an absence of attentional modulation. Here, we clearly dissociated attention allocated to the intended saccade goal from attention allocated to the endpoint of the saccade and found no benefit at the averaging saccade endpoint. This result is theoretically consistent with the idea that attention is not restricted to the endpoint of a saccade [11,44] and provides behavioral evidence against the main hypothesis of the premotor theory of attention, which postulates that the deployment of visual attention is derived from oculomotor programming [7,8].

We illustrate our results in a theoretical framework (Fig 4), inspired by both behavioral and neurophysiological findings, linking visual attention and oculomotor programming [67]. This theoretical framework neither provides a strict model nor a computational framework. It aims at putting our results in the context of the current view on saccade programming and yielding new testable predictions. We propose that our attentional effects rely on a top-down modulation [5,19] of feature-selective areas of the visual cortex by the priority maps [68]. Initially, the onsets of the saccade targets strongly activate neurons with corresponding receptive fields within columns of the feature and priority maps (Fig 4A). Their activity will then decay until the saccade target-selection process begins. We propose that, before an accurate saccade, one of the saccade targets is selected, such that oculomotor cells centered on the saccaded location become more active in comparison to those encoding the nonsaccaded target location (Fig 4B). Because our 2 targets were physically identical, saccade target selection probably occurs within the priority maps and propagates via a top-down mechanism to the corresponding feature map columns [5,69–71]. Oculomotor cells within the priority maps are connected to the areas of the brainstem circuitry controlling the horizontal (e.g., pons and medulla) and vertical (e.g., rostral midbrain) components of an eye movement [72,73]. Given that only 1 saccade can be executed at a time, a winner-takes-all integration of the motor output [47,74,75] from the priority maps is typically assumed such that the most active population will determine the subsequent saccade vector. The exact nature of this integration is, however, beyond the scope of this study. Thus, in our framework, an accurate saccade towards the selected saccade target (i.e., the saccade target that is represented as the most active population at the level of the priority maps) is triggered by the saccade generator, and the activity state within the feature maps leads to higher sensitivity at the saccade endpoint before the eyes start to move (Fig 4B).

Following the same rationale, we propose that averaging saccades arise from an unresolved saccade target-selection process. Given the behavioral nature of our data, we can only speculate about the neural correlates of averaging saccades at the level of the priority maps in this experiment. We will, however, discuss our results in the light of 2 alternative accounts concerning the representation of averaging saccades at the level of the SC. While Edelman and Keller [54] found evidence for a bimodal distribution of collicular activity before averaging saccades at express latencies, an earlier study by Glimcher and Sparks [52] argued for an intermediate unimodal distribution in case of regular-latency averaging saccades.

Because averaging saccades were executed at regular latencies in this experiment, they might indeed have been associated with a unimodal distribution of activity at an intermediate collicular site (early oculomotor selection—Fig 4C) at saccade onset. According to this view, averaging saccades were initially reflected by 2 equally enhanced collicular populations coding for the 2 saccade targets. This bimodal distribution of activity propagates to the feature maps, leading to an equal enhancement of visual sensitivity at the 2 saccade targets. However, the initial bimodal collicular activity distribution then progresses into a unimodal distribution centered at an intermediate collicular site to subsequently allow for the execution of a single saccade. Such a scenario is in line with evidence from a recent study performing dual-site electrical stimulation in the intermediate layers of the SC [55]. If the absence of attentional

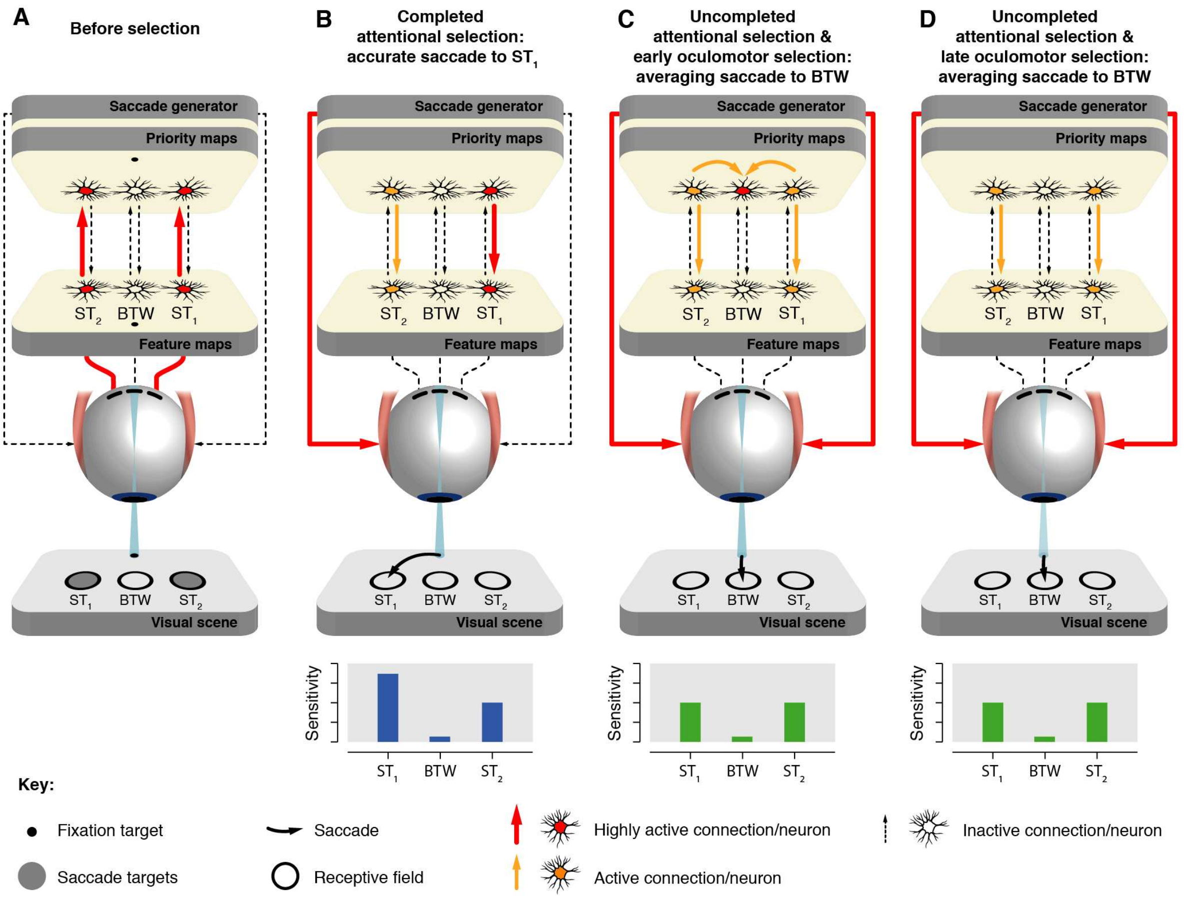

Fig 4. Attentional selection determines saccade endpoint. Two nearby saccade targets (gray dots) are flashed in the periphery from the fixation target and projected onto the retina, triggering a cascade of bottom-up (upward arrows) and top-down (downward arrows) processes throughout the visual processing hierarchy. Colors of the neurons and arrows indicate the level of activation. Each retinal projection connects to a specific neuron (in fact, a population of neurons) in retinotopic feature maps (V1–V4, MT). Feature map neurons, in turn, are linked to priority maps (FEF, LIP, SC). Priority map activity is later integrated by the saccade generator (brainstem) driving the extra-oculomotor muscles. Note that the priority maps and the saccade generator are distinct components within the processing hierarchy. The data panels show the predicted sensitivity at the saccade targets (ST_1 and ST_2) and in between them (BTW), and curved black arrows show the predicted saccade path. (A) Before attentional selection, ST_1 and ST_2 neuronal columns are highly activated by bottom-up connections driven by the saccade target onset. (B) Following a decay in the activity of both ST_1 and ST_2 neuronal columns, a completed attentional selection leads to a high activation of either ST_1 or ST_2 neurons in the priority maps (in this example, ST_1 is selected), propagating via top-down connections to the feature maps. This leads to a presaccadic enhancement of sensitivity at the selected target and subsequently to an accurate saccade towards it (in this example, towards ST_1). (C, D) Uncompleted attentional selection leads to an equal and moderate presaccadic sensitivity enhancement at the saccade targets, but not in between. Subsequently, the bimodal collicular activity distribution merges into a unimodal distribution around the intermediate collicular site (panel C) or remains bimodal and is later integrated by the saccade generator (panel D). In either case, an averaging saccade is executed towards the intermediate location (BTW). BTW, position in between the saccade targets; DT, discrimination target; FEF, Frontal Eye Field; LIP, Lateral Intraparietal Cortex; MT, Middle Temporal Visual Area; SC, Superior Colliculus; ST_1, saccade target 1; ST_2, saccade target 2; V, Visual Area.

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deployment at the averaging saccade endpoint observed here was indeed associated with a single active population located at an intermediate site of the SC, our results would clearly refute the premotor theory of attention.

Alternatively, averaging saccades may result from a bimodal collicular activity distribution at saccade onset (late oculomotor selection—Fig 4D). In this case, the collicular sites of enhanced activity would match with the observed attentional benefits at the 2 saccade targets, and oculomotor averaging across the active collicular populations would be achieved by integration downstream of the SC. This conception could be considered compatible with a weak version of the premotor theory of attention because one could argue that the output from the SC—which is likely the last node for visuomotor transformation—is simultaneously recruited to guide attention and eye movements. However, while the final oculomotor program was averaged, attention clearly was not in this experiment. Thus, attentional and oculomotor programming are necessarily dissociable at some processing level. One possible option to account for the observed dissociation at the behavioral level is to assume that the brainstem circuitry and the attentional system deploy different algorithms to read out the collicular code.

Disentangling the 2 options discussed above (early versus late oculomotor selection) would constitute an important step in the understanding of the link between attention and action and would require simultaneous behavioral and neural recordings. In regard to the neural recording, one should, however, carefully distinguish between the different classes of neurons (fixation, visual, motor, and visuomotor), which appear to reside along a continuum with variable response properties depending on the experimental conditions [76].

According to our view, attentional selection is not completed at the onset of averaging saccades, as reflected by the equal and moderate attentional benefits at the saccade targets. This proposal is supported by electrophysiological recordings showing that averaging saccades are associated with 2 distinct peaks within the intermediate layers of the SC [53,54]. A similar, general conception of oculomotor programming was expressed by He and Kowler [44], who proposed a 2-stage process in which a single mechanism resolves attentional selection before the oculomotor program is computed at a later stage based on attentional weighting. Our results, moreover, go against a recent proposal that a merged activation within the superficial layers of the SC would feed back into the visual system [55] because this should have led to some attentional enhancement in between the saccade targets before an averaging saccade.

Our framework leads to some predictions in regard to the global effect. First, it predicts that any experimental manipulation modifying the difficulty of saccade target selection will directly impact the occurrence of averaging saccades. For example, specifying the location, the identity, or the probability of a saccade target appearing at a certain location will decrease the task difficulty, thereby increasing the speed of the attentional selection process and reducing the occurrence of averaging saccades [40–44,77]. Also, it predicts that, at a given latency, an easy saccade task should lead to fewer averaging saccades as compared to a more difficult one. Using a simple 2-saccade target task, it was shown that monkeys make averaging saccades only for express but not for normal saccade latencies [50], whereas they execute averaging saccades even for normal saccade latencies in a task rendered harder by a visual search display [49]. Similarly, Viswanathan and colleagues [78] showed that—at a saccade latency for which no consistent global effect was found with a distractor shown nearby a prosaccade target—a clear global effect was evident with the same distractor shown nearby an antisaccade target. These results are in line with our first prediction, as antisaccades are associated with a slower attentional selection [79]. Second, our framework predicts that one should not find any incremental presaccadic attentional benefit at one of the competing saccade targets before an averaging saccade, irrespective of the observed saccade latency. Future studies could directly test this prediction by measuring neuronal activity associated with the saccade targets before an averaging saccade. Third, we proposed 2 alternative explanations that could account for the observed behavioral dissociation between attention and the saccade endpoint before averaging saccades at the neuronal level. Both accounts question the validity of the premotor theory of attention in a saccade task rather than in a covert attention task [21–23].

Combining a measure of presaccadic visual sensitivity with a free-choice saccade task, we spatially dissociated attention allocated to the intended saccade goal from attention allocated to the saccade endpoint. We report here that attention is not obligatorily coupled to the endpoint of the oculomotor program, providing evidence against the strict view that oculomotor processes precede attention. Instead, we propose that saccadic responses depend on the state of attentional selection at saccade onset.

Materials and methods

Ethics statement

This experiment was approved by the Ethics Committee of the Faculty for Psychology and Pedagogics of the Ludwig-Maximilians-Universität München (approval number 13_b_2015) and conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

Participants

Thirteen participants (aged 20–28, 7 females, 12 right-eye dominant, 1 author) completed the experiment for a compensation of 50€. The study was run over 2 experimental sessions (on different days) of 12 blocks of approximately 150 minutes each (including breaks). All participants except for 1 author (LW) were naive as to the purpose of the study, and all had normal or corrected to normal vision.

Setup

Participants sat in a quiet and dimly illuminated room, with their head positioned on a chin and forehead rest. The experiment was controlled by an Apple iMac computer (Cupertino, CA). Manual responses were recorded via a standard keyboard. The dominant eye's gaze position was recorded and made available online using an EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The experimental software controlling the display and the response collection as well as the eye tracking were implemented in Matlab (The MathWorks, Natick, MA), using the Psychophysics [80,81] and EyeLink toolboxes [82]. Stimuli were presented at a viewing distance of 60 cm, on a 24-in Sony GDM F900 CRT screen (Tokyo, Japan) with a spatial resolution of 1,024 × 640 pixels and a vertical refresh rate of 120 Hz [83].

Experimental design

Each trial began with participants fixating on a central fixation target forming a black (approximately 0 cd/m^2) and white (approximately 57 cd/m^2) "bull's eye" (0.4° radius) on a gray background (approximately 19.5 cd/m^2). When the participant's gaze was detected within a 2.0°-radius virtual circle centered on the fixation point for at least 200 ms, the trial began. At that time, 24 distractor streams appeared equally distributed along a 10°-radius imaginary circle centered on the fixation target (see Fig 1A). Distractor streams consisted of flickering stimuli (40 Hz), alternating every 25 ms between a vertical Gabor patch (frequency: 2.5 cpd; 100% contrast; random phase selected each stream refresh; SD of the Gaussian window: 1.1°; mean luminance: approximately 28.5 cd/m^2) and a Gaussian pixel noise mask (made of approximately 0.22°-width pixels with the same Gaussian envelope as the Gabors). After a random fixation period between 300 and 600 ms (in steps of 1 screen refresh: approximately 8 ms), the fixation target switched off together with the onset of 2 saccade targets. Saccade targets, ST$_1$ and ST$_2$, were gray circles (approximately 39 cd/m^2; 1.1° radius; 0.2° width) surrounding 2 randomly chosen streams with an intertarget angular distance of 90° or 30°. They were either presented transiently (50 ms) or continuously (until the end of the trial). When presented transiently, the saccade targets had always disappeared from the screen at the time the discrimination target appeared on the screen. When presented continuously, on the other hand, the saccade targets always temporally overlapped with the presentation of the discrimination target. Our motivation to include these 2 saccade target durations was to check for a potential masking effect of the saccade targets on the discriminability of a discrimination target. Participants were instructed to select 1 of the saccade targets by moving their eyes towards it as fast and as accurately as possible. In 96.5% of all trials, between 75 and 175 ms after the saccade target onset (a time determined to maximize discrimination target offsets in the last 200 ms before the saccade), 1 of the 24 distractor streams was replaced by a discrimination target stream in which a tilted Gabor was played (25 ms, rotated clockwise or counterclockwise by 12° relative to the vertical). The discrimination target could appear at any of the 24 distractor streams with equal probability, and subjects were explicitly informed about this fact at the beginning of the experiment. In 3.5% of all the trials, we did not present any discrimination target, in order to evaluate its influence on saccade metrics (note that all other analyses are based on the discrimination-target-present trials). At 500 ms after the saccade target onset, all stimuli disappeared, and participants were instructed to report the orientation of the discrimination target using the keyboard (right or left arrow key). Incorrect responses were followed by a negative feedback sound. On trials in which no discrimination target was shown, participants' responses were followed by a random feedback sound.

Three participants were excluded from the analysis because their performance stayed at chance level irrespective of the position of the discrimination target. The remaining 10 participants completed between 6,972 and 7,055 trials of the saccade task. Correct fixation within a 2.0°-radius virtual circle centered on the fixation point was checked online. Trials with fixation breaks were repeated at the end of each block, together with trials during which a saccade started (i.e., crossed the virtual circle around the fixation target) within the first 50 ms or after more than 350 ms following the saccade target onset (participants repeated between 46 to 395 trials across all blocks).

In our experiment, we did not indicate the location of the discrimination target. Therefore, the perceptual task required participants to base their decision on multiple potential locations. One might therefore argue that the low sensitivity at the intermediate location BTW was observed because participants did not take the intermediate location into account as a decision variable for the perceptual task. In order to validate that our results reflect attentional effects and were not selectively biased by varying decision criteria across the different locations, we ran a control experiment, in which the position of the discrimination target was revealed by the presentation of a report cue at the end of each trial. Consequently, participants knew which location to base their discrimination judgment upon in this control experiment, which was—except for the presentation of the report cue—identical to the main experiment. Participants were instructed to give their discrimination judgment only after the report cue had appeared. The report cue (a black circle; approximately 0 cd/m^2) was presented right after the offset of the distractor streams and stayed on the screen until the trial end. Overall, we tested 8 participants (4 participated in the main experiment) on an equal amount of blocks and trials as in the main experiment. S7 Fig shows the results of this control experiment in the same format as those of the main experiment (see Fig 3).

Data preprocessing

Before proceeding to the analysis of the behavioral results, we scanned offline the recorded eye-position data. Saccades were detected based on their velocity distribution [84] using a moving average over 20 subsequent eye-position samples. Saccade onset and offset were detected when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within a 2.0° radius centered on the fixation target, if a correct saccade started at the fixation target and landed at a distance between 7° and 13° from the fixation target (±30% of the instructed saccade size), and if no blink occurred during the trial. Finally, only trials in which the discrimination target offset was included in the last 200 ms preceding the saccade onset were included in the analysis (mean ± SEM discrimination target offset relative to the saccade onset for the selected trials: −50.2 ± 1.3 ms). In total, we included 53,117 trials in the analysis (78.2% of the online-selected trials; 75.7% of all trials played) corresponding to an average of 106.0 ± 2.1 trials (115.9 ± 3.3 no-discrimination-target trials) and 105.3 ± 1.8 trials (125.0 ± 4.4 no-discrimination-target trials) per discrimination target location and participant, in the 90° and 30° conditions, respectively.

Corrective saccades were defined as the saccades directly following the offline-selected main saccades sequence and landing at a distance between 7° and 13° from the fixation target. Corrective saccades were included only if they started before the participant's behavioral response and within the first 500 ms following the main saccade sequence. In total, we obtained 14,714 corrective saccade trials in the analysis (21.7% of the online-selected trials; 21.0% of all trials played).

Behavioral data analysis

Before proceeding to any behavioral analysis, we first rotated the trial configuration as to align the 2 saccade target locations (ST1: +45°, ST2: −45° and ST1: +15°, ST2: −15° for the conditions in which they were separated by 90° and 30°, respectively) symmetrically around the geometrical angle 0 (BTW). We then determined the sensitivity to discriminate the orientation of the discrimination targets (d'): d' = z(hit rate) − z(false alarm rate). To do so, we defined a clockwise response to a clockwise discrimination target (arbitrarily) as a hit and a clockwise response to a counterclockwise discrimination target as a false alarm. Corrected performance of 99% and 1% were substituted if the observed proportion correct was equal to 100% or 0%, respectively. Performance below the chance level (50% or d' = 0) were transformed to negative d' values [83]. We analyzed sensitivity as a function of the discrimination position in space irrespective of the saccade landing direction (Fig 3A and 3B) but also as a function of the discrimination target position relative to the saccade landing direction (Fig 3C–3F). To do so, we redefined the position of the discrimination target relative to the saccade direction binned across 24 even, angular sectors of 15° (±7.5° from each distractor stream center angle). This binning was chosen to match with the locations at which we tested visual attention.

We initially computed single-subject means and then averaged these means across participants for each of the compared conditions to get the presented results. For all statistical comparisons, we drew (with replacement) 10,000 bootstrap samples from the original pair of compared values. We then calculated the difference of these bootstrapped samples and derived 2-tailed *p*-values from the distribution of these differences.

Individual raw data and averaged processed data can be found in the Open Science Framework (OSF) online repository at https://osf.io/762up/.

Supporting information

S1 Fig. Saccade direction as a function of saccade latency. (A, B) Plots show the saccade landing direction relative to BTW for all trials as a function of the saccade latency in the 90° (panel A) and 30° (panel B) condition for each participant individually. Dot color indicates the DT location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). Note the overall consistency across

participants and DT locations. BTW, position in between the saccade targets; CTRL, control position; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S2 Fig. Absolute saccade direction and sensitivity as a function of saccade latency. (A, B) Lines show the mean absolute saccade direction relative to BTW grouped into 4 quartiles of saccade latency for the 90° (panel A) and 30° (panel B) condition across all participants irrespective of the discrimination target location. Note that a homogenous distribution of averaging and accurate saccades in the 30° condition should lead to an averaged angle of 10°. (C, D) Mean visual sensitivity (d'), averaged across participants, for trials grouped into 4 quartiles of saccade latency for the 90° (panel C) and 30° (panel D) position. Line color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). The vertical and horizontal dimensions of the shaded areas around each point represent the SEM. BTW, position in between the saccade targets; CTRL, control position; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S3 Fig. Absolute saccade direction as a function of saccade latency. (A, B) Lines show the mean absolute saccade direction relative to BTW as a function of the saccade latency grouped into 4 quartiles of saccade latency in the 90° (panel A) and 30° (panel B) condition for each participant individually. Dot color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). BTW, position in between the saccade targets; CTRL, control position; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S4 Fig. Sensitivity as a function of saccade latency. (A, B) Lines show sensitivity (d') as a function of the saccade latency binned into quartiles of trials in the 90° (panel A) and 30° (panel B) condition for each participant individually. Line color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). BTW, position in between the saccade targets; CTRL, control position; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S5 Fig. Corrective saccades. (A) Circular plot shows averaged frequency distribution of the corrective saccade landing direction following an averaging saccade. (B) Bar graph illustrates averaged frequency of trials as a function of the corrective saccade landing direction following an averaging saccade for 3 positions of interest (ST_1, BTW, and ST_2). (C) Bar graph illustrates sensitivity observed for DT shown at the correctively saccaded (purple) and the correctively nonsaccaded (light purple) positions for trials in which the main saccade was directed in between the saccade target. Conventions are as in Figs 2 and 3. BTW, position in between the saccade targets; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S6 Fig. Visual sensitivity for different saccade direction grouping procedures in the 30° condition. (A, B) Visual sensitivity (d'), averaged across participants, as a function of the saccade direction. Data are grouped using ±7.5° (panel A) and ±2.5° (panel B) bins centered on the discrimination target location (in panel B, data are from a running average at each saccade direction degree). Bottom panel shows the amount of trials per data point. Line color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2). Shaded areas represent the SEM. BTW, position in between the saccade targets; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

S7 Fig. Visual sensitivity in a control experiment, in which the position of the DT was revealed to the participant (*n* = 8; 4 participated in the main experiment) via the

presentation of a report cue similar to the saccade targets at the end of each trial. (A, B) Circular plots show averaged visual sensitivity (d') as a function of the DT position in the 90° (panel A) and 30° (panel B) conditions, irrespective of the duration of the saccade targets and across all saccade directions observed. Bar graphs illustrate visual sensitivity for 4 positions of interest (ST_1, BTW, ST_2, CTRL). (C, D) Visual sensitivity as a function of the DT position relative to the saccade landing direction in the 90° (panel C) and 30° (panel D) conditions, irrespective of the duration of the saccade targets (blue: saccade to ST_1; green: saccade to BTW; red: saccade to ST_2). For each saccade direction, we took the average sensitivity for each DT location. For example, the blue line plots visual sensitivity when saccades were made towards ST_1 and the DT was either at ST_1 (+15° on the polar plot), BTW (15° counterclockwise to ST_1; 0° on the polar plot), or ST_2 (30° counterclockwise to ST_1; +345° on the polar plot), and so on. (E, F) Bar graphs illustrate sensitivity observed for DT shown at the saccaded (purple: e.g., DT at ST_1 and saccade to ST_1) and the nonsaccaded (light purple: e.g., DT at ST_1 and saccade to ST_2 or BTW) positions in the 90° (panel E) and the 30° (panel F) conditions. Conventions are as in Fig 3. As evident when comparing the results of this control experiment to those of the main experiment (see Fig 3), revealing the location of the DT at the end of the trial did not change the overall pattern of the results. The report cue increased discrimination performance overall but not selectively at any specific location. This control experiment thus demonstrates that the attentional effects reported in the main experiment are immune to potential decision biases. BTW, position in between the saccade targets; CTRL, control position; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.
(TIF)

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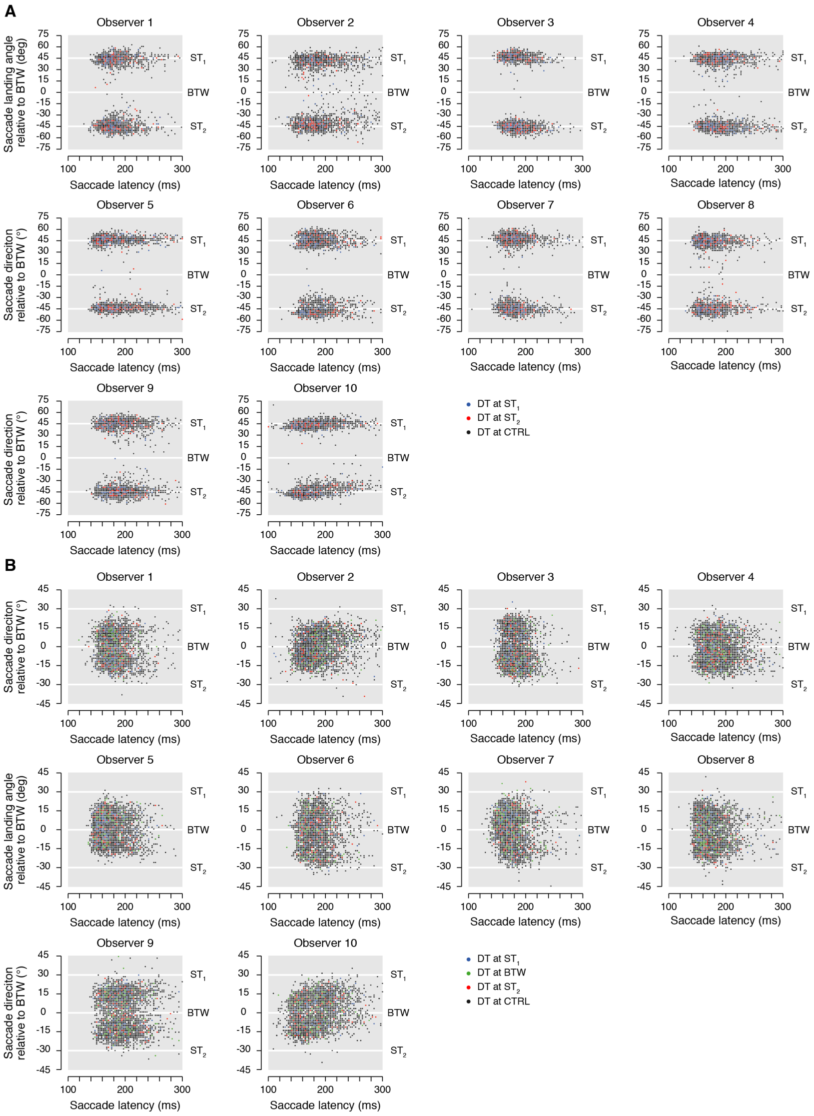

S1 Fig. Saccade direction as a function of saccade latency.
(A, B) Plots show the saccade landing direction relative to BTW for all trials as a function of the saccade latency in the 90° (panel A) and 30° (panel B) condition for each participant individually. Dot color indicates the DT location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). Note the overall consistency across participants and DT locations. BTW, position in between the saccade targets; CTRL, control position; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.
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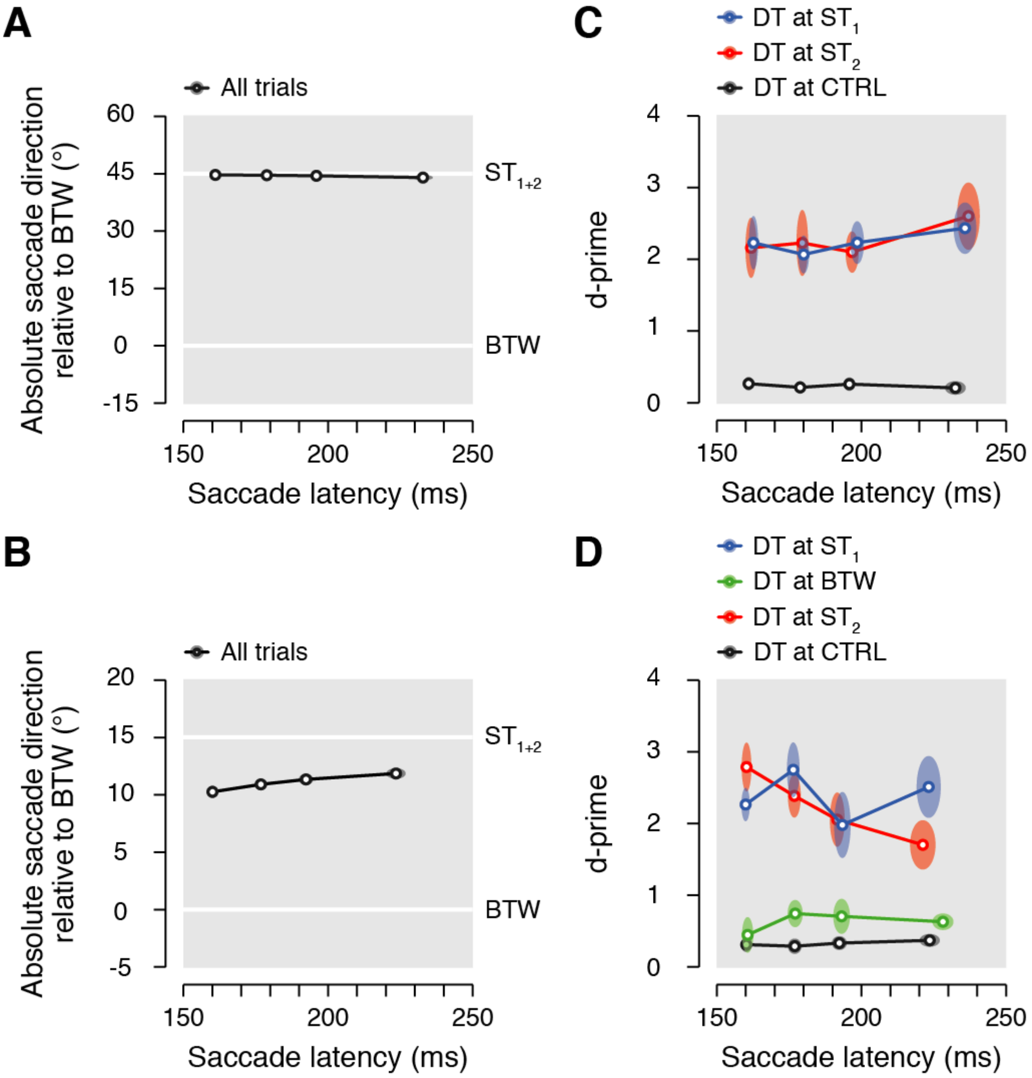

S2 Fig. Absolute saccade direction and sensitivity as a function of saccade latency.
(A, B) Lines show the mean absolute saccade direction relative to BTW grouped into 4 quartiles of saccade latency for the 90° (panel A) and 30° (panel B) condition across all participants irrespective of the discrimination target location. Note that a homogenous distribution of averaging and accurate saccades in the 30° condition should lead to an averaged angle of 10°. (C, D) Mean visual sensitivity (d'), averaged across participants, for trials grouped into 4 quartiles of saccade latency for the 90° (panel C) and 30° (panel D) position. Line color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). The vertical and horizontal dimensions of the shaded areas around each point represent the SEM. BTW, position in between the saccade targets; CTRL, control position; ST_1, saccade target 1; ST_2, saccade target 2.
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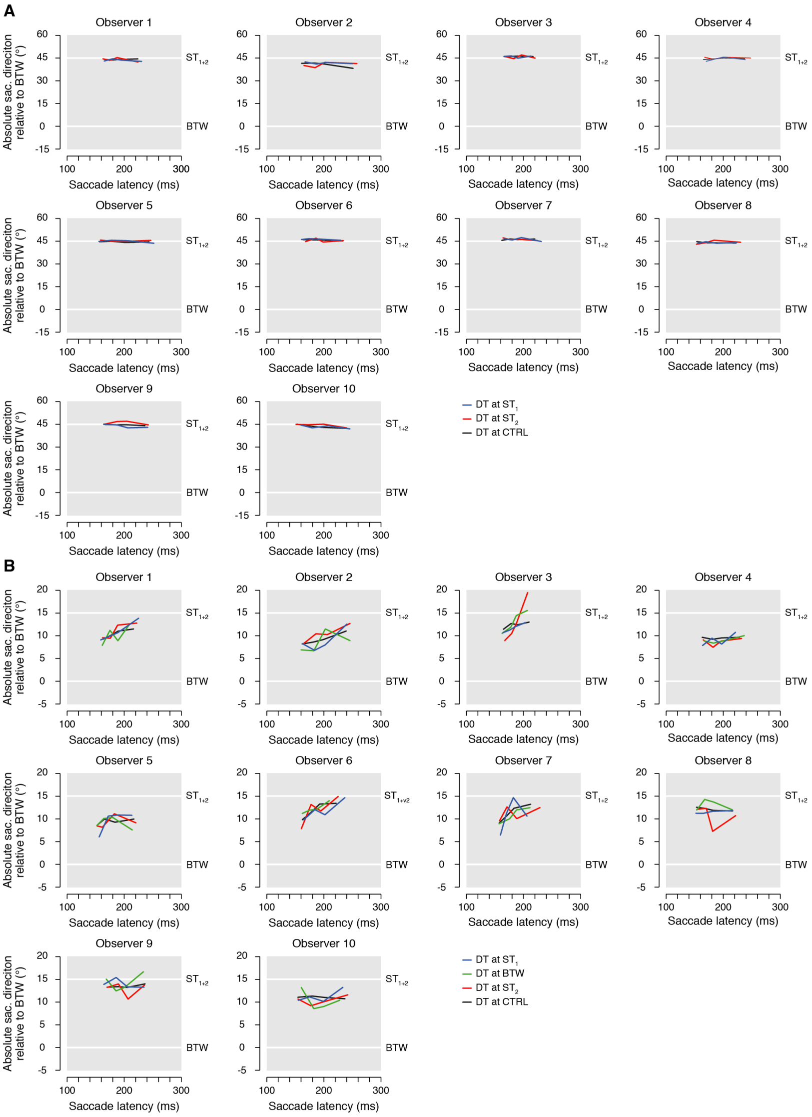

S3 Fig. Absolute saccade direction as a function of saccade latency.
(A, B) Lines show the mean absolute saccade direction relative to BTW as a function of the saccade latency grouped into 4 quartiles of saccade latency in the 90° (panel A) and 30° (panel B) condition for each participant individually. Dot color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2; gray: CTRL). BTW, position in between the saccade targets; CTRL, control position; ST_1, saccade target 1; ST_2, saccade target 2.
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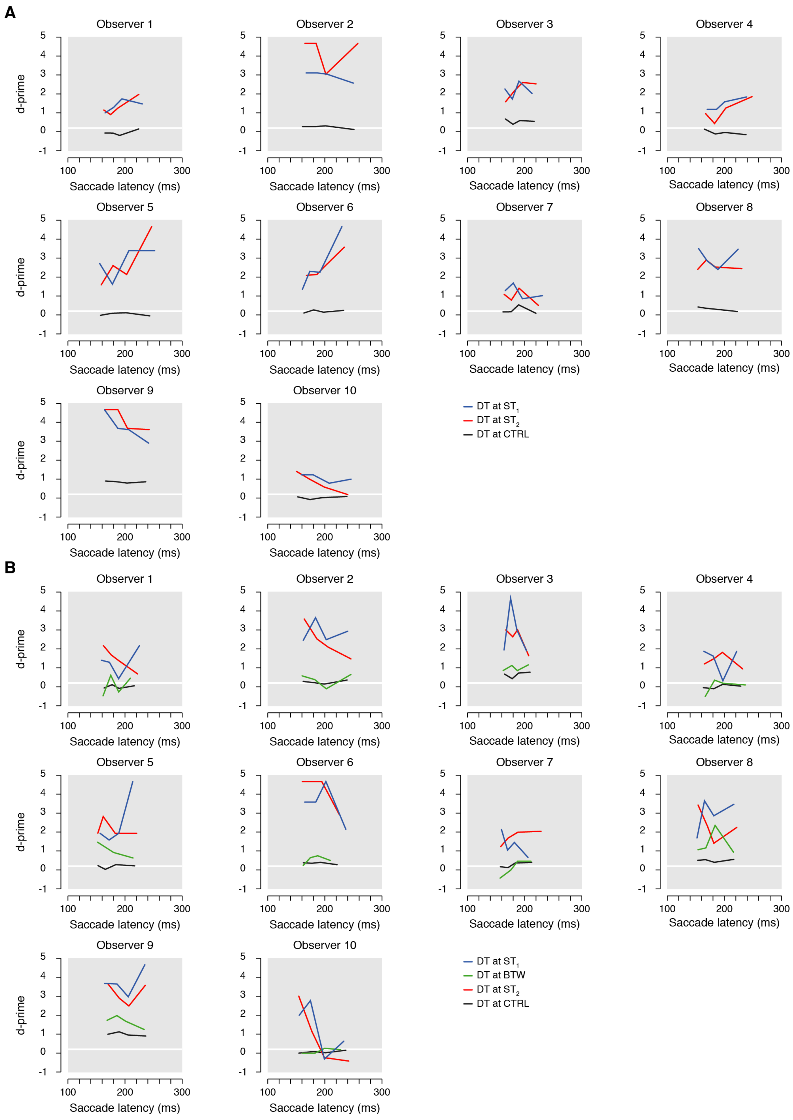

S4 Fig. Sensitivity as a function of saccade latency.
(A, B) Lines show sensitivity (d’) as a function of the saccade latency binned into quartiles of trials in the 90° (panel A) and 30° (panel B) condition for each participant individually. Line color indicates the discrimination target location (blue: ST$_1$; green: BTW; red: ST$_2$; gray: CTRL). BTW, position in between the saccade targets; CTRL, control position; ST$_1$, saccade target 1; ST$_2$, saccade target 2.
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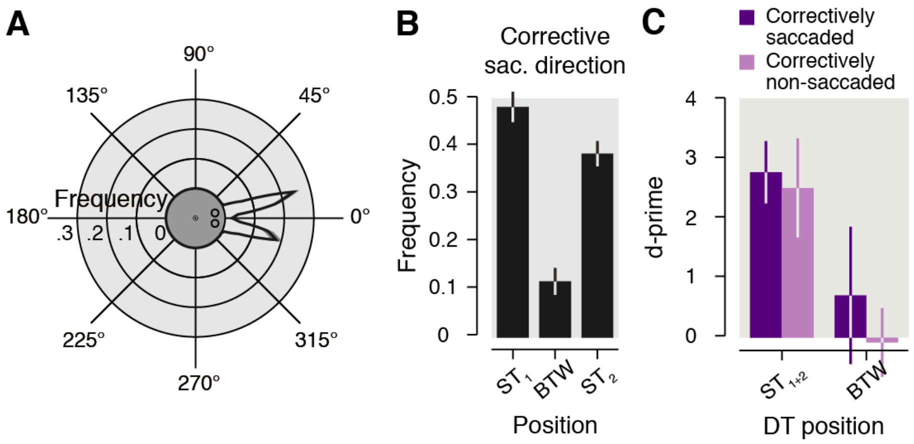

S5 Fig. Corrective saccades.

(A) Circular plot shows averaged frequency distribution of the corrective saccade landing direction following an averaging saccade. (B) Bar graph illustrates averaged frequency of trials as a function of the corrective saccade landing direction following an averaging saccade for 3 positions of interest (ST_1, BTW, and ST_2). (C) Bar graph illustrates sensitivity observed for DT shown at the correctively saccaded (purple) and the correctively nonsaccaded (light purple) positions for trials in which the main saccade was directed in between the saccade target. Conventions are as in Figs 2 and 3. BTW, position in between the saccade targets; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.

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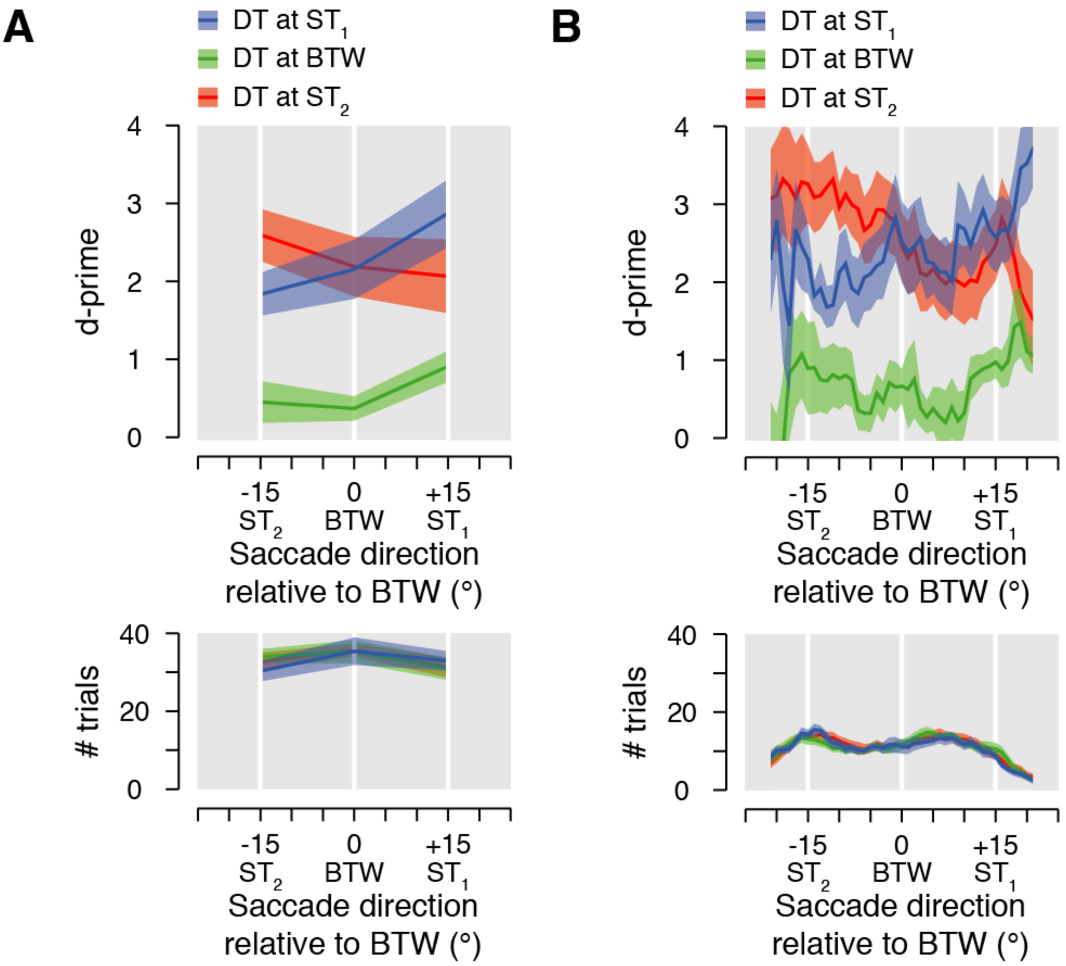

S6 Fig. Visual sensitivity for different saccade direction grouping procedures in the 30° condition.

(A, B) Visual sensitivity (d'), averaged across participants, as a function of the saccade direction. Data are grouped using ±7.5° (panel A) and ±2.5° (panel B) bins centered on the discrimination target location (in panel B, data are from a running average at each saccade direction degree). Bottom panel shows the amount of trials per data point. Line color indicates the discrimination target location (blue: ST_1; green: BTW; red: ST_2). Shaded areas represent the SEM. BTW, position in between the saccade targets; ST_1, saccade target 1; ST_2, saccade target 2.

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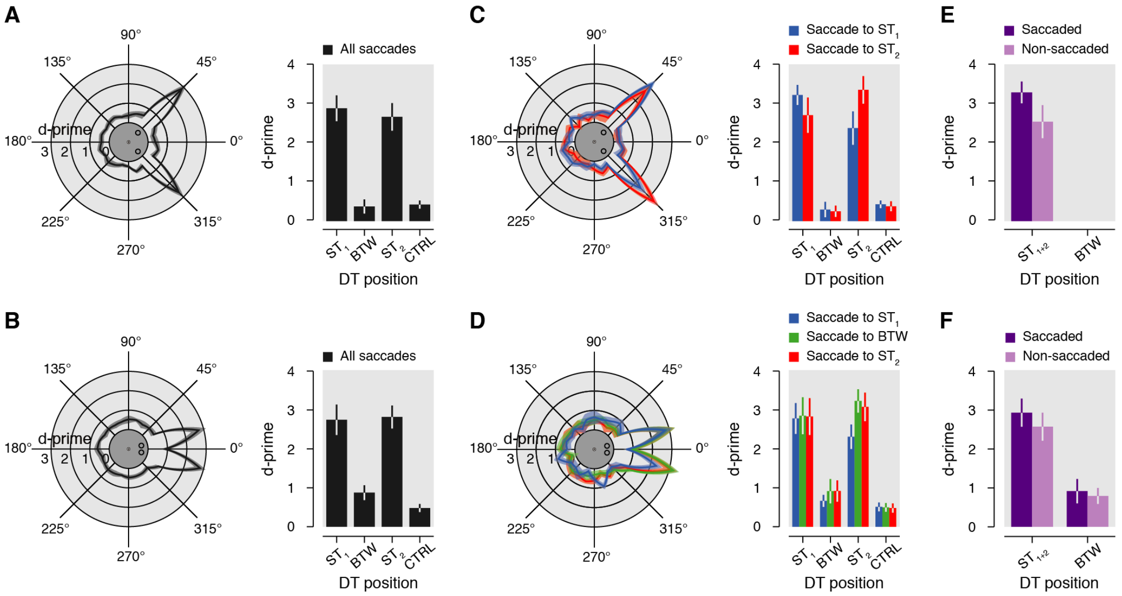

S7 Fig. Visual sensitivity in a control experiment, in which the position of the DT was revealed to the participant (*n* = 8; 4 participated in the main experiment) via the presentation of a report cue similar to the saccade targets at the end of each trial.

(A, B) Circular plots show averaged visual sensitivity (d') as a function of the DT position in the 90° (panel A) and 30° (panel B) conditions, irrespective of the duration of the saccade targets and across all saccade directions observed. Bar graphs illustrate visual sensitivity for 4 positions of interest (ST_1, BTW, ST_2, CTRL). (C, D) Visual sensitivity as a function of the DT position relative to the saccade landing direction in the 90° (panel C) and 30° (panel D) conditions, irrespective of the duration of the saccade targets (blue: saccade to ST_1; green: saccade to BTW; red: saccade to ST_2). For each saccade direction, we took the average sensitivity for each DT location. For example, the blue line plots visual sensitivity when saccades were made towards ST_1 and the DT was either at ST_1 (+15° on the polar plot), BTW (15° counterclockwise to ST_1; 0° on the polar plot), or ST_2 (30° counterclockwise to ST_1; +345° on the polar plot), and so on. (E, F) Bar graphs illustrate sensitivity observed for DT shown at the saccaded (purple: e.g., DT at ST_1 and saccade to ST_1) and the nonsaccaded (light purple: e.g., DT at ST_1 and saccade to ST_2 or BTW) positions in the 90° (panel E) and the 30° (panel F) conditions. Conventions are as in Fig 3. As evident when comparing the results of this control experiment to those of the main experiment (see Fig 3), revealing the location of the DT at the end of the trial did not change the overall pattern of the results. The report cue increased discrimination performance overall but not selectively at any specific location. This control experiment thus demonstrates that the attentional effects reported in the main experiment are immune to potential decision biases. BTW, position in between the saccade targets; CTRL, control position; DT, discrimination target; ST_1, saccade target 1; ST_2, saccade target 2.

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2.2 Visual attention and eye movement control during oculomotor competition

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Author contributions:

Luca Wollenberg designed the study, programmed the experiment, collected, analyzed, interpreted, and visualized the data, and wrote the manuscript.

Nina M. Hanning contributed to the study design, participated in interpreting the results, and commented on the manuscript.

Heiner Deubel contributed to the study design, participated in interpreting the results, and commented on the manuscript.

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Visual attention and eye movement control during oculomotor competition

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Saccadic eye movements are typically preceded by selective shifts of visual attention. Recent evidence, however, suggests that oculomotor selection can occur in the absence of attentional selection when saccades erroneously land in between nearby competing objects (saccade averaging). This study combined a saccade task with a visual discrimination task to investigate saccade target selection during episodes of competition between a saccade target and a nearby distractor. We manipulated the spatial predictability of target and distractor locations and asked participants to execute saccades upon variably delayed go-signals. This allowed us to systematically investigate the capacity to exert top-down eye movement control (as reflected in saccade endpoints) based on the spatiotemporal dynamics of visual attention during movement preparation (measured as visual sensitivity). Our data demonstrate that the predictability of target and distractor locations, despite not affecting the deployment of visual attention prior to movement preparation, largely improved the accuracy of short-latency saccades. Under spatial uncertainty, a short go-signal delay likewise enhanced saccade accuracy substantially, which was associated with a more selective deployment of attentional resources to the saccade target. Moreover, we observed a systematic relationship between the deployment of visual attention and saccade accuracy, with visual discrimination performance being significantly enhanced at the saccade target relative to the distractor only before the execution of saccades accurately landing at the saccade target. Our results provide novel insights linking top-down eye movement control to the operation of selective visual attention during movement preparation.

Introduction

Saccadic eye movements play a pivotal role in visual perception. They successively shift our fovea toward objects of interest, allowing us to process their details at high resolution during intermittent fixations. Importantly, to account for the multitude of objects typically competing for in-depth processing within our crowded visual environment, efficient eye movement control is contingent upon top-down selection via attentional mechanisms. Whereas bottom-up (stimulus-driven) processes contribute to visual selection via extraction of the most salient aspects in the visual field, top-down (goal-driven) mechanisms bias selection as a function of the observer's current goals (e.g. Wolfe, 1994; Itti & Koch, 2001). It is generally believed that bottom-up visual selection occurs fast and transiently, whereas top-down control emerges only slower and operates in a more sustained fashion (e.g. Nakayama & Mackeben, 1989; Carrasco, 2011). Crucially, a substantial body of empirical evidence argues for an intriguing coupling between

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the mechanisms underlying selective visual attention and the control of saccadic eye movements. For instance, both mechanisms have been found to recruit largely overlapping neuronal circuitries (e.g. Corbetta, 1998). Furthermore, selective perceptual benefits can be evoked via subthreshold microstimulation within oculomotor key structures, such as the frontal eye fields (FEF; Moore & Fallah, 2004) and the superior colliculus (SC; Müller, Philiastides, & Newsome, 2005) of the monkey. In humans, psychophysical dual-task paradigms consistently showed that visual processing is selectively enhanced at the target of an impending saccade during oculomotor preparation (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996). Some authors even conceptualized visual attention as an obligatory consequence of motor programming (see *Premotor Theory of Attention:* Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994), or in terms of a common selection mechanism for perceptual processing and motor programming (Schneider, 1995; Deubel & Schneider 1996).

Despite the ability to accurately move our eyes in a voluntary fashion, the oculomotor system is susceptible to systematic inaccuracies when multiple nearby objects compete for selection. Under these circumstances, saccades frequently land at an intermediate location between the competing objects (Coren & Hoenig, 1972; Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1984; Van der Stigchel & Nijboer, 2014). This phenomenon – commonly referred to as the global effect or saccade averaging – has been linked to competition in a retinotopically organized saccade map characterized by excitatory connections among proximal neuronal populations (Van Opstal & Van Gisbergen, 1989; Kopecz & Schöner, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001; Godijn & Theeuwes, 2002). It has been proposed that the SC constitutes a likely substrate for the implementation of such a saccade map, representing movement vectors based on the population activity of neurons with large and coarsely tuned movement fields (Schiller & Stryker, 1972; Wurtz & Goldberg, 1972). Indeed, simultaneous microstimulation at two spatially separate sites in the primate SC was shown to elicit averaging saccades landing in between the locations corresponding to each stimulation site (Robinson, 1972; Schiller & Sandell, 1983). However, whether naturally occurring averaging saccades are represented as two separate loci of collicular activity residing at the sites of the competing stimuli (Edelman & Keller, 1998), or a single activity peak located in between the competing stimuli (Glimcher & Sparks, 1993), has not yet been consistently resolved. Due to the observation that saccade averaging is most pronounced at short saccade latencies (Findlay, 1982; Ottes, Van Gisbergen, & Eggermont, 1985; Coëffé & O'Regan, 1987; Edelman & Keller, 1998; Chou, Sommer, & Schiller, 1999), the global effect has originally been interpreted as an automatic oculomotor response originating from bottom-up processing of visual information (Findlay, 1982). More recent accounts, however, hold that the activity profile of the saccade map implements target selection via the integration of bottom-up and top-down signals (Findlay & Walker, 1999; Trappenberg et al., 2001; Meeter, Van der Stigchel, & Theeuwes, 2010), suggesting that higher level information can effectively bias low-level visual competition. In line with this idea, it was shown that the occurrence of averaging saccades can be reduced by increasing target predictability (Coëffé & O'Regan, 1987; He & Kowler, 1989; Aitsebaomo & Bedell, 2000). More recently, the perceptual correlates of saccade averaging were investigated in dual-task paradigms inducing oculomotor competition between nearby objects (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018; Wollenberg, Deubel, & Szinte, 2019). In our recent work (Wollenberg et al., 2018), we asked participants to move their eyes toward one of two nearby saccade targets at free choice and assessed visuospatial orientation sensitivity during movement preparation. We observed a selective enhancement of visual orientation sensitivity at the endpoint of saccades accurately landing at a saccade target, but – consistent with the results of Van der Stigchel and de Vries (2015) – not at the endpoint of averaging saccades. Instead, visual orientation sensitivity was equally enhanced at the two competing saccade targets prior to the execution of averaging saccades, suggesting that oculomotor competition was not readily resolved at the perceptual level before movement onset. These results emphasize the role of top-down attentional mechanism in resolving bottom-up visual competition for efficient oculomotor control.

The time course of top-down control on saccade averaging was recently investigated in a fixation gap paradigm (Heeman, Theeuwes, & Van der Stigchel, 2014). Without an instruction about the identity of the saccade target, saccades consistently landed in between the saccade target and a nearby distractor. However, when participants received an explicit task instruction specifying the identity of the saccade target, the saccade endpoint deviations linearly decreased with increasing saccade latency. This top-down modulation already emerged at the shortest saccade latencies observed, suggesting an early involvement of top-down mechanisms for the control of saccadic eye movements (see also: Aagten-Murphy & Bays, 2017). Likewise, the proportion of saccades directed to the saccade target rather than to a simultaneously presented distractor was found to increase as a function of saccade latency in visual search tasks (van Zoest, Donk, & Theeuwes, 2004; van Zoest & Donk, 2005). The authors therefore concluded that bottom-up and top-down control operate at different temporal scales: whereas saccade target selection is susceptible to visual saliency early on during saccade preparation, the influence of stimulus-related top-down control emerges only later. In summary, previous literature suggests that top-down mechanisms play a major role for efficient oculomotor control. Yet, despite the well-documented spatiotemporal coupling between saccade programming and visual attention (Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996), the perceptual correlates of top-down eye movement control during oculomotor competition have not yet been systematically investigated.

Here, we asked participants to move their eyes to a saccade target in the presence of a nearby distractor (saccade task), and to report the orientation of a discrimination target presented at different locations and time points during movement preparation (visual discrimination task). Importantly, we systematically manipulated (1) the predictability of the saccade target and the distractor location (via different pre-block instructions) as well as (2) visual processing time prior to saccade onset (via variable saccadic go-signal delays). Consequently, the analysis of presaccadic visual discrimination performance and saccade endpoints allowed us to concurrently evaluate the influence of varying top-down control on saccade target selection at the perceptual and oculomotor level. To our knowledge, this is the first study to directly assess how the spatiotemporal dynamics of visual attention, which affect visual perception during movement preparation, relate to top-down eye movement control.

We reasoned that saccade target selection would be initially challenged by bottom-up competition between the saccade target and the distractor (induced via salient visual onsets at the respective locations). Increasing spatial predictability and visual processing time prior to movement onset should, however, enhance the emergence of top-down control mechanisms (van Zoest et al., 2004; van Zoest & Donk, 2005; Heeman et al., 2014; Aagten-Murphy & Bays, 2017), thereby counteracting bottom-up competition and facilitating efficient saccade target selection.

More specifically, we assumed that rendering the saccade target or distractor location predictable would particularly facilitate top-down control when visual processing time is limited before movement onset, leading to an improvement in the accuracy of short-latency saccades. Furthermore, a prolongation of visual processing time should more generally improve top-down control, leading to enhanced saccade accuracy at longer movement latencies. Importantly, based on the tight spatiotemporal coupling between visual attention and oculomotor programming (Hoffman & Subramaniam, 1995; Kowler et al., 1995; Deubel & Schneider, 1996), we assumed that the anticipated top-down improvements in saccade accuracy would be reflected at the perceptual level during movement preparation. In particular, based on recent evidence demonstrating that attentional resources are split between two proximal stimuli before the execution of averaging saccades (Van der Stigchel & de Vries 2015: page 11, lines 9–14; Wollenberg et al., 2018: page 10, lines 10–13), we hypothesized that the expected improvements in saccade accuracy should be associated with a reduction of presaccadic attentional competition between the saccade target and the distractor. This reduction of attentional competition should affect visual discrimination capabilities during movement preparation and lead to selectively enhanced visual discrimination performance at the saccade target relative to the distractor.

Materials and methods

Ethics statement

This experiment was conducted in accordance with the Declaration of Helsinki and approved by the Ethics Committee of the Faculty for Psychology and Pedagogics of the Ludwig-Maximilians-Universität München (approval number 13_b_2015). All participants gave written informed consent before participation.

Participants

Based on the sample size range of previous studies on presaccadic visual attention (e.g. Deubel & Schneider, 1996; White, Rolfs, & Carrasco, 2013; Wollenberg et al., 2018; Hanning, Szinte, & Deubel, 2019), 9 healthy participants (aged 24–31 years, 5 women, 8 right-eye dominant, and 1 author) with normal or corrected to normal vision completed the experiment over the course of 2 sessions (approximately 150 minutes each, including intermittent breaks) on different days in exchange for 50 €. All participants, except for one author (L.W.), were unaware of the study objectives.

Setup

The experiment was conducted in a dimly illuminated room. Participants were seated at a viewing distance of 60 cm in front of a 19-inch Silicon Graphics CRT screen (resolution: 800 × 600 pixels; vertical refresh rate: 120 Hz), with their head stabilized by a chin and forehead rest. Stimulus presentation and the collection of manual responses and eye data were implemented in Matlab (The MathWorks, Natick, MA) via the

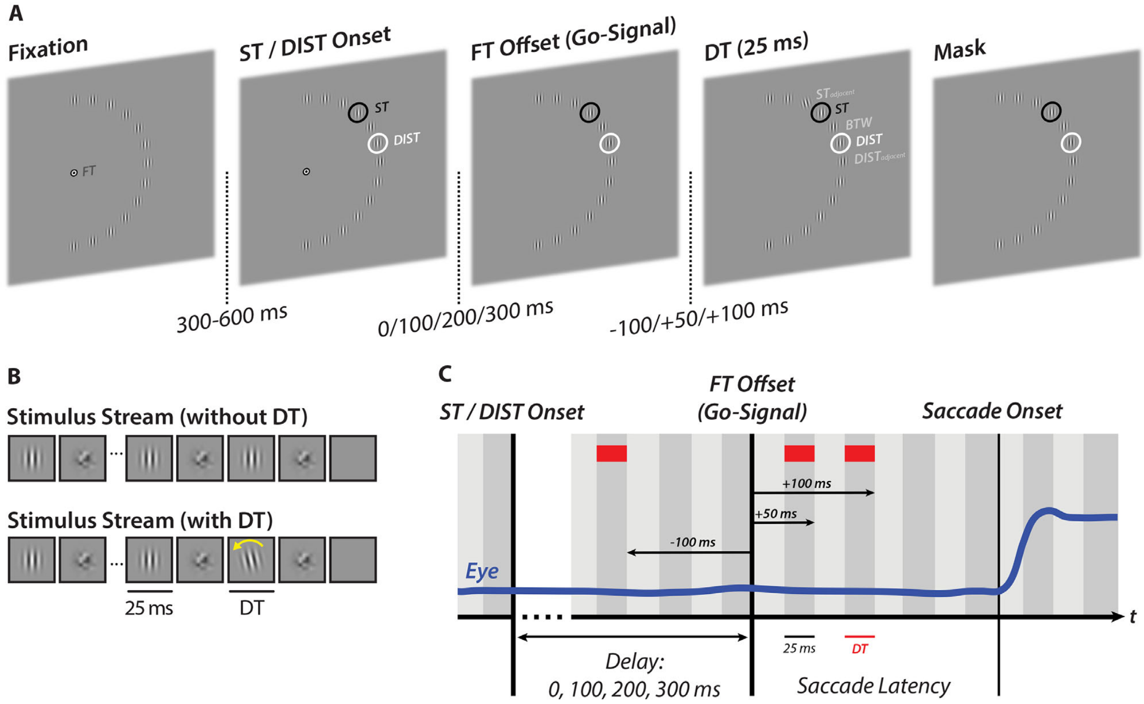

Figure 1. Experimental procedure. Participants performed a dual-task, comprising a saccade task and a visual discrimination task, during episodes of competition between a saccade target (ST) and a nearby distractor (DIST). Experimental blocks varied depending on the predictability of the ST and DIST locations: $ST/DIST^{variable}$, ST^{fixed}, and $DIST^{fixed}$. (**A**) Trial chronology. *Fixation:* At the beginning of each trial, 13 flickering stimulus streams (see **B**) appeared on the screen and participants had to maintain fixation at the fixation target (FT). *ST/DIST Onset:* After 300 to 600 ms, a black and a white circle appeared at an angular distance of 30 degrees from each other, surrounding two of the stimulus streams to indicate the ST and DIST locations. *FT Offset (Go-Signal):* Upon a variable delay (0, 100, 200, or 300 ms relative to ST/DIST onset), the FT disappeared and participants had to move their eyes as fast as possible toward ST. *DT (25 ms):* Before saccade onset, a discrimination target (DT, see **B**) – a slightly clockwise or counterclockwise tilted Gabor — was randomly flashed for 25 ms within 1 of 5 predefined stimulus streams (ST, DIST, BTW, $ST_{adjacent}$, and $DIST_{adjacent}$). The DT disappeared at either −100 ms, +50 ms, or +100 ms after the FT offset (see **C**). *Mask:* The DT was subsequently masked by the continuation of the flickering stimulus streams and participants had to report the orientation of the DT via the keyboard at trial end. (**B**) Flickering stimulus streams without (upper depiction) or with (lower depiction) a DT (here, a counterclockwise rotated DT; yellow arrow superimposed for illustration). (**C**) Schematic illustration of stimulus timing (x-axis represents time). The blue line depicts the position of the eye, which is expected to move on average approximately 200 ms after the FT offset (i.e. saccadic go-signal). The dotted line segment of the x-axis indicates the variability of the delay between ST/DIST onset and FT offset. Red squares highlight the 25 ms intervals during which the DT was presented, with arrows indicating the different DTOAs applied. Temporal contingencies were identical in all spatial predictability conditions.

Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink (Cornelissen, Peters, & Palmer, 2002) toolboxes. Gaze position of the dominant eye was recorded at a sampling rate of 1 kHz by an EyeLink 1000 Desktop Mount eye-tracker (SR Research, Osgoode, Ontario, Canada). Manual responses were recorded via a standard keyboard and auditory feedback (upon incorrect manual responses) was played via external loudspeakers.

Experimental design

Figure 1 illustrates the experimental procedure. On each trial, participants had to initially fixate within a 2.0 degree radius around a central fixation target (FT) – a black (approximately 0 cd/m^2) and white (approximately 44 cd/m^2) bull's eye (radius: 0.4 degrees) – presented on a gray background (approximately 22 cd/m^2). Upon correct fixation for 200 ms, 13 equidistant flickering stimulus streams were presented along an imaginary semicircle (radius: 10°) to the right side of the FT. Stimulus streams alternated every 25 ms (40 Hz) between a vertical Gabor patch (spatial frequency: 2.5 cpd; 100% contrast; random phase selected at each stream refresh; SD of the Gaussian window: 1.1 degrees; mean luminance: approximately 22 cd/m^2) and a Gaussian pixel noise mask (consisting of 0.23 degree width pixels with the same Gaussian envelope as the Gabors; see Wollenberg et al., 2019 for a video demonstration, and Hanning, Deubel, & Szinte, 2019 for a sample code). Between 300 and 600 ms after the onset of the stimulus streams, we presented a saccade target (ST) to which participants had to move their eyes, together with a nearby distractor (DIST), which participants should ignore. ST and DIST were equiluminant relative to the background and appeared in the form of black (approximately 0 cd/m^2) and white (approximately 44 cd/m^2) circles (radius: 1.1 degrees; width: 0.2 degrees) surrounding 2 stimulus streams separated by an angular distance of 30 degrees until trial end. The color configuration of ST and DIST was counterbalanced across participants but constant for each participant across the experiment (5 participants: white ST/black DIST; 4 participants: black ST/white DIST). Importantly, we systematically varied the spatial predictability of the ST and DIST locations via pre-block instructions (8 blocks of each type played in random order). Depending on the block type, participants were either unaware of the ST and DIST locations (ST/DIST$^{\text{variable}}$), informed about the fixed location of ST (ST$^{\text{fixed}}$), or informed about the fixed location of DIST (DIST$^{\text{fixed}}$). Note that, as ST and DIST always appeared at an angular distance of 30 degrees, participants could also predict the DIST location in the ST$^{\text{fixed}}$ condition and the ST location in the DIST$^{\text{fixed}}$ condition with a probability of 50% (i.e. either two stimulus streams clockwise or counterclockwise to the fixed location). Moreover, to investigate the dynamics of attentional and oculomotor selection as a function of visual processing time prior to saccade onset, we systematically delayed saccades. Participants were instructed to move their eyes as fast and accurately as possible upon the offset of FT (rather than the onset of ST and DIST), which was randomly delayed by 0, 100, 200, or 300 ms (delay^0, delay^{100}, delay^{200}, and delay^{300}) relative to ST and DIST onset. In order to assess the deployment of visual attention during saccade preparation, a discrimination target (DT) was presented shortly before saccade onset. The DT consisted of a slightly tilted Gabor (either clockwise or counterclockwise at a rotation angle of 12 degrees relative to the vertical), which was presented for a duration of 25 ms and disappeared at either −100, +50, or +100 ms relative to the FT offset (saccadic go-signal). Note that, whereas the positive discrimination target offset asynchronies (DTOAs, defined as the duration between FT offset and DT offset) of +50 and +100 ms were used across all saccadic go-signal delays (delay^0, delay^{100}, delay^{200}, and delay^{300}), the negative DTOA of −100 ms was only introduced in half of the trials without a saccadic go-signal delay (i.e. delay^0). These trials were used to evaluate potential effects of spatial predictability on the endogenous deployment of visual attention prior to the actual presentation of ST and DIST. The DT location was randomly selected among five possible stimulus streams at: the saccade target (ST), the distractor (DIST), in between the saccade target and the distractor (BTW), adjacent to the saccade target (ST$_{\text{adjacent}}$), or adjacent to the distractor (DIST$_{\text{adjacent}}$). Discrimination performance was averaged across the latter two locations to derive a robust baseline measure (CTRL) of visual orientation sensitivity. On approximately 2% of trials, no DT was presented in order to evaluate potential influences of the DT appearance on saccade latencies. Eight hundred ms after the onset of ST and DIST, all stimuli were erased from the screen. At the end of each trial, participants reported the DT orientation (two alternative forced choice: clockwise versus counterclockwise) via button press on the keyboard (right versus left arrow). A feedback sound was played upon incorrect manual responses and the next trial was launched once the manual discrimination response was registered.

Overall, participants completed 24 blocks, each consisting of 230 trials. Incorrect trials, in which online saccade onset was not detected between 50 and 350 ms relative to the FT offset (saccadic go-signal) upon correct fixation (within a 2.0 degree radius around the FT) were repeated at the end of each block.

Data preprocessing

Saccades were detected based on the velocity distribution of the sampled eye data (Engbert & Mergenthaler, 2006). We registered saccade onsets/offsets whenever the eye's velocity was greater/smaller than the median of a moving average across 20 subsequent eye-position samples by 3 SDs for at least 20 ms. For further analyses, we only included trials without intermittent eye blinks, in which (1) initial fixation was maintained within a radius of 2.0 degrees around FT, (2) saccade onset fell between 50 ms and 350 ms relative to the saccadic go-signal, and (3) a saccade landed between 7 degrees and 13 degrees from FT. Moreover, to base our measures of visual orientation sensitivity on the deployment of visual processing resources before saccade onset, only trials in which the DT offset occurred before the eyes started to move were further considered. After preprocessing the data as described, a total number of 46,400 trials were included in the final analyses, corresponding to 81.74%

of all trials played and an average of 5156 ± 59 (mean ± SEM) trials per participant.

Data analysis

Our analyses focused on the evaluation of saccade endpoints and presaccadic visual discrimination performance obtained under conditions varying with regard to the predictability of the saccade target and distractor locations (ST/DIST$^{\text{variable}}$, ST$^{\text{fixed}}$, and DIST$^{\text{fixed}}$) and movement preparation time (delay^{0}, delay^{100}, delay^{200}, and delay^{300}).

For the analysis of saccade endpoints, we first divided the stimulus stream semicircle into 13 even angular sectors of 15 degrees (±7.5 degrees from each stimulus stream center angle) and computed the percentage of saccade endpoints recorded within a given sector. This allowed us to derive saccade endpoint distributions reflecting the proportion of target saccades (landing closest to the saccade target), distractor saccades (landing closest to the distractor), and averaging saccades (landing in the sector between the saccade target and the distractor).

Presaccadic visual discrimination performance was computed as the percentage of correct orientation discrimination responses observed for the stimulus streams located at ST, DIST, and BTW (between ST and DIST), respectively. Data obtained at the streams surrounding ST and DIST were collapsed into a baseline measure of visual discrimination performance (CTRL).

All results are reported as M ± SEM (mean ± standard error of mean). Reported effect sizes represent the standardized mean difference Cohen's d_z among the compared groups (Lakens, 2013).

Results

Basic analyses

Before focusing on the analyses of saccade endpoints and visual discrimination performance, we first verified central assumptions underlying the interpretation of our data.

Figure 2 shows mean saccade latencies separately for each spatial predictability condition and saccadic go-signal delay. In order to validate the effectiveness of our saccadic delay manipulation, we collapsed data across the different spatial predictability conditions and subjected the mean saccade latency (measured relative to saccade target and distractor onset) of each saccadic go-signal delay to a 1-way repeated measures ANOVA. We observed that saccade latencies significantly increased as a function of the saccadic go-signal delay (delay^{0}: 190.34 ± 3.28 ms, delay^{100}: 278.68 ± 6.11 ms, delay^{200}: 360.39 ± 6.96 ms, and delay^{300}: 450.18 ± 6.75; F(1.85, 14.77) = 964.52, $p < 0.001$, Greenhouse Geisser corrected). Thus, as expected, our saccadic delay manipulation led to a systematic prolongation of visual processing time prior to saccade onset. Saccadic go-signal delays did, however, not increase saccade latencies exactly proportional to their duration, which becomes evident when computing the mean saccade latency increase relative to the corresponding saccadic go-signal delay duration (delay^{100}: −11.66 ms, delay^{200}: −29.95 ms, and delay^{300}: −40.16 ms). This effect likely indicates that oculomotor processing already started (to some degree) with the onset of the oculomotor cues rather than strictly contingent upon the go-signal. Importantly, despite this relative acceleration of movement execution, the observed saccade latencies clearly indicate that the DT offset (at −100, +50, or +100 ms relative to the go-signal) consistently occurred before movement onset.

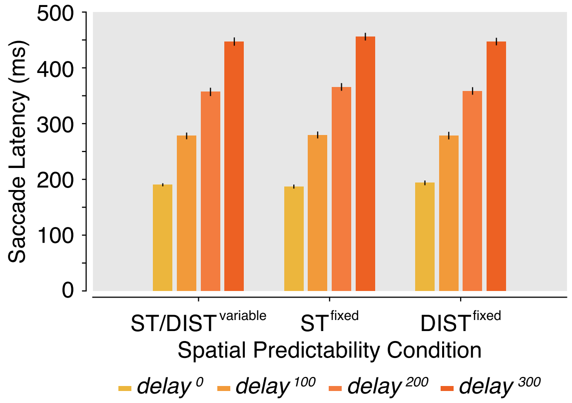

Figure 2. Saccade latencies. Mean saccade latencies relative to saccade target and distractor onset observed in the different spatial predictability conditions for each saccadic go-signal delay (0 - 300 ms; light to dark orange). Error bars represent SEM ($n = 9$).

Next, we verified that the mere presence of the discrimination target did not inherently capture attention, which would be reflected in saccade latency modulations. We collapsed data across all spatial predictability conditions and saccadic go-signal delays, and subsequently compared the mean saccade latency between trials in which DT was presented (DT$^{\text{present}}$; approximately 98% of trials) and trials without DT (DT$^{\text{absent}}$; approximately 2% of trials). We only included trials in which DT occurred after the go-signal (i.e. DT offset at either +50 or +100 ms relative to FT offset) to ensure that this comparison was based on the presence of the discrimination target shortly before saccade onset. A paired t-test did not reveal a significant saccade latency difference (DT$^{\text{present}}$: 319.91 ± 5.03

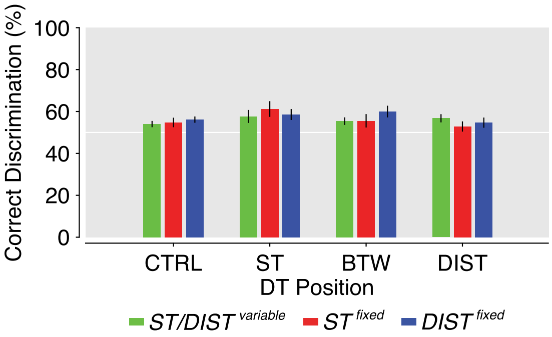

Figure 3. Visual discrimination performance before cue onset. Mean percentage of correct orientation discrimination at the CTRL, ST, BTW, and DIST location observed in the different spatial predictability conditions (ST/DIST^{variable}: green; ST^{fixed}: red; and DIST^{fixed}: blue) prior to the visual onset of saccade target and distractor. Error bars represent SEM ($n = 9$).

ms versus DT^{absent}: 316.28 ± 5.18 ms; $t(8) = 1.48$, $p > 0.05$, $d_z = 0.49$). Accordingly, our discrimination target signal allowed to probe visual attention during the presaccadic interval without interfering with oculomotor preparation.

Last, we examined whether spatial predictability systematically affected the endogenous deployment of visual attention. To this end, we combined all trials in which the discrimination target appeared before the onset of the saccade target and the distractor (i.e. only trials associated with a DTOA of −100 ms at delay^0) and computed visual discrimination performance at the CTRL, ST, BTW, and DIST location separately for each spatial predictability condition (see Figure 3). Subsequently, visual discrimination performance at ST and DIST in the ST^{fixed} and DIST^{fixed} conditions was compared to the ST/DIST^{variable} condition using paired t-tests (at a Bonferroni-corrected alpha of 0.025 for both the ST and DIST comparisons). Interestingly, visual discrimination performance at ST in both the ST^{fixed} (61.18 ± 3.75%) and DIST^{fixed} (58.56 ± 2.62%) condition did not significantly differ from the ST/DIST^{variable} condition (57.64 ± 3.10%; both p values > 0.05). Similarly, no significant modulation of visual discrimination performance at DIST was observed in the ST^{fixed} (52.84 ± 2.45%) and DIST^{fixed} (54.68 ± 2.44%) relative to the ST/DIST^{variable} condition (56.77 ± 1.96%; both p values > 0.05). Thus, being able to predict the upcoming location of the saccade target or the distractor did not systematically affect the endogenous deployment of visual attention prior to saccade target and distractor onset at the respective locations. Consequently, any top-down effects on saccade accuracy and visual discrimination performance emerging after the visual onsets of saccade target and distractor did not result from a predictive deployment of attention.

Main analyses

Saccade accuracy

To investigate the influence of our experimental manipulations on the accuracy of saccades, we computed the distribution of saccade endpoints across the angular sectors surrounding the ST, BTW, and DIST location (see saccade endpoint binning procedure described in Data analysis) separately for each spatial predictability condition and saccadic go-signal delay (see Figure 4A). These data were subjected to a 2-way repeated measures ANOVA (spatial predictability × saccadic go-signal delay) taking the proportion of target saccades landing closest to ST as the dependent measure. Interestingly, even though spatial predictability tended to increase the proportion of target saccades (ST/DIST^{variable}: 80.48 ± 1.70, ST^{fixed}: 85.96 ± 3.50, and DIST^{fixed}: 86.34 ± 1.67), the main effect of spatial predictability only approached statistical significance ($F(2,16) = 3.48$, $p = 0.06$). There was, however, a highly significant main effect of the saccadic go-signal delay duration ($F(1.29,10.30) = 38.07$, $p < 0.001$, Greenhouse Geisser corrected), demonstrating that the proportion of target saccades generally increased with prolonged movement preparation time. Yet, as revealed by the average proportion of target saccades observed for the different go-signal delays (delay^0: 75.19 ± 2.42, delay^{100}: 86.26 ± 2.03, delay^{200}: 88.01 ± 1.96, and delay^{300}: 87.58 ± 2.20), movement accuracy did not linearly increase with movement preparation time but rather reached a plateau after a 100 ms go-signal delay. Moreover, we found a highly significant interaction effect of spatial predictability and saccadic-go signal delay ($F(6,48) = 18.79$, $p < 0.001$). The distribution of saccade endpoints (see Figure 4A) suggests that this interaction is driven by the sharp increase in target directed saccades in the ST/DIST^{variable} condition from delay^0 to delay^{100}. A more detailed insight into the distribution of saccade endpoints can be obtained from Supplementary Figure S1, which depicts saccade endpoint data at a finer resolution.

Based on the assumption that spatial predictability would lead to a fast improvement in saccade accuracy, we subsequently used paired t-tests (at a Bonferroni-corrected alpha of 0.0167) to compare the proportion of undelayed target saccades (delay^0) between the different spatial predictability conditions (see leftmost plot in Figure 4A). Indeed, relative to the ST/DIST^{variable} condition (63.64 ± 3.15%), the proportion of target saccades was significantly larger in the ST^{fixed} (82.79 ± 4.05%; $t(8) = 4.14$, $p < 0.01$, $d_z = 1.38$) and DIST^{fixed} condition (79.15 ± 2.26%; t(8)

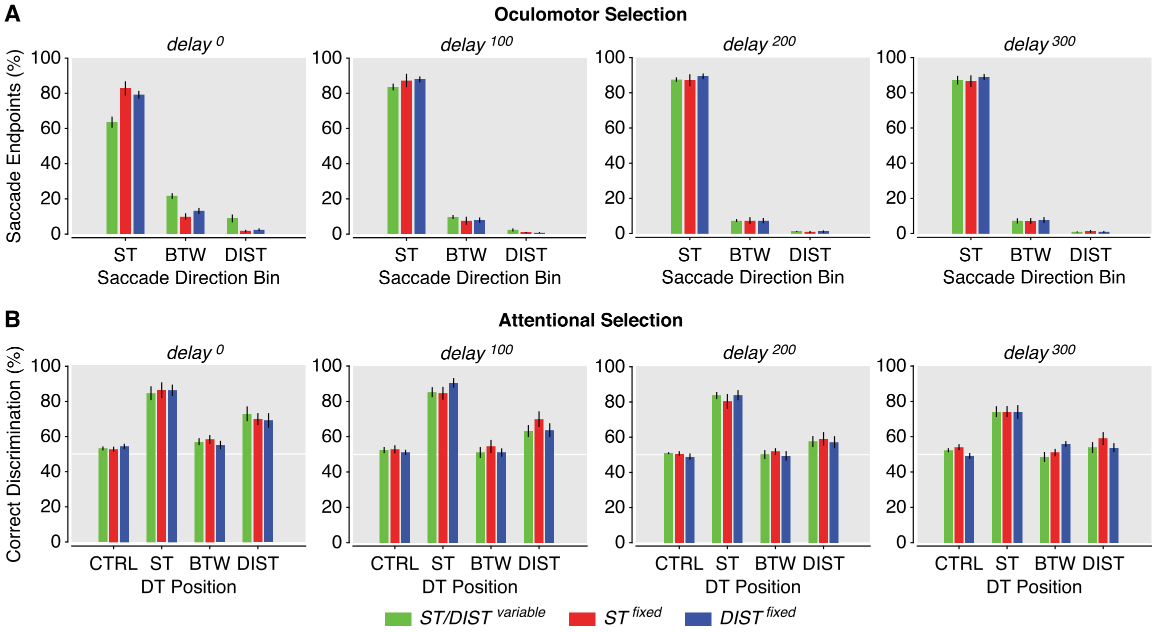

Figure 4. Saccade endpoints and visual discrimination performance during movement preparation. (**A**) *Oculomotor Selection*. Mean proportion of saccades landing around the ST, BTW, and DIST location for each spatial predictability condition (ST/DIST^{variable}: green; ST^{fixed}: red; and DIST^{fixed}: blue) for a given saccadic go-signal delay (0 - 300 ms; from left to right). (**B**) *Attentional Selection*. Mean percentage of correct orientation discrimination at CTRL, ST, BTW, and DIST for the respective conditions. Note that only trials in which the DT appeared after ST/DIST onset were included. Error bars represent SEM ($n = 9$).

$= 4.45$, $p < 0.01$, $d_z = 1.48$), but did not differ between the ST^{fixed} and DIST^{fixed} conditions (t(8) = 1.27, $p > 0.05$, $d_z = 0.42$). Thus, when either the saccade target or the distractor location was predictable, eye movements were more frequently directed to the instructed target location as compared to when saccade target and distractor locations were unpredictable.

We further investigated the observed interaction effect by comparing the proportion of target saccades within each spatial predictability condition between delay^0 and delay^{100} using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167). Here, we found that the proportion of target saccades significantly increased by approximately 20% to 83.61 ± 1.93% in the ST/DIST^{variable} condition (t(8) = 7.69, $p < 0.001$, $d_z = 2.56$). Similarly, the proportion of target saccades significantly increased by approximately 9% to 87.91 ± 1.73% in the DIST^{fixed} condition (t(8) = 6.49, $p < 0.001$, $d_z = 2.16$). Although the proportion of target saccades increased by approximately 4% to 87.25 ± 3.79% in the ST^{fixed} condition, this improvement in saccade accuracy did not reach statistical significance at corrected alpha (t(8) = 2.81, $p > 0.0167$, $d_z = 0.94$).

Taken together, these data show that a saccadic go-signal delay of 100 ms systematically improved voluntary eye movement control such that saccades more frequently landed at the instructed target location (whereas conversely reducing saccade averaging as well as the occurrence of distractor saccades). Importantly, as reflected by the differential increase in the proportion of target saccades across the spatial predictability conditions (ST/DIST^{variable}: 19.97%, ST^{fixed}: 4.46%, and DIST^{fixed}: 8.76%), this facilitatory effect of additional visual processing time was most pronounced when the saccade target and distractor locations were unpredictable.

Before proceeding with the analysis of visual discrimination performance, we evaluated whether the latency of saccades had a systematic effect on movement accuracy. As the global effect (saccade averaging) was shown to be most pronounced for short latency saccades (e.g. Findlay, 1982; Ottes et al., 1985; Coëffé & O'Regan, 1987), we compared the mean latency of target saccades (landing closest to ST) and averaging saccades (landing closest to BTW in between ST and DIST). To do so, we again collapsed data across the different spatial predictability conditions and ran a 2-way repeated measures ANOVA on the mean saccade latency for the factors saccadic go-signal delay and saccade landing bin (ST versus BTW). We found a significant main effect of go-signal delay (F(3,24) = 1149.43, $p < 0.001$), but, importantly, there was neither a significant main effect of saccade landing bin (F(1,8) = 2.64, $p > 0.05$), nor a significant interaction between go-signal delay and saccade landing bin (F(3,24) = 0.18, $p > 0.05$). In contrast to previous reports (e.g. Findlay, 1982; Ottes et al., 1985; Coëffé & O'Regan, 1987), our data therefore do not allow to conclude on a latency dependence of saccade averaging.

Visual discrimination performance

In order to assess the attentional correlates associated with the oculomotor effects obtained by the analysis of saccade endpoints, we proceeded with the analysis of visual discrimination performance after the onset of ST and DIST (i.e. only trials with a DTOA of either +50 or +100 ms).

Based on the accuracy improvements in the $\mathrm{ST}^{\mathrm{fixed}}$ and $\mathrm{DIST}^{\mathrm{fixed}}$ relative to the $\mathrm{ST/DIST}^{\mathrm{variable}}$ condition at delay^{0}, we evaluated whether spatial predictability modulated the deployment of visual attention during the preparation of undelayed saccades. In particular, we focused on assessing the influence of spatial predictability on the extent of attentional competition between the saccade target and the distractor. We therefore computed the difference in visual discrimination performance between ST and DIST (i.e. percent correct at ST - percent correct at DIST) at delay^{0} and compared respective measures between the different spatial predictability conditions using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167).

Despite the significant improvements in saccade accuracy associated with spatial predictability, the difference in visual discrimination performance between ST and DIST did not significantly differ between the $\mathrm{ST/DIST}^{\mathrm{variable}}$ (0.12 ± 0.03%), $\mathrm{ST}^{\mathrm{fixed}}$ (0.17 ± 0.05%), and $\mathrm{DIST}^{\mathrm{fixed}}$ condition (0.17 ± 0.03%), with all three comparisons yielding a $p > 0.05$. Yet, it should be noted that the difference in visual discrimination performance was quantitatively smallest in the $\mathrm{ST/DIST}^{\mathrm{variable}}$ condition (for which we observed the lowest proportion of target saccades), suggesting that attentional competition was most pronounced when both saccade target and distractor were unpredictable (see leftmost plot in Figure 4B).

Next, we focused on potential modulations of visual discrimination performance associated with the differential saccade accuracy improvements across the spatial predictability conditions, which we observed for a saccadic go-signal delay of 100 ms. To this end, we compared the difference in visual discrimination performance at ST and DIST between delay^{0} and delay^{100} for each spatial predictability condition using paired *t*-tests (at a Bonferroni-corrected alpha of 0.0167).

When ST and DIST were unpredictable ($\mathrm{ST/DIST}^{\mathrm{variable}}$), the visual discrimination benefit at ST increased significantly from delay^{0} to delay^{100} (0.12 ± 0.03% vs. 0.22 ± 0.03%; t(8) = 3.87, $p < 0.01$, $d_z = 1.29$). Thus, the pronounced facilitatory effect of a 100 ms go-signal delay on saccade accuracy in the absence of spatial predictability was indeed reflected in a reduction of attentional competition between saccade target and distractor. Contrasting with this effect, the saccade target benefit did not significantly increase when the saccade target location was fully predictable (0.17 ± 0.05% vs. 0.15 ± 0.03%; t(8) = 0.53, $p > 0.05$, $d_z = 0.18$). This absence of a statistically significant reduction of attentional competition matches with the observation that saccade accuracy improved only slightly, but not significantly, with a 100 ms go-signal delay in the $\mathrm{ST}^{\mathrm{fixed}}$ condition. When the distractor location was fully predictable – leading to a modest and statistically significant improvement in saccade accuracy – the difference in visual discrimination performance between ST and DIST only approached statistical significance at the corrected alpha (0.17 ± 0.03% vs. 0.27 ± 0.04%; t(8) = 2.91, p = 0.02, $d_z = 0.97$).

In sum, these results point toward a systematic relationship between the spatiotemporal dynamics of selective visual attention and eye movement control, which might explain the relatively low accuracy of short-latency saccades under spatial uncertainty and the improving accuracy with increasing visual processing time.

Given the emergence of perceptual effects within the rather short time window induced by a saccadic delay of 100 ms, we next evaluated the time course of selective attentional processing by analyzing visual discrimination performance across longer go-signal delays. We first collapsed data across the different spatial predictability conditions within each go-signal delay for all trials with a positive DTOA (of either +50 or +100 ms) and computed visual discrimination performance for the ST, DIST, and CTRL locations. Subsequently, we compared the measures for ST and DIST to CTRL for each go-signal delay by means of paired *t*-tests (at a Bonferroni-corrected alpha of 0.0125 for both ST and DIST comparisons). This allowed us to assess the general time course underlying the selective deployment of attentional resources to the saccade target and the distractor relative to baseline (CTRL). Visual discrimination performance at ST was significantly enhanced relative to CTRL across all go-signal delays (all p values < 0.001), that is for delay^{0} (85.53 ± 3.71% vs. 53.37 ± 1.10%; $d_z = 3.04$), delay^{100} (86.77 ± 2.96% vs. 52.12 ± 1.28%; $d_z = 4.29$) delay^{200} (82.69 ± 2.89% vs. 50.24 ± 0.96%; $d_z = 4.10$), and delay^{300} (74.24 ± 3.12% vs. 51.74 ± 0.89%; $d_z = 2.37$). At DIST, visual discrimination performance only remained significantly enhanced relative to CTRL for delay^{0} (70.50 ± 3.75%; t(8) = 5.34, $p < 0.001$, $d_z = 1.78$) and delay^{100} (65.66 ± 3.44%; t(8) = 4.16, $p < 0.01$, $d_z = 1.39$), but not for delay^{200} (57.94 ± 3.17%; t(8) = 3.18,

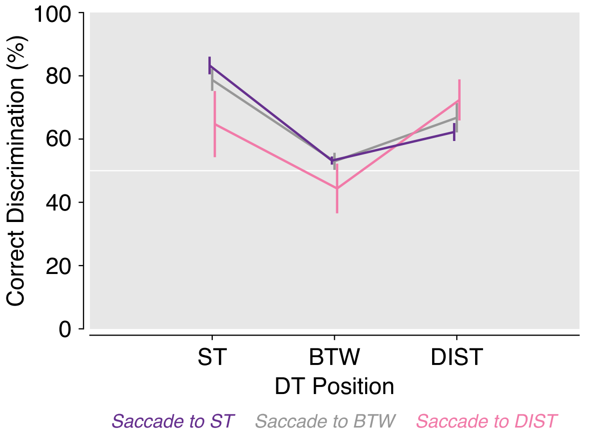

Figure 5. Visual discrimination performance depending on the saccade endpoint. Mean percentage of correct orientation discrimination at the ST, BTW, and DIST location before the execution of target saccades landing at ST (purple), averaging saccades landing at BTW (in between ST and DIST; grey), and distractor saccades landing at DIST (pink). Data were collapsed across all spatial predictability conditions (ST/DIST^{variable}, ST^{fixed}, and DIST^{fixed}), saccadic go-signal delays (0, 100, 200, and 300 ms), and positive DTOAs (+50 and +100 ms). Error bars represent SEM ($n = 9$).

$p > 0.0125$, $d_z = 1.06$) and delay^{300} (55.54 ± 2.71%; $t(8) = 1.83$, $p > 0.05$, $d_z = 0.61$).

Thus, whereas attentional resources were deployed to both the saccade target and the distractor shortly after their onset (i.e. delay^{100} and delay^{200}), they were selectively sustained across time only at the saccade target but not at the distractor.

Finally, we directly investigated the spatial relationship between the presaccadic deployment of visual attention and the saccade endpoint. To this end, we computed separate measures of visual discrimination performance at ST, BTW, and DIST for each saccade endpoint bin (see Figure 5), which allowed us to contrast the attentional correlates of target saccades, averaging saccades, and distractor saccades. To exclusively evaluate the deployment of visual attention shortly before saccade onset, we again only included trials with a positive DTOA (i.e. +50 and +100 ms relative to FT offset). Moreover, due to the low amount of averaging and distractor saccades in several conditions (especially for longer go-signal delays), we collapsed data across the different spatial predictability conditions and saccadic go-signal delays. For each subpopulation of saccades, we then conducted a paired *t*-test comparing visual discrimination performance between ST and DIST (at a Bonferroni-corrected alpha of 0.0167).

Before the execution of target saccades, visual discrimination performance was significantly enhanced at ST relative to DIST (83.27 ± 2.79% vs. 62.23 ± 2.84%; $t(8) = 7.89$, $p < 0.001$, $d_z = 2.63$). Thus, target saccades were clearly associated with a selective allocation of attentional resources to the instructed saccade target.

We also observed that visual discrimination performance was enhanced at ST (78.70 ± 3.46%) relative to DIST (66.76 ± 4.65%) prior to the execution of averaging saccades. This effect did, however, not reach statistical significance at the corrected alpha ($t(8) = 2.84$, $p > 0.0167$, $d_z = 0.95$), indicating that attentional competition between the saccade target and the distractor was not successfully resolved before the execution of averaging saccades. Following up on this comparison, to investigate whether visual attention was allocated to the endpoint of averaging saccades, we ran a one-sample *t*-test comparing visual discrimination performance at BTW (i.e. in between ST and DIST) to chance level (50%) for the subpopulation of averaging saccades. In line with previous studies (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018), we did not find a significant enhancement of visual discrimination performance at the endpoint of averaging saccades (52.96 ± 2.71%; $t(8) = 1.09$, $p > 0.05$, $d_z = 0.36$). Thus, contrary to the selective enhancement at the endpoint of target saccades, the locus of visual attention was clearly dissociated from the endpoint of averaging saccades.

Last, for the subpopulation of distractor saccades, visual discrimination performance did not significantly differ between ST and DIST (64.72 ± 10.46% vs. 72.37 ± 6.50%; $t(8) = 0.65$, $p > 0.05$, $d_z = 0.22$). Interestingly, other than for target and averaging saccades, these data show that visual discrimination performance was quantitatively most enhanced at DIST rather than ST prior to distractor saccades (note, however, the comparably large variability in these data due to the small number of distractor saccades).

In sum, the differential pattern of results observed here provides evidence for a systematic relationship between the deployment of visual attention prior to saccade onset and the endpoint of saccades. Importantly, however, the absence of a selective enhancement of visual discrimination performance at the endpoint of averaging saccades demonstrates that the locus of visual attention does not necessarily coincide with the saccade endpoint.

Discussion

This study aimed to investigate the perceptual correlates of top-down eye movement control during episodes of oculomotor competition between a saccade target and a proximal distractor. We manipulated the predictability of target and distractor locations and variably delayed movement execution in a dual-task paradigm consisting of a saccade task and a visual discrimination task. This design allowed us to concurrently assess the influence of increasing top-down control on saccade accuracy (i.e. saccade endpoint distributions) and the deployment of visual attention during movement preparation (i.e. visual discrimination performance). To our knowledge, this is the first study to systematically examine the spatiotemporal dynamics of visual attention associated with the capacity to exert top-down control over saccadic eye movements, which was solely inferred from the assessment of saccade endpoints in similar, previous studies.

The influence of spatial predictability on saccade accuracy and attentional selection

We assumed that efficient oculomotor control would be challenged by bottom-up visual competition between the saccade target and the distractor, presumably dominating the dynamics of saccade target selection early on during movement preparation (van Zoest et al., 2004; van Zoest & Donk, 2005). Accordingly, our first main hypothesis implicated that spatial predictability of target and distractor locations would provide an efficient top-down signal counteracting initial bottom-up competition, thereby enhancing movement accuracy even for short-latency saccades. Furthermore, we expected that this improvement in saccade accuracy would be reflected at the perceptual level prior to saccade onset, with attentional resources being more selectively deployed to the saccade target relative to the distractor.

Interestingly, 100 ms prior to saccade target and distractor onset, visual discrimination performance at both locations was comparable (and close to chance level) across all spatial predictability conditions. Thus, being able to predict the saccade target or the distractor location did not affect the endogenous deployment of visual attention. This indicates that the beneficial effect of spatial predictability on oculomotor selection emerged only during movement preparation. We believe that the variability of the saccadic go-signal can account for the absence of an early endogenous attentional effect. Because the fixation target offset indicated the saccadic go-signal, participants had to maintain attentional resources at fixation, which likely interfered with their ability to predictively attend to a location in the periphery.

In line with our prediction, we observed a distinct effect of spatial predictability on the accuracy of short-latency saccades. Without a saccadic delay (i.e. delay^0), the proportion of target saccades significantly increased (whereas, conversely, the proportion of averaging and distractor saccades decreased) when either the saccade target or the distractor location was predictable (ST$^{\text{fixed}}$ and DIST$^{\text{fixed}}$) compared to when both were unpredictable (ST/DIST$^{\text{variable}}$). Thus, spatial predictability improved oculomotor control even though only little time had elapsed between the presentation of the oculomotor cues and movement onset. Consistent with earlier observations (Heeman et al., 2014; Aagten-Murphy & Bays, 2017), this demonstrates that top-down mechanisms can effectively attenuate adverse effects of bottom-up competition on eye movement control in a rather fast fashion. Interestingly, our data furthermore suggest that this facilitatory effect does not depend on whether the saccade target or the distractor location could be predicted, as the proportion of target saccades did not differ between the ST$^{\text{fixed}}$ and DIST$^{\text{fixed}}$ condition. Yet, even though these two conditions likewise reduced spatial uncertainty, they differed in an important way. Whereas the saccade target was fully predictable in the ST$^{\text{fixed}}$ condition, it could appear at one out of two possible locations in the DIST$^{\text{fixed}}$ condition (clockwise or counterclockwise from the distractor). Accordingly, one might have expected a higher proportion of target saccades in the former compared to the latter condition. The absence of such an effect therefore may indicate that the mechanism subserving an early top-down modulation of oculomotor control incorporates spatial predictability in a rather unspecific manner, insensitive to the exact contingencies underlying the prediction. Alternatively, the oculomotor system might simultaneously prioritize two potentially task-relevant locations (saccade targets) without costs, such that potential differences between the two conditions were obscured. Future research may resolve this issue via assessing the effects of increased target and distractor ambiguity on saccade accuracy in dual-task designs similar to ours.

However, other than expected, we did not observe a systematic effect of spatial predictability on the deployment of attentional resources (measured as visual discrimination performance) to the saccade target and the distractor during the preparation of undelayed saccades (i.e. delay^0). This indicates that top-down signals facilitating fast eye movement control do not necessarily transfer to perception. Yet, whereas the mean difference in visual discrimination performance between saccade target and distractor was comparably large in the ST$^{\text{fixed}}$ and DIST$^{\text{fixed}}$ conditions, it was quantitatively less pronounced in the ST/DIST$^{\text{variable}}$ condition, for which we observed the lowest proportion of undelayed saccades landing at the saccade target. This may indicate that the facilitatory effect of spatial predictability on rapid eye movement control was associated with more efficient attentional target selection.

The influence of visual processing time on saccade accuracy and attentional selection

Our second main hypothesis was deduced from observations indicating that top-down mechanisms increasingly influence saccade target selection as a function of time (van Zoest et al., 2004; van Zoest & Donk, 2005; van Zoest & Donk, 2006; Carrasco, 2011; Heeman et al., 2014). Thus, we predicted that delayed saccadic go-signals – by increasing saccade latencies and thereby visual processing time prior to saccade onset – would facilitate voluntary eye movement control and attentional selection of the saccade target.

In line with this prediction, we observed a significant effect of the saccadic go-signal delay on the proportion of target saccades, replicating previously reported effects of increased movement preparation time on top-down eye movement control during oculomotor competition (Heeman et al., 2014; Aagten-Murphy & Bays, 2017). On top of this general effect, our data indicate that spatial predictability differentially affected the early time course of top-down eye movement control. A saccadic go-signal delay of 100 ms yielded a large and significant increase in the proportion of target saccades in the ST/DIST^{variable} condition. The same delay, however, yielded only a moderate (but significant) improvement in saccade accuracy in the DIST^{fixed} condition and no significant improvement in the ST^{fixed} condition. Thus, while being able to predict the saccade target or the distractor location accelerated top-down eye movement control (at delay^{0}), additional visual processing time was required to achieve a similar level of oculomotor control when saccade target and distractor locations were unpredictable. Indeed, the saccade endpoint distributions obtained in the different spatial predictability conditions for a go-signal delay of 100 ms approached each other, which suggests that already a short prolongation of visual processing time can compensate for the adverse effect of spatial uncertainty on saccade accuracy. Such a dependency of top-down oculomotor control on exposure to task-relevant visual input is in line with recent evidence from a study on memory guided saccades (Arkesteijn, Donk, Smeets, & Belopolsky, 2020), which showed that sufficient target and distractor presentation time reduces saccade averaging.

As evident in the distribution of saccade endpoints, longer delays of 200 ms and 300 ms did not notably alter saccade accuracy. This suggests that top-down control over saccadic eye movements was effectively deployed within the first 300 ms upon the visual presentation of the oculomotor cues, such that the large majority of saccades landed at the saccade target. A similar temporal pattern was reported by Aagten-Murphy and Bays (2017). Our data further add up to the proposal that saccade endpoint deviations away from a saccade target linearly decrease across a saccade latency range of up to 320 to 340 ms (Heeman et al., 2014). The current data indicate that saccade accuracy does not further improve at latencies above this range. More generally, our data support a framework in which bottom-up and top-down mechanisms operate at a different time scale, controlling saccade target selection at short and longer latencies, respectively (van Zoest et al., 2004; van Zoest & Donk, 2005; van Zoest & Donk, 2006).

In line with our prediction, the distinct improvement in saccade accuracy associated with a saccadic go-signal delay of 100 ms in the ST/DIST^{variable} condition was reflected in a reduction of attentional competition between saccade target and distractor. For this condition, the visual discrimination benefit of the saccade target over the distractor significantly increased from delay^{0} to delay^{100}. Further, in line with the far less pronounced improvements in saccade accuracy, a saccadic go-signal delay of 100 ms did not significantly improve visual discrimination at the saccade target relative to the distractor in the ST^{fixed} and DIST^{fixed} conditions. These differential effects suggest that bottom-up visual competition between saccade target and distractor was initially (at delay^{0}) highest when their locations were unpredictable, such that voluntary eye movement control improved only later (at delay^{100}), once attentional resources could be more efficiently biased toward the saccade target.

Across longer saccadic delays (delay^{200} and delay^{300}), visual discrimination performance (obtained after collapsing data across the different spatial predictability conditions) decreased both at the saccade target and the distractor. This general decline in visual discrimination benefits most likely reflects a decay of automatic bottom-up attentional effects elicited by the salient visual onsets at saccade target and distractor. Importantly, however, whereas discrimination performance at the distractor approached chance level upon a saccadic delay of 200 ms, it remained selectively enhanced at the saccade target across the entire latency range. Thus, despite a general decay of the initial bottom-up attentional effects at both the saccade target and the distractor, our data indicate that the operation of selective top-down mechanisms allowed for more sustained attentional facilitation of the saccade target. Future studies could extend our insights by systematically varying visual processing time (i.e. the presentation time of the saccade target and the distractor) independent from movement preparation time (i.e. the saccadic go-signal delay). Such a design will allow to determine whether the improvement of saccade accuracy over time depends on prolonged visual processing per se or more generally on extended movement preparation time.

The link between visual attention and saccade accuracy

Finally, the current study directly examined the relationship between visuospatial attention and the accuracy of saccadic eye movements. The analysis of visual discrimination performance as a function of the saccade endpoint allowed us to separately approximate the perceptual correlates of target saccades, averaging saccades, and distractor saccades.

Indeed, our data provide evidence linking the selective deployment of visual attention during movement preparation to the accuracy of subsequently executed saccades. For the subpopulation of target saccades, visual discrimination performance was markedly and significantly enhanced at the saccade target relative to the distractor. Thus, consistent with previous work (see also: Van der Stigchel & de Vries, 2018: page 2, lines 5–9; Wollenberg et al., 2018: page 10, lines 8–10), these data suggest that prior to saccades successfully landing at an intended target, attentional resources were selectively deployed to the movement endpoint.

This attentional benefit at the saccade target was reduced before the execution of averaging saccades, such that we observed no significant discrimination benefit for the saccade target over the distractor for these saccades. Interestingly, whereas our recent work (Wollenberg et al., 2018) demonstrated that saccade averaging is associated with an equal deployment of attentional resources to both competing oculomotor cues, the current data indicate that visual attention may be biased toward the saccade target even before the execution of averaging saccades. Note, however, that in the former study we used two physically identical saccade targets among which participants could freely choose, whereas in the current study we differentiated target and distractor by color. This increased visual discriminability of saccade target and distractor may well explain the perceptual bias toward the target observed here. Importantly, our data further showed that visual discrimination performance remained around chance level at the location between saccade target and distractor (BTW) before the execution of averaging saccades, which demonstrates that the endpoint of averaging saccades was not visually selected before movement onset. This decoupling between the locus of visual attention and the endpoint of averaging saccades is consistent with previous reports (Van der Stigchel & de Vries, 2015; Wollenberg et al., 2018). Together with similar dissociations observed at the behavioral (Belopolsky & Theeuwes, 2012; Smith, Schenk, & Rorden, 2012; Born, Mottet, & Kerzel, 2014; Hanning et al., 2019) and neuronal level (Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Thompson, Biscoe, & Sato, 2005; Gregoriou, Gotts, & Desimone, 2012), our data argue against an obligatory coupling between selective attention and the operations of the oculomotor system: Presaccadic attention is not necessarily deployed to the movement endpoint, but rather to the intended motor goal.

Finally, before the execution of distractor saccades, we observed that visual discrimination performance was not significantly enhanced at the saccade target relative to the distractor, but visual processing resources rather were slightly biased toward the distractor. However, as the total number of distractor saccades was very low, these data were much noisier compared to the data obtained for target saccades and averaging saccades, which limits interpretation. Still, our results point toward an interesting perceptual correlate of distractor saccades: Compared to target and averaging saccades, the discrimination benefit at the distractor was notably highest prior to distractor saccades. Distractor saccades therefore may reflect selection errors rather than systematic saccadic inaccuracies explained by an incomplete saccade target selection process that precedes averaging saccades.

Top-down control of saccade target selection at the neuronal level

At the neuronal level, the increase in saccade accuracy over time observed in this study can be explained by reduced competition among neuronal populations encoding the saccade target and the distractor as potential motor goals within a retinotopic saccade map (e.g. Trappenberg et al., 2001; Godijn & Theeuwes, 2002). Upon initial feed-forward (bottom-up) excitation of neuronal populations encoding both potential motor goals, active suppression of distractor-related activity within the saccade map across time may have facilitated accurate downstream oculomotor programming at longer latencies. For instance, Bichot and Schall (2002) showed that distractor-related activity in the monkey FEF starts to decay after an initial buildup, which matches with the deterioration of visual discrimination performance at the distractor over time observed in this study. Similarly, it has been suggested that visual attention can be transiently allocated at two separate locations at short latencies, but subsequently narrows down on a single target location due to competitive interactions within oculomotor key structures (Dubois, Hamker, & Van Rullen, 2009; Zirnsak, Beuth, & Hamker, 2011). Moreover, the described dynamics are in line with the model of Trappenberg et al. (2001), which proposes that visual bottom-up signals can modulate activity within the saccade map very quickly, whereas cortical top-down processes can modulate activity only after a delay. Therefore, once the exogenous effect of bottom-up excitation via the visual onsets vanishes, top-down inhibition may lead to a decay of activity at the site of the distractor in the saccade map. Similarly, top-down selection of the saccade target emerging over time presumably may lead to a more pronounced sustainment of activity at the site of the saccade target. Crucially, despite their well-established involvement in the programming of saccadic eye movements, both FEF and SC are known to carry signals underlying visual selection (Corbetta, 1998; Moore & Armstrong, 2003; McPeek & Keller, 2004; Moore & Fallah, 2004; Müller et al., 2005). We therefore propose that both FEF and SC serve as neuronal substrates underlying the perceptual and oculomotor dynamics observed in our study.

Conclusions

Our study concurrently assessed the influence of top-down control on the spatiotemporal dynamics of visual attention and the accuracy of saccadic eye movements during episodes of competition between a saccade target and a proximal distractor. In line with earlier observations, our results demonstrate that both spatial predictability and longer visual processing time can effectively facilitate voluntary eye movement control. While being able to predict either the location of the upcoming target or the distractor likewise improves the capability to rapidly move the eyes in a goal-directed fashion, prolonged visual processing time prior to saccade onset allows for improved saccade accuracy even under spatial uncertainty. Interestingly, our data indicate that the top-down signals underlying the rapid control of saccadic eye movements do not affect visual perception prior to movement preparation. Over time, however, top-down eye movement control appears to emerge concurrently with the operation of selective attentional mechanisms, which allow to better distinguish the intended saccade target from the proximal distractor at the perceptual level. Finally, we report strong evidence for a systematic interaction between the presaccadic deployment of visual attention and the endpoint of saccades: Our data demonstrate that perceptual target selection is most efficiently resolved prior to the execution of saccades accurately landing at the saccade target, whereas target selection is not readily resolved before saccades deviating away from it. The systematic relationship between visual attention and saccade accuracy does, however, not entail a mandatory coupling between the locus of visual attention and the saccade endpoint, as attentional resources are not deployed to the endpoint of averaging saccades.

Keywords: saccade, attention, saccade averaging, competition, selection

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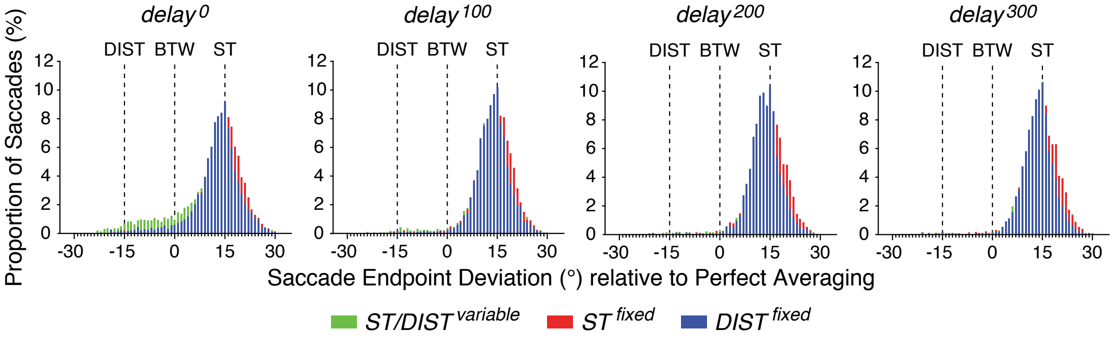

Supplementary Figure S1. Saccade endpoint distributions. Saccade endpoint data for each spatial predictability condition ($\text{ST/DIST}^{\text{variable}}$: green; ST^{fixed}: red; $\text{DIST}^{\text{fixed}}$: blue) and each saccadic go-signal delay (0 - 300 ms; from left to right) collapsed across all participants. We computed the angular deviation (in degree) of saccade endpoints relative to perfect averaging, i.e. the intermediate stimulus stream BTW. Negative values indicate deviation towards the distractor, positive values indicate deviation towards the saccade target. Dashed vertical lines mark the saccade target (ST at 15 degree), the intermediate stimulus stream (BTW at 0 degree), and the distractor (DIST at -15 degree).

2.3 Eye and hand movements disrupt attentional control

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Author contributions:

Nina M. Hanning designed the study, programmed the experiment, collected, analyzed, interpreted, and visualized the data, and wrote the manuscript.

Luca Wollenberg contributed to the study design, participated in interpreting the results, and commented on the manuscript.

Donatas Jonikaitis contributed to the study design, participated in interpreting the results, and participated in writing the manuscript.

Heiner Deubel contributed to the study design, participated in interpreting the results, and commented on the manuscript.

Eye and hand movements disrupt attentional control

Abbreviated title: Failed attentional control

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Abstract

Voluntary attentional control is the ability to selectively focus on a subset of visual information in the presence of other competing stimuli. While it is well established that this capability is a marker of cognitive control that allows for flexible, goal-driven behavior, it is still an open question how robust it is. In this study we contrasted voluntary attentional control with the most frequent source of automatic, involuntary attentional orienting in daily life—shifts of attention prior to goal-directed eye and hand movements. In a multi-tasking paradigm, we asked participants to attend at a location while planning eye or hand movements elsewhere. We observed that voluntary attentional control suffered with every simultaneous action plan. Crucially, this impairment occurred even when we reduced task difficulty and memory load—factors known to interfere with attentional control. Furthermore, the performance cost was limited to voluntary attention. We observed simultaneous attention benefits at two movement targets without attentional competition between them. This demonstrates that the visual system allows for the concurrent representation of multiple attentional foci. It further reveals that voluntary attentional control is extremely fragile and dominated by automatic, premotor shifts of attention. We propose that action-driven selection disrupts voluntary attention and plays a superordinate role for visual selection.

Introduction

Attentional control is the ability to select relevant visual information in the presence of other, non-relevant stimuli [Posner, 1980; Treisman, 1982]. This selection is also referred to as top-down, or task-driven attention, and can be contrasted to bottom-up attention which automatically selects stimuli based on their unique properties [Müller & Rabbitt, 1989; Theeuwes, Kramer, Hahn, Irwin, 1998; Klein, 2000; Carrasco, 2004; Carrasco, 2011]. Top-down selection is typically investigated by having humans and non-human animals attend to one out of several stimuli, either by instruction or manipulating reward probabilities [Found & Müller, 1996; Ciaramitaro, Cameron, Glimcher, 2001; Anderson, Laurent, Yantis, 2011; Baruni, Lau, Salzman, 2015]. Generally, attentional control is proposed to play a crucial role in the transition from automatic to flexible, adaptive behavior [Aston-Jones, Desimone, Driver, Luck, & Posner, 1999; Munoz & Everling, 2004; Schütz, Trommershäuser, & Gegenfurtner, 2012].

A separate line of research has focused on visual attention in the context of motor actions. Eye movements [Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Montagnini & Castet, 2007; Jonikaitis, Klapetek, Deubel, 2017; Hanning, Szinte, Deubel, 2019] as well as hand movements [Deubel, Schneider, & Paprotta, 1998; Baldauf, Wolf, & Deubel, 2006; Hesse & Deubel 2011; Rolfs, Lawrence & Carrasco, 2013] are preceded by shifts of attention to their motor targets. These premotor shifts of attention are thought to occur automatically when we explore or interact with our environment; in other words, without any instructions or reward manipulations [Baldauf & Deubel, 2010]. Attentional control and premotor attention frequently share a common goal: Behaviorally relevant or rewarded objects are typically also motor targets [Land & Lee, 1994; Land & McLeod, 2000]. However, given that premotor attention is thought to be automatic while attentional control is task-driven and voluntary, the relationship between the two has not yet been defined.

Several frameworks can be used to describe the relationship between attentional control and premotor attention. The key approach to study attentional control is the *visual search* paradigm, which requires top-down or voluntary attention to select task relevant information [Treisman, 1982]. Unfortunately, visual search paradigms frequently require gaze to be maintained stable and do not measure eye movements. They typically assume that, under free-viewing conditions, gaze would be directed to the attended location [McPeek, Skavenski, Nakayama, 2000; Peters, Iyer, Itti, & Koch, 2005; Bichot, Rossi, & Desimone, 2005]. Thus, even though it is implied in these studies that attentional control drives premotor attention, the relationship between the two is not directly investigated. Based on the visual search paradigm, a more formal framework has been proposed, referred to as *salience maps or priority maps* [Itti & Koch, 2001; Thompson & Bichot, 2005; Fecteau & Munoz, 2006; Bisley & Goldberg, 2010]. Within these maps, bottom-up and top-down signals are thought to be integrated in a winner-take-all process. Subsequently, the highest activity peak on the map determines the attentional focus, to which eye movements can be potentially directed [Itti & Koch, 2001]. This framework again links attentional control and premotor attention without explicitly testing their relationship.

While visual-search-based theories assume that eye movements *follow* the attentional focus, the *premotor theory of attention* proposes the opposite, namely that visual attention is a product of the motor system. In order to shift attention covertly (i.e., without moving the eyes) a motor program still has to be prepared, yet not necessarily executed [Rizzolatti, Riggio, Dascola, Umiltá, 1987; Craighero, Fadiga, Rizzolatti, Umiltà, 1999]. While this theory can explain automatic attention shifts to motor targets in the absence of any instruction or reward manipulation, a tight coupling does not prove that visual attention in fact arises from motor preparation. Instead, the reverse might be true, and visual attention is necessary to successfully perform a motor action. This alternative account states that attentional selection is required to specify the motor coordinates for an upcoming movement [Schneider, 1995; Baldauf & Deubel, 2010]. Baldauf and Deubel (2010) proposed an *attentional landscapes* framework which explicitly deals with multiple attentional foci, as they can occur during simultaneous eye-hand movements [Jonikaitis & Deubel, 2011; Hanning, Aagten-Murphy, & Deubel, 2018; Kreyenmeier, Deubel, & Hanning, 2020]. While cognitive control and premotor attention are closely linked in both frameworks, the implied direction of this relationship is opposite.

The above discussed frameworks vary markedly in their assumptions. The relationship between attentional control and premotor attention is either not directly specified (visual search & priority maps), or attention is necessarily driven by motor selection (premotor theory of attention), or, the contrary, motor selection requires attention, but not the other way around (attentional landscapes). Crucially, these contrasting assumptions have not yet been addressed. It is therefore still an open question how reflexive, automatic information selection in the context of motor actions interacts with adaptive, controlled attentional selection.

We investigated these two components of attentional selection using a classical dissociation approach in which we pitted premotor attention shifts against the capability to maintain voluntary spatial attention. This approach can reveal competition or prioritization between premotor and voluntary attention. Our participants were required to attend to a given location (*voluntary attention*) while simultaneously preparing an eye movement (*premotor attention to eye*) and/or hand movement (*premotor attention to hand*) to another location. If all three tasks interact equally with each other, this would indicate dual-task costs, whereas distinct interaction patterns can differentially support or refute the above discussed frameworks. We used local visual discrimination performance as a proxy of visuospatial attention during premotor and voluntary selection, and systematically biased participants' deployment of voluntary attention by informing them about which location was most likely to contain the discrimination signal—a briefly presented oriented noise patch. Our data revealed that any type of attentional selection, voluntarily as well as premotor, was associated with improved discrimination performance at the target location. Furthermore, we observed no indication of attentional competition between the eye and the hand motor target. In striking contrast, voluntary attentional selection suffered with every motor action being planned, revealing that eye and hand movement preparation abolishes attentional control. This demonstrates that the visual system selectively prioritizes automatic shifts of attention to motor targets over top-down attentional control.

Results

In **Experiment 1** participants were instructed to perform different combinations of three possible tasks: endogenously attending to a specific location (*Attention*), executing an eye movement (*Eye*), and executing a hand movement (*Hand*) to a centrally cued target. Concurrently, they performed a two-alternative forced-choice discrimination task (***Figure 1a***) based on oriented pink noise patches [Hanning, Deubel, Szinte, 2019] (***Figure 1b***). Orientation discrimination performance at the endogenously attended location, at the motor target location(s), and at neutral locations (i.e., movement-irrelevant, non-target control locations) served as a proxy for visuospatial attention during motor target and endogenous perceptual selection. Altogether, the experiment comprised seven tasks: *Attention-only*, *Eye-only*, *Hand-only*, *Eye-Hand*, *Attention-Eye*, *Attention-Hand*, *Attention-Eye-Hand* (see ***Figure 1c*** for stimulus timing).

First, we measured the pattern of attentional selection during each of the above conditions (***Figure 2a***). In the *Attention-only* task, we biased discrimination signal probability to guide voluntary attention: the discrimination signal was most likely to appear at the to be attended location (75% probability). Performance at the attention target was better than at the non-targets (p = 0.001), indicating that participants deployed voluntary attention to the most probable discrimination signal location [Carrasco, 2004; Müller & Rabbit, 1989]. In the *Eye-only* and the *Hand-only* task, performance at the eye target (p = 0.001) and the hand target

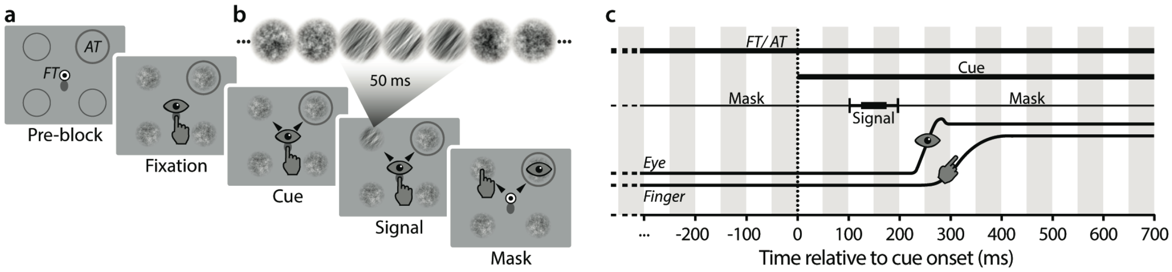

Figure 1. Methods. (**a**) Example trial sequence of the *ATT-EYE-HAND* task (Experiment 1). Throughout the block, the endogenous attention target (AT) was marked by a dark gray circle. Participants maintained central eye and finger fixation until two black arrow cues occurred that marked two of four noise patches as motor targets. Participants reached towards one and simultaneously saccaded towards the other motor target. Before movement onset, one of the noise streams showed a clockwise or counterclockwise orientation signal. After the movements and a masking period, participants indicated their discrimination judgement via button press. (**b**) Noise streams used as discrimination stimuli. Each of the four noise streams consisted of a succession of randomly generated 1/f noise patches.The test stream comprised a 50 ms sequence of orientation filtered 1/f noise patches showing a clockwise or counterclockwise tilt. (**c**) Stimulus timing. Fixation (FT) and attention target (AT) remained on the screen throughout the trial. 400 to 800 ms after the onset of four noise pre-masks (M), the motor cues were presented. 100 ms after cue onset, one of the noise streams contained the orientation test signal, which was masked after 50 ms.

(*p* = 0.004) was similarly enhanced relative to the movement-irrelevant locations which were equally likely to contain the discrimination signal. This demonstrates that attention shifted automatically to the motor targets, independent of discrimination signal probability.

Next, we investigated interactions between these three sources of attentional selection (***Figure 2b***). In the *Eye-Hand* task, participants simultaneously performed eye and hand movements to either shared or separate targets. When the two movements were made to separate target locations, we observed improved performance both at the eye (*p* = 0.003) and the hand target (*p* = 0.007) compared to the movement-irrelevant locations, and the attentional benefit at the two motor targets did not differ (*p* = 0.219). When participants made simultaneous eye-hand movements to a shared target, performance at that location was also significantly improved (*p* = 0.005), and comparable to performance when eye and hand movements were directed to separate locations (compared to the eye target: *p* = 0.431; compared to the hand target: *p* = 0.515). Importantly, relative to single effector movements (i.e. *Eye-only* and *Hand-only*), combined effector movements to separate locations did neither reduce discrimination performance at the eye target (*p* = 0.819) nor at the hand target (*p* = 0.366). In summary, this demonstrates that during simultaneous eye-hand movements, attention is deployed to both motor targets in parallel without any observable cost, which is in line with previous studies [Jonikaitis & Deubel, 2011; Hanning et al., 2018; Kreyenmeieret al., 2020; but see Khan, Song, & McPeek, 2011].

To investigate how voluntary attentional control interacts with motor planning, we asked participants to attend at one location while preparing an eye or hand movement to another (*Attention-Eye* task, *Attention-Hand* task). These two tasks create a conflict: while the discrimination signal was most likely to appear at the voluntary attention target, the movement target was more likely to be at a different, non-predictable location. In the *Attention-Eye* task, when eye movement target location and voluntarily attended location coincided, this mutual target, as expected, received a discrimination benefit (*p* = 0.001). When voluntary attention and eye movement were directed to separate locations, we observed enhanced performance at the eye target (*p* = 0.001) and a small performance benefit at the attention target (*p* = 0.015; note that $p_{corrected}$ = 0.060). Moreover, performance at the attention target was worse than at the eye target (*p* = 0.001). We observed similar results for voluntary attention during hand movement preparation. In the *Attention-Hand* task,

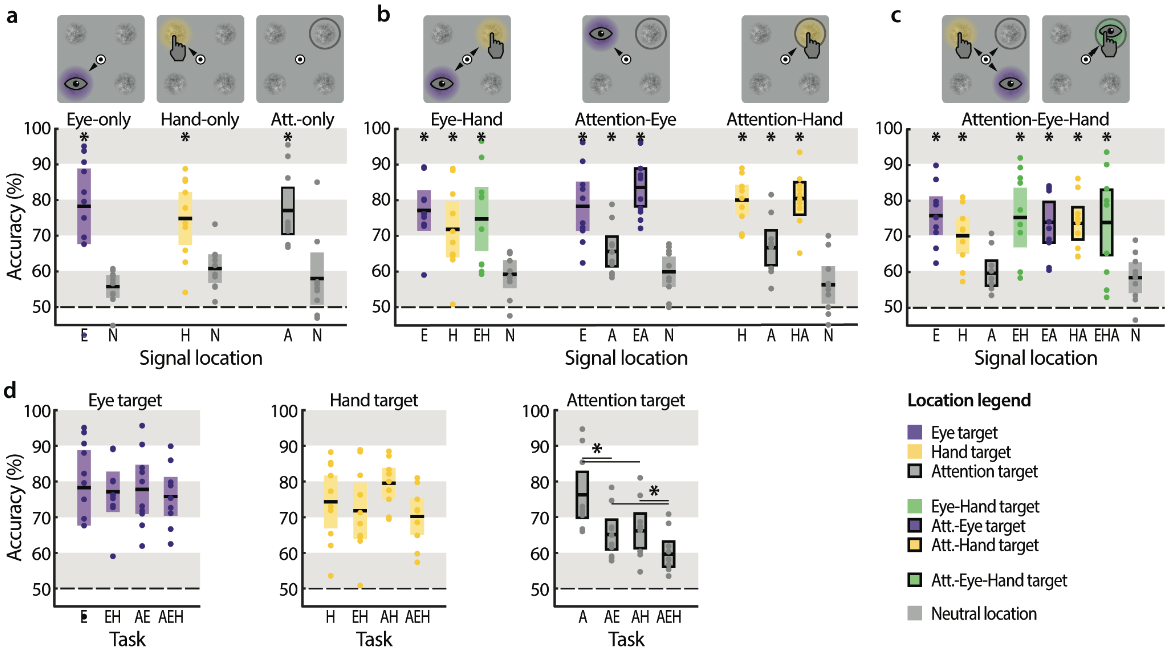

Figure 2. Voluntary and premotor attentional selection. Discrimination performance at the different test locations of the single target tasks (**a**), double target tasks (**b**), and tripe target task (**c**) of Experiment 1. Black lines within each whisker plot indicate the group average. Colored bars depict the 95% confidence interval, dots represent individual subject data, and dashed lines mark chance performance. *$p < 0.05$, significant difference between a location and the neutral location of the respective task. (**d**) Discrimination performance at the eye target (left), hand target (middle), and attention target (right) as a function of the experimental task. *$p < 0.05$, all significant difference between tasks are indicated by horizontal lines. Other conventions as in (a).

performance at the attention target (p = 0.007), the hand target (p = 0.001), and the shared hand-attention target (p = 0.001) was significantly enhanced. Again, the attentional benefit at the attention target was smaller than at the hand target (p = 0.001). To summarize, in contrast to the *Eye-Hand* task, in which attention was equally distributed to both motor targets, attention was clearly biased towards the motor target in the *Attention-Eye* and the *Attention-Hand* tasks.

We put further stress on attentional control by asking participants to simultaneous attend to a location while preparing both an eye and a hand movement (***Figure 2c***, *Attention-Eye-Hand*). As before, we observed a clear attentional benefit at the eye target (p = 0.001), the hand target (p = 0.002), and the combined eye-hand target (p = 0.001). However, even though the discrimination signal was most likely to appear at the voluntary attention target, participants were not able to maintain voluntary attention there (p = 0.534).

A direct comparison of performance across the different motor tasks showed that this decrease in performance was limited to voluntary attention and did not apply to motor targets (***Figure 2d***). Performance at the eye target was consistently enhanced whether only an eye movement was prepared, or the eye movement was accompanied by either a hand movement (p = 0.819), voluntary attentional selection (p = 0.893), or both (p = 0.645). Likewise, attention was consistently deployed to the hand target, independently of whether the hand movement was accompanied by an eye movement (p = 0.366), voluntary attentional selection (p = 0.180), or both (p = 0.150). In other words, performance at the motor targets in the combined eye-hand movement task was indistinguishable from the respective performance in the single (eye only or hand only) tasks, demonstrating that the attentional selection of one motor target did not affect the selection of the other. In direct contrast, voluntary attentional control was hampered by motor programming: performance at the attention target was reduced whenever a single eye movement (p = 0.001) or single

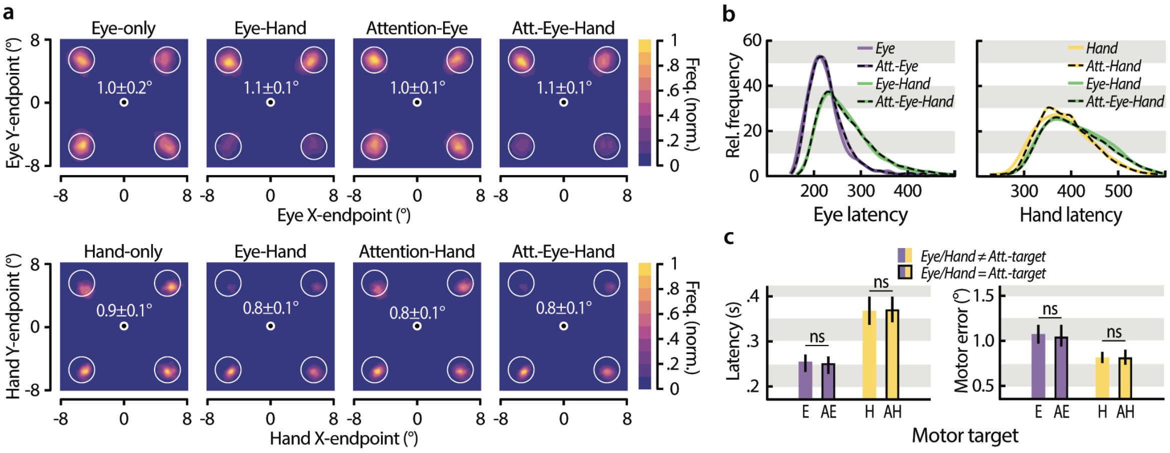

Figure 3. Movement latencies and precision. (**a**) Normalized eye (top row) and hand (bottom row) landing frequency maps averaged across participants in the respective tasks. White values depict the average distance between movement endpoint and target center as well as the the 95% confidence interval. (**b**) Relative frequency of eye (left) and hand right) latencies in the respective tasks. (**c**) Eye and hand movement latencies (left) landing errors (middle) and endpoint variance (right) across all tasks split as to whether the movement was made to an endogenously attended location (AE, AH) or not (E, H). Error bars denote the 95% confidence interval.

hand movement (*p* = 0.003) were planned. Importantly, performance decreased even further when both an eye and a hand movement simultaneously were directed away from the attended location (compared to single eye movement: *p* = 0.001; compared to single hand movement: *p* = 0.009). Thus, while attentional control was already affected by single movements, it was practically annihilated during simultaneous eye and hand movement preparation.

We observed that voluntary attention was reduced when participants made an eye or hand movement. Conversely, however, voluntary attention did not affect perceptual performance at the motor targets. We next investigated whether voluntary attention interfered with eye or hand movement preparation in any other way, for example by decreasing movement accuracy or prolonging movement latencies.

We first compared eye and hand landing positions across the different motor tasks (***Figure 3a***). Generally, when two motor targets were cued (*Eye-Hand* and *Attention-Eye-Hand* task) participants tended to select the upper locations as eye targets and the lower locations as hand targets. However, neither eye nor hand movement precision—measured as the average distance of the movement endpoint from motor target center—differed between the respective single movement tasks (*Eye-only* / *Hand-only*) and the multiple target tasks (Eye movement precision: *Eye-only* vs. *Eye-Hand*: *p* = 0.229*3, vs. *Attention-Eye*: *p* = 0.957*3, vs. *Attention-Eye-Hand*: *p* = 0.308*3; Hand movement precision: *Hand-only* vs. *Eye-Hand*: *p* = 0.060*3, vs. *Attention-Hand*: *p* = 0.721, vs. *Attention-Eye-Hand*: *p* = 0.037). Thus, neither the requirement to program a second movement nor to deploy voluntary attention affected eye and hand movement precision. In contrast, we observed interactions between eye and hand movement control with respect to movement latencies. Compared to the *Eye-only* task (***Figure 3b***; left), eye movement onsets were significantly delayed in tasks in which also a hand movement had to be prepared (*Eye-only* vs. *Eye-Hand*: *p* = 0.001, vs. *Attention-Eye-Hand*: *p* = 0.001), which is in line with earlier work [Jonikaitis & Deubel, 2011]. Having to attend voluntarily, however, did not slow down eye movement execution (*Eye-only* vs. *Attention-Eye*: *p* = 0.106). Likewise, hand movement latencies (***Figure 3b***; right) were slightly prolonged by simultaneous eye movement preparation (*Hand-only* vs. *Eye-Hand*: *p* = 0.019, vs. *Attention-Eye-Hand*: *p* = 0.012), but again

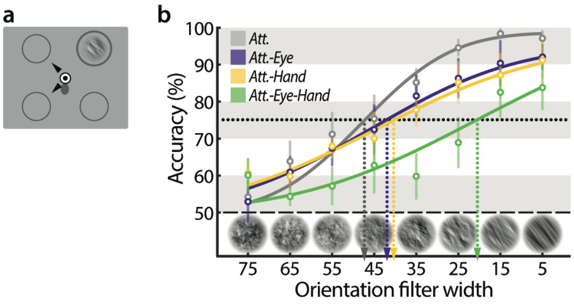

Figure 4. Costs of action-selection for voluntary attention. (**a**) Stimuli configuration in Experiment 2. One noise stream was presented at a fixed location, marked by a circle. Participants maintained central eye and finger fixation until one (*Attention-Eye* or *Attention-Hand*) or two (*Attention-Eye-Hand*) black arrow cues occurred, indicating the motor target(s). Participants reached and / or saccaded towards the motor target(s) upon cue onset. In the *Attention* task no cue occurred and participants maintained fixation. After 100 - 200 ms the noise stream displayed a brief orientation, which participants discriminated via button press at the end of the trial. (**b**) Group-averaged psychometric functions (discrimination performance vs. orientation filter width) for each task. Error bars denote the between subject SEM.

not by voluntary attention (*Hand-only* vs. *Attention-Hand*: $p = 0.301$). Note that the effect of hand movement on eye movement execution was considerably more pronounced than vice versa.

To investigate the influence of voluntary attentional control on movement execution, we evaluated movement latencies (***Figure 3c***; left) and landing errors (defined as the distance between movement endpoint and target center; ***Figure 3c***; right) depending on whether the movement was made to the voluntarily attended location or not. Neither for eye nor for hand movements we observed a significant difference in latencies (*Eye-only* vs. *Attention-Eye*: $p = 0.164$*1; *Hand-only* vs. *Attention-Hand*: $p = 0.118$*1) or landing errors (*Eye-only* vs. *Attention-Eye*: $p = 0.517$; *Hand-only* vs. *Attention-Hand*: $p = 0.865$*1), demonstrating that attentional control affected neither movement onset nor precision.

Our results showed that preparing eye or hand movements interferes with voluntary attention. In an attempt to reduce the interference of motor preparation on attentional control, we optimized conditions to favor voluntary attention deployment in **Experiment 2**. In this experiment, we presented only one noise stream that always contained the discrimination signal, which removes any potential uncertainty as to where to attend or respond (***Figure 4a***). Participants either attended to that location (*Attention-only*), or attended and made eye (*Attention-Eye*), hand (*Attention-Hand*), or simultaneous eye-hand movements (*Attention-Eye-Hand*) away from this location. In this experiment, we varied the width of the orientation filter used to create the discrimination signal (the smaller the width, the clearer the orientation) and assessed perceptual performance by measuring psychometric thresholds—an alternative approach to quantify attention [Carrasco, 2011].

In line with our previous findings, motor preparation consistently reduced participants' ability to voluntary attend (***Figure 4b***). This was evident in the psychometric functions' slopes and thresholds. In the *Attention-only* task, the slope ($m = 0.59$ [0.37, 1.58]) was steeper than in the *Attention-Eye* task ($m = 0.37$ [0.26, 0.65]) and the *Attention-Hand* task ($m = 0.32$ [0.17, 0.57]). In the hardest version of the task (*Attention-Eye-Hand*), the detrimental effect of motor-preparation on attentional control was even more pronounced ($m = 0.29$ [0.07, 1.38]). When estimating thresholds at a fixed discrimination performance level of 75% we observed a matching pattern: the highest threshold in the *Attention-only* task ($\alpha = 47.21$ [41.89, 53.51]), followed by the two single movement tasks (*Attention-Hand*: $\alpha = 42.09$ [31.11, 49.12], *Attention-Hand*: $\alpha = 40.16$ [31.40, 47.22]). Correspondingly, performance in the *Attention-Eye-Hand* task yielded the lowest threshold (*Attention-Eye-Hand*: $\alpha = 20.50$ [0.98, 36.44]). In summary, even though we provided optimal conditions for voluntary attentional control by decreasing task difficulty and memory load, motor preparation nonetheless markedly impaired voluntary attentional selection.

Discussion

We studied the relationship between voluntary attentional selection and automatic attention shifts before goal-directed motor actions. We observed robust perceptual benefits (a marker for attention deployment) under the typically investigated single-task conditions: at eye movement targets [Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Montagnini & Castet, 2007; Jonikaitis, Klapetek, Deubel, 2017; Hanning, Szinte, Deubel, 2019], hand movement targets [Deubel et al., 1998; Baldauf et al., 2006; Rolfs et al., 2013], as well as endogenously attended locations [Posner, 1980; Müller & Rabbitt, 1989; Montagna, Pestilli, & Carrasco, 2009]. Under multiple-task conditions, when participants either had to select two or even three locations, we observed a dissociation between the investigated sources of attention. There was no attentional competition between the eye and the hand motor targets. In striking contrast, voluntary attentional selection suffered from every simultaneous action plan.

Our results reveal that the visual system selectively prioritizes automatic, premotor shifts of attention over voluntary attentional control, and demonstrate that voluntary attentional selection is extremely fragile. Even though task instructions and stimulus probabilities particularly facilitated voluntary attentional orienting, it was consistently susceptible to disruption by both eye and hand movements. Indeed, one could have expected the opposite, namely that in order to maintain attentional control, discrimination performance should have dropped at motor goals.

Earlier studies observing that eye movements compete with voluntary attention or vice versa [Montagnini & Castet, 2007; Deubel, 2008] cannot rule out that participants prioritized one task over the other due to increased difficulty (dual- as compared to a single-task condition). Using different levels of task difficulty (one to three attention targets), we show that voluntary attention was increasingly impaired, whereas, crucially, performance at eye and hand movement targets did not suffer. This dissociation—a cost for endogenous attention yet no interference for eye and hand premotor attention—rules out that increased task or attentional selection difficulty can explain the loss of attentional control. Further, even when there was only a single location to be voluntarily attended (Experiment 2), we observed a decrease in attentional control whenever an eye or hand movement was planned away from this location. This shows that neither reduced stimulus location uncertainty nor the attention target being the only salient stimulus presented could prevent the observed loss of attentional control.

Different aspects of our results are not compatible with other major frameworks referring to the relationship between attentional control and premotor attention. First, our and earlier observations of multiple, simultaneous attentional peaks [Baldauf & Deubel, 2009; Jonikaitis & Deubel, 2011; Gilster, Hesse, & Deubel, 2012; Hanning et al., 2018; Kreyenmeier et al., 2020], are not compatible with *priority map* models assuming a strict winner-take-all attentional selection, in which performance benefits should occur only at the highest peak [Itti & Koch, 2001; Thompson & Bichot, 2005; Fecteau & Munoz, 2006; Bisley & Goldberg, 2010]. Second, our finding that eye and hand movements draw attention away from the voluntary attended location is incompatible with the view that motor actions merely follow the current focus of voluntary attention, as is assumed in visual search frameworks [Treisman, 1982; Itti & Koch, 2001; Müller & Krummenacher, 2006; Theeuwes & Burger, 1998]. Third, the *premotor theory of attention* [Rizzolatti et al., 1987; Craighero et al., 1999] assumes that any shift of attention is equivalent to a saccade plan, which offers two testable predictions. First, when the saccade target matches the endogenously attended location, saccadic latencies should be shorter. Our data show that they are not. Second, when the saccade is directed away from the endogenously attended location, two “saccade plans” are technically required. As these should compete with each other, attention allocation to both locations should decrease. Our data show that this also was not the case. In summary, our findings cannot be explained by priority map, visual search, or the premotor theory of attention frameworks without modifying their core assumptions.

Our findings are in line with the proposal of an *attentional landscape*—a map representing the attentional distribution across space [Baldauf & Deubel, 2010]. This framework allows for a simultaneous deployment of visual attention to several action-relevant locations, observed as multiple "attentional peaks". These peaks can vary in magnitude to reflect different degrees of attentional allocation. Indeed, our results demonstrate that attention can be allocated to multiple locations at a time. Multiple stimuli are typically assumed to compete for attentional selection [Bundesen, 1990; Bundesen & Habekost, 2014]. We found that motor goals are prioritized in this attentional selection. Further in line with this view, we observed that the peak performance associated with endogenous attentional selection decreases gradually with every motor action added.

Some of our behavioral effects can be linked to earlier neurophysiological studies. First, activity within visual areas is consistently modulated by visual attention [Moran & Desimone, 1985; McAdams, Maunsell, 1999], and this modulation is thought to result in corresponding changes in perceptual performance [Moore & Fallah, 2004; Lovejoy & Krauzlis, 2010; Fernández & Carrasco, 2020]. Several studies focusing on voluntary attention, or attentional control, have observed this modulation throughout the hierarchy of the visual system, ranging from occipital [Mazer & Gallant, 2003; Reynolds & Chelazzi, 2004; Serences, 2008] over parietal [Colby, Duhamel, & Goldberg, 1996; Ipata, Gee, Bisley, & Goldberg, 2009] to frontal cortex [Juan, Shorter-Jacobi, & Schall, 2004; Schafer & Moore, 2007; Cosman, Lowe, Zinke, Woodman, & Schall, 2018; Jonikaitis & Moore, 2019]. Second, eye movement preparation modulates neuronal activity in visual cortical areas in a manner indistinguishable from voluntary attention [Moore & Armstrong, 2003]. The neural sources for this modulation are assumed to be fronto-parietal feedback connections converging onto earlier visual areas [Moore & Fallah, 2004; Armstrong & Moore, 2007; Ekstrom, Roelfsema, Arsenault, Bonmassar, & Vanduffel, 2008; Rolfs & Szinte, 2016]. This has led to multiple proposals that oculomotor areas could serve as an attentional source or map [Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Bisley & Mirpour, 2019]. Third, our behavioral observation of multiple attentional peaks can be related to simultaneous and distinct activity peaks observed in human and monkey neurophysiology studies [Morawetz, Holz, Baudewig, Treue, & Dechent, 2007; Baldauf, Cui, & Andersen, 2008; Niebergall, Khayat, Treue, & Martinez-Trujillo, 2011; Steinmetz & Moore, 2014; Saber, Pestilli, & Curtis, 2015].

The neurophysiological basis for other key aspects of our findings however is still lacking. First, there is no evidence of the source of premotor attention signals to visual cortex before hand movements. These feedback-signals could originate from reach-related or oculomotor areas—but this has not yet been investigated. Thus, it is not known whether neuronal activity associated with premotor attention before eye and hand movements occurs simultaneously in the same area, or in separate areas. Given how consistently attention is shifted before reaching [Deubel et al., 1998; Baldauf et al., 2006; Rolfs et al., 2013] and grasping movements [Hesse & Deubel, 2011; Hesse, Schenk, & Deubel, 2012], understanding the underlying neural circuitry is crucial to comprehend the mechanisms that govern attentional selection in real-life situations.

Second, interactions between endogenous and premotor attention likewise have not yet been explained neurophysiologically. Oculomotor areas are thought to be the common source for presaccadic and covert voluntary attention [Moore & Fallah, 2004; Armstrong & Moore, 2007; Ekstrom et al., 2008]. It is therefore unclear why both eye movement and hand movement planning do compete with voluntary attention, but no competition is observed between multiple motor targets [Godijn, Theeuwes, 2003; Baldauf & Deubel, 2008; Baldauf & Deubel, 2009; Jonikaitis & Deubel, 2011; Hanning et al., 2018; Kreyenmeier et al., 2020]. Third, we do not know whether the neuronal modulations associated with eye, hand, and voluntary spatial attention can be observed in a common area (e.g., frontal, parietal, visual or subcortical areas), suggesting a common attentional map, or whether they arise from different areas. In the latter case, attention to multiple targets could activate separate areas without integrating activity between them (and thus limiting premotor competition between attentional goals). As evidence in favor of a common attentional map has mainly been collected under experimental conditions requiring eye and hand fixation, those conclusions may be biased. It is equally possible that separate, effector-specific maps show attentional modulation during eye and hand movement target selection. Such separate maps could explain the absence of premotor attentional competition between different effectors. In sum, our results show that there are multiple questions to be answered if one wants to explain everyday attentional selection.

In everyday life we continuously explore and interact with our environment. Our findings reveal that whenever our eye or hand movement goals do not match our attentional control settings, attentional control cannot be maintained. Thus, attentional control is likely to fail as frequently as we move. We typically avoid this failure by aligning our attentional control and movement goals. While the classical understanding of attention underscores covert attentional orienting in the absence of motor actions, such situations of immobility are rare, if not artificial. Actions are typically considered the *consequence* of attentional control. Our data however show that actions take precedence over attentional control. We therefore propose to refocus from considering action as the strict consequence of voluntary attentional control to viewing action as the main determinant of successful or failed visual selection.

Materials and Methods

Participants and setup

The sample sizes were determined based on previous work [Jonikaitis & Deubel, 2011; Hanning et al., 2018]. Ten participants (ages 23–31 years, 7 female) completed Experiment 1, six participants (ages 23–28 years, 4 female) took part in Experiment 2. All participants were healthy, had normal vision and, except for one author (N.M.H.), were naive as to the purpose of the experiments.

Gaze position was recorded using an EyeLink 1000 Tower Mount (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. Manual responses were recorded via a standard keyboard. The experimental software controlling display, response collection, as well as eye tracking was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics [Brainard, 1997; Pelli, 1997] and EyeLink toolboxes [Cornelissen, Peters, & Palmer, 2002]. Stimuli were presented on a 45° inclined touchscreen (Elo 2700 IntelliTouch, Elo Touchsystems, Menlo Park, CA) with a spatial resolution of 1280x1024 pixels and a refresh rate of 60 Hz.

Experimental Design

Experiment 1 comprised seven tasks (randomized block design): *Attention-only*, *Eye-only*, *Hand-only*, *Eye-Hand*, *Attention-Eye*, *Attention-Hand*, *Attention-Eye-Hand*. ***Figure 1a*** depicts the sequence for the *Attention-Eye-Hand* task: Participants initially fixated a central fixation target (FT) comprising a black (~0 cd/m2) and white (~98 cd/m2) “bull's eye” (radius 0.5°) on a gray background (~60 cd/m2). Their right index finger remained on a gray oval (0.6° x 0.65°, ~22 cd/m2) slightly below the eye fixation. At the beginning of each block, four equally spaced locations were marked by gray circles (radius 1.7°) at an eccentricity of 8° from fixation. One of the four locations (randomly selected) was framed in dark gray (~24 cd/m2), indicating the attention target (AT), i.e. the location which participants should aim to attend to endogenously. Note that no such attention target was indicated in the *Eye-only*, the *Hand-only*, and the *Eye-Hand* task. Once stable eye and finger fixation was detected within a 2.5° radius virtual circle centered on the fixation targets, four streams of 1/f spatial noise patches (radius 1.7°) appeared at the marked locations. Each noise stream consisted of randomly generated 1/f noise patches windowed by a symmetrical raised cosine (radius 1.7°, sigma 0.57), refreshing at 60 Hz (***Figure 1b***). After 400 - 800 ms, two arrow cues appeared nearby the FT, indicating the eye and the hand movement targets (MT1 & MT2). The motor targets were selected randomly for each trial and could coincide with the attention target as well as with each other. The onset of the arrow cues was the go-signal for both movements, which had to be executed as fast and precise as possible. Participants reached towards either of the two potential motor targets while simultaneously making a saccade towards the other—at free choice. Note that in the *Attention-only* task no cues occurred, and in the single movement tasks (*Eye-only*, *Hand-only*, *Attention-Eye,* and *Attention-Hand*) only one arrow occurred—and only one movement was executed while the other effector remained at the fixation target. 100 - 150 ms after cue onset (within the movement latency), one of the 1/f noise streams was briefly replaced by an orientation-filtered noise stimulus, showing a 40° clockwise or counterclockwise orientation. Participants were informed that this test signal would appear at the attention target location in 75 % of trials (in tasks without an attention target, the test was equally likely to appear at any of the four locations). After 50 ms the test was masked by the reappearance of non-oriented 1/f noise for another 700 ms (***Figure 1c*** provides an overview of stimulus timing). Afterwards, the screen turned blank and participants indicated via button press in a non-speeded manner whether they had perceived the orientation to be tilted clockwise or counterclockwise. They received auditory feedback for incorrect responses.

A threshold task preceded the experiment to ensure a consistent level of discrimination difficulty across participants. The threshold task visually matched the main experiment but no arrow cues were presented and participants were instructed to maintain eye and finger fixation. Furthermore, they were informed at which of the 4 locations the test would be presented in 100 % of trials. We used a procedure of constant stimuli and randomly selected the orientation filter strength *alpha* (corresponding to the visibility of the orientation tilt) out of six linear steps of filter widths. By fitting cumulative Gaussian functions to the discrimination performance via maximum likelihood estimation, we determined the filter width corresponding to 75% correct discrimination performance for each participant and used this value for the main experiment.

Participants performed 66 experimental blocks (2 *Attention-only*, 3 *Eye-only*, 2 *Hand-only*, 8 *Eye-Hand*, 11 *Attention-Eye*, 8 *Attention-Hand*, and 32 *Attention-Eye-Hand* blocks) of at least 66 trials each, resulting in a total of 4,356 trials per participant. We controlled online for violations of eye and finger fixation (outside

2.5° from FT before the cue onset), too short (<170 ms) or too long (>700 ms) movement latencies, and incorrect eye or hand movements (not landing within 2.5° from motor target center). Erroneous trials were repeated in random order at the end of each block. Overall, 567 ± 117 (mean ± SEM) trials per participant were repeated due to eye movement errors, 441 ± 73 due to finger movement errors.

Task, stimuli, and timing of **Experiment 2** were equivalent to Experiment 1, except that only one stream of 1/f noise patches was presented to which participants were endogenously attending throughout. The location of this noise stream (attention target; AT) again was indicated at the beginning of each block (either the upper right or the upper left location, randomly selected). As in the previous experiment, depending on the pre-block instruction, participants had to either exclusively attend to the noise stream (*Attention-only*), or attend to the noise stream and perform eye- (*Attention-Eye*), hand- (*Attention-Hand*), or simultaneous eye-hand-movements (*Attention-Eye-Hand*) to randomly selected motor target(s) indicated by centrally presented arrow cue(s). Unlike in Experiment 1, attention and motor targets never coincided. Furthermore, for each trial we randomly selected the orientation filter strength out of eight linear steps of filter widths (i.e. visibility level; *alpha* 5 to 75) and fitted cumulative Gaussian functions to the obtained group average discrimination performance via maximum likelihood estimation.

After an initial training (one block of 30 trials for each movement condition), participants performed 13 experimental blocks (3 *Attention-only*, 3 *Attention-Eye*, 3 *Attention-Hand*, and 4 *Attention-Eye-Hand* blocks) of at least 80 trials each, resulting in a total of 1,130 trials per participant. We controlled online for violations of eye and finger fixation (outside 2.5° from the FT before the cue onset), too short (<170 ms) or too long (>700 ms) movement latencies, and incorrect eye or hand movements (not landing within 2.5° from motor target center). Erroneous trials were repeated in random order at the end of each block. Overall, 145 ± 67 trials per participant were repeated due to eye movement errors, 130 ± 29 due to finger movement errors.

Eye data pre-processing

We scanned the recorded eye-position data offline and detected saccades based on their velocity distribution [Engbert & Mergenthaler, 2006] using a moving average over twenty subsequent eye position samples. Saccade onset and offset were detected when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within a 2.5° radius centered on FT until cue onset and landed within 2.5° from the cued location no later than 700 ms following cue onset, and if no blink occurred during the trial. In total we included 39,751 trials in the analysis of the behavioral results for Experiment 1 (on average 3,975 ± 79 trials per participant) and 6,015 trials (1,003 ± 29 per participant) for Experiment 2.

Statistical analysis and data visualization

For Experiment 1, we determined percentage correct discrimination performance separately for each task and location, depending on the respective motor and attention target configuration. Whisker plots show single participant discrimination performance (represented by dots) averaged across participants (represented by black lines) and corresponding 95% confidence intervals (indicated by colored bars). All comparisons were contrasted to the average performance at the movement-irrelevant (non-target) locations in the respective task (referred to as “neutral” / “N”), unless otherwise stated. Psychometric functions for the four tasks of Experiment 2 were obtained by fitting cumulative Gaussian functions to the group average orientation discrimination performance via maximum likelihood estimation. For all statistical comparisons we used permutation tests to determine whether the performance between two conditions (e.g. at cued vs. uncued locations) differed significantly. We resampled our data to create a permutation distribution by randomly rearranging the labels of the respective conditions for each participant and computed the difference in sample means for 1000 permutation resamples (iterations). We then derived p-values by locating the actually observed difference (difference between the group-averages of the two conditions) on this permutation distribution, i.e. the p-value corresponds to the proportion of the difference in sample means that fell below or above the actually observed difference. Unless otherwise stated, all reported differences remained significant after Bonferroni multiple-comparison correction. All files will be available via the OSF database upon manuscript publication (https://osf.io/q8nbd).

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Additional information

Competing interests

The authors declare that no competing interests exist.

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Author contributions

Nina M. Hanning: Conceptualization, Methodology, Software, Validation, Formal Analysis, Investigation, Writing - Original Draft Preparation, Writing - Review & Editing, Visualization, Project Administration; Luca Wollenberg: Conceptualization, Investigation, Writing - Review & Editing; Donatas Jonikaitis: Conceptualization, Writing - Original Draft Preparation, Writing - Review & Editing; Heiner Deubel: Conceptualization, Writing - Review & Editing, Funding Acquisition, Supervision;

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Ethics

The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München (approval number 13_b_2015), in accordance with German regulations and the Declaration of Helsinki. All participants gave written informed consent.

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2.4 Investigating the deployment of visual attention before accurate and averaging saccades via eye tracking and assessment of visual sensitivity

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Author contributions:[1]

Luca Wollenberg wrote the manuscript, compiled all supplementary materials, and scripted the video demonstration published together with the manuscript.

Heiner Deubel commented on the manuscript.

Martin Szinte commented on the manuscript.

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[1] Note that this is a methodological manuscript which did not comprise any author contributions regarding study design, experimental programming, original data collection, data analysis, and data visualization.

Video Article

Investigating the Deployment of Visual Attention Before Accurate and Averaging Saccades via Eye Tracking and Assessment of Visual Sensitivity

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Abstract

This experimental protocol was designed to investigate whether visual attention is obligatorily deployed at the endpoint of saccades. To this end, we recorded the eye position of human participants engaged in a saccade task via eye tracking and assessed visual orientation discrimination performance at various locations during saccade preparation. Importantly, instead of using a single saccade target paradigm for which the saccade endpoint typically coincides roughly with the target, this protocol comprised the presentation of two nearby saccade targets, leading to a distinct spatial dissociation between target locations and saccade endpoint on a substantial number of trials. The paradigm allowed us to compare presaccadic visual discrimination performance at the endpoint of accurate saccades (landing at one of the saccade targets) and of averaging saccades (landing at an intermediate location in between the two targets). We observed a selective enhancement of visual sensitivity at the endpoint of accurate saccades but not at the endpoint of averaging saccades. Rather, before the execution of averaging saccades, visual sensitivity was equally enhanced at both targets, suggesting that saccade averaging follows from unresolved attentional selection among the saccade targets. These results argue against a mandatory coupling between visual attention and saccade programming based on a direct measure of presaccadic visual sensitivity rather than saccadic reaction times, which have been used in other protocols to draw similar conclusions. While our protocol provides a useful framework to investigate the relationship between visual attention and saccadic eye movements at the behavioral level, it can also be combined with electrophysiological measures to extend insights at the neuronal level.

Video Link

The video component of this article can be found at https://www.jove.com/video/59162/

Introduction

Accumulated evidence argues for strong coupling between oculomotor and attentional control. The influential premotor theory of attention[1,2] provides a particularly strict account regarding this coupling, suggesting that covert shifts of visual attention correspond to saccade programming without subsequent execution. Indeed, shared neuronal correlates of attentional and oculomotor control have been identified via functional magnetic resonance imaging (fMRI)[3] and sub-threshold micro-stimulation of the Frontal Eye Fields (FEF) and the Superior Colliculi (SC) produces attentional benefits measured both behaviorally and electrophysiologically at the stimulated movement field position, even if no eye movements are induced[4,5,6,7]. Psychophysical experiments furthermore revealed that visual attention is consistently shifted towards the target of a saccade during oculomotor preparation[8,9]. However, dissociations at the neuronal level[10,11,12] and observations that saccade preparation does not necessarily entail a corresponding shift of attention[13,14,15,16] cast some doubt on an obligatory coupling between saccade programming and visual spatial attention.

Here, we revisited the nature of the coupling between attention and oculomotor programming at the behavioral level using a dual task which entailed a free choice saccade task and a visual discrimination task. Crucially, two saccade targets were presented at an angular distance of 30° on half of the trials, producing a distinct global effect[17,18,19,20] associated with a substantial number of saccades landing in between the two targets (averaging saccades). Since we randomly presented a discrimination target shortly before saccade onset at one out of 24 equidistant locations (including the two saccade target locations, the location in between them and 21 control locations), we were able to assess and compare the presaccadic deployment of visual attention when saccade goal and saccade endpoint were either spatially associated (accurate saccades) or dissociated (averaging saccades).

To test whether visual attention is an obligatory consequence of oculomotor programming, and, therefore, always shifted towards the saccade endpoint, we analyzed visual sensitivity for all 24 locations as a function of the saccade landing direction. While accurate saccades were associated with a consistent presaccadic enhancement of visual sensitivity at their endpoint, we found no such enhancement at the endpoint of averaging saccades. This dissociation rules out an obligatorily coupling of visual attention to the executed oculomotor program at the behavioral level and suggests that attentional and oculomotor control are dissociable at some cortical or subcortical processing stage. Importantly, we observed an equal enhancement of visual sensitivity at the two saccade targets before averaging saccades, suggesting that the global effect arises from unresolved saccade target selection before saccade onset.

Protocol

This protocol was designed according to the ethical requirement specified by the Ludwig-Maximilians-Universität München and with the approval of the ethics board of the department.

1. Participants

1. Recruit a sufficient number of naive participants with normal or corrected-to-normal vision and without neurological or psychiatric disorders. 10 participants are recommended based on similar, recent protocols[21,22].
   NOTE: Overall, we recruited 13 participants (aged 20-28, 7 females, 12 right-eye dominant, 1 author) from which 3 were excluded from final analysis since their orientation discrimination performance remained at chance level for all tested locations.

2. Experimental Setup

1. Conduct the experiment in a quiet and dimly illuminated room under the supervision of an experienced experimenter familiar with eye tracking and all other experimental components.
2. **Prepare an experimental setup consisting of a computer, a cathode-ray tube (CRT) monitor, a standard keyboard, two loudspeakers, and an eye tracker (see Table of Materials).**
   1. Sequence and control the experiment using an appropriate software (see **Table of Materials**). Write a script which can be run on the software to load and launch the experiment automatically for each participant (https://github.com/mszinte/CompAttExo). Ensure that the script encodes all necessary experimental parameters and implements stimulus presentation as well as behavioral and eye data collection.
   2. Display all visual stimuli on a CRT screen with a minimum vertical refresh rate of 120 Hz. Ensure the proper display of visual Gabors via gamma linearization of the experimental screen.
   3. Assess participants' evaluation of the discrimination target orientation (counterclockwise vs. clockwise) via the left and right arrow keys on a standard keyboard.
   4. Provide auditory feedback via loudspeakers upon incorrect manual responses.

3. Eye Tracking

1. Record the gaze of participants' dominant eye at a sampling rate of at least 1 kHz throughout the entire experiment via an eye tracker.
2. Ask the participant to sit down comfortably on a chair, place their chin on a chinrest, and lean their forehead against a bar to restrain head movement during the experiment. Individually adjust the height of the chair, the chinrest and the forehead bar such that participants' eyes align with the center of the experimental monitor.
3. **Individual Eye Tracker Calibration**
   1. Before each experimental block (duration: approximately 10 min) and whenever necessary (e.g. after noticeable head movements and resulting shifts of the estimated fixation), run a calibration procedure to guarantee that participants' gaze can be accurately tracked within a radius of 1°.
      NOTE: Here, we used a 13-point calibration procedure to get an accurate estimate of the characteristic light reflections (pupil and corneal reflection) of the tracked eye as a function of the gaze.
      1. Ask the participant to follow a dot moving across different locations on the screen with their eyes to estimate their gaze position.
      2. Repeat the procedure with a dot rotation of 30° and compare the measured gaze position to the estimated gaze position to validate the initial calibration. The calibration can be considered accurate when the averaged difference between the estimated gaze position following the calibration stage and the measured gaze position in the validation stage is below 1°.
      3. Repeat the calibration procedure whenever the participant breaks fixation repetitively to guarantee high tracking accuracy throughout the experiment.

4. During the experiment, monitor correct fixation at the screen center at the beginning of each trial. Only start a trial if the gaze stays within a radius of 2° around the central fixation target for at least 200 ms.

4. Instructions

1. **Provide participants with clear task instructions. Present the task instructions at least once at the beginning of each experimental session in the form of a written text, together with a visualization of the trial chronology. Encourage participants to carefully read through the instructions and to ask remaining questions to the experimenter.**
   NOTE: The instructions, as presented to the participants before each block, are shown in **Figure 1**.
   1. Instruct the participant to fixate at the center of the screen at the beginning of each trial.
   2. Inform the participant that 24 flickering distractor streams will appear on the screen and that two of them will be cued by white frames, which will either be flashed shortly or remain on the screen until the trial end.
   3. Ask the participant to execute a saccade towards the center of one of the two cued distractor streams at free choice. Emphasize that participants should move their eyes as fast and as accurately as possible upon the onset of the cues.

4. Inform the participant that, for a short duration during the trial, a tilted Gabor will be presented randomly at one of the 24 distractor streams.
5. Ask the participant to manually report whether the tilted Gabor was rotated clockwise or counterclockwise relative to the vertical by pressing the right or left arrow on the keyboard, respectively. Explain that a sound will be played if the orientation of the tilted Gabor is being reported incorrectly.

5. Experimental Design, Stimuli, and Trial Chronology

1. Ensure to partition the experiment into at least two experimental sessions on different days to guarantee participants' concentration across the entire duration of the experiment. Within an experimental session, prompt participants to take short breaks in between consecutive blocks.
   NOTE: This experiment consisted of 24 blocks, each including 290 online correct trials (all trials without fixation breaks and with a saccade onset between 50 and 350 ms after the saccade targets onset; incorrect trials were repeated at the end of a block), amounting to a total duration of about 5 h.
2. Deliberately predefine stimulus features (color, luminance, and size), stimulus timing, and a viewing distance which ensures the desired angular stimulus size. While most features of the visual stimuli (e.g., size, luminance, and contrast) can be adjusted to account for specific experimental purposes based on piloting, precise stimulus timing is crucial to assess visual attention during the presaccadic interval.
3. **Stimuli and Trial Chronology**
   1. Present all stimuli on a gray (~19.5 cd/m^2) background in order to minimize visual and screen aftereffects.
      NOTE: A visualization of the experimental procedure can be found in **Figure 2**.
   2. Present a fixation target (FT) in the form of a black (~0 cd/m^2) and white (~57 cd/m^2) "bull's eye" (0.4° radius) at the screen center at trial start. Remove the fixation target from the screen together with the onset of the saccade targets.
   3. Display 24 evenly spaced distractor streams (DS) at a radius of 10° from the fixation target at the trial start. Use dynamic stimuli, alternating every 25 ms (40 Hz) between a vertical Gabor patch (frequency: 2.5 cpd; 100 % contrast; random phase selected each stream refresh; SD of the Gaussian window: 1.1°; mean luminance: ~28.5 cd/m^2) and a Gaussian pixel noise mask (made of approximately 0.22° width pixels with the same Gaussian envelope as the Gabors).
      NOTE: The use of flickering noise helps to minimize attentional capture due to sudden onsets that are normally associated with static stimuli and thus reduces discrimination target detectability without concurrent selective deployment of attention[21].
   4. Between 300 and 600 ms (in steps of the screen refresh rate of ~8 ms) after the onset of the fixation target, present two saccade targets (ST_1 and ST_2) in the form of gray circles (~39 cd/m^2; 1.1° radius; 0.2° width) surrounding two randomly chosen distractor streams. Ensure to vary the time of saccade target onset from trial to trial to avoid that participants adopt a predictive saccade execution pattern.
      1. Randomly present the two saccade targets at an angular distance of either 30° or 90° across trials.
      2. Randomly display the saccade targets for either 50 ms (transient cueing condition: tST_{1+2}) or until the end of the trial (continuous cueing condition: cST_{1+2}) across trials.

   5. Randomly present a discrimination target (DT) at one of the 24 distractor streams and between 75 and 175 ms after the onset of the saccade targets. Display the discrimination target, a tilted Gabor patch, rotated clockwise or counterclockwise by 12 ° relative to the vertical, for 25 ms to replace the vertical Gabor patch within the randomly selected distractor stream. Select the time window for discrimination target presentation to maximize the number of trials in which the discrimination target offset occurred before saccade onset.
      NOTE: The applied tilt level of the discrimination target was derived from pretests with the objective of producing visual discrimination performance above chance level at attended locations. The tilt level can be generally changed but experimenters should first test whether participants can properly discriminate the target angle at least at the cued locations.
   6. Erase all stimuli from the screen 500 ms after the onset of the saccade targets such that only the gray background remains.
   7. Wait for the participant to indicate the orientation of the discrimination target via the keyboard (by pressing the left arrow for counterclockwise orientations and the right arrow for clockwise orientations) and play a feedback sound whenever participants report the discrimination target orientation incorrectly. Automatically launch the next trial once a manual response was given.

6. Data Preprocessing and Analysis

1. Process the recorded eye data before proceeding to final data analysis. Only include trials in which the participant maintained fixation within a 2° radius around the fixation target without blinking and initiated a saccade landing between 7° and 13° from the fixation target (i.e. within ± 30 % of the instructed saccade size). Ensure that any measure of visual sensitivity was collected during the presaccadic interval by including only those trials in which the discrimination target offset occurred before the saccade onset.
   NOTE: In total, 75.7% of all trials were included in the final analyses after eye data preprocessing.
2. In order to analyze data as a function of the location of the discrimination target relative to the location of the saccade targets, rotate the stimulus configuration of each trial as to align the saccade target locations symmetrically around the geometrical angle 0 of the stimulus stream orbit.
3. Split trials as a function of the saccade landing direction. To do so, divide the entire stimulus stream orbit into 24 even angular sectors of 15° (±7.5°) centered on each distractor stream and combine trials entailing saccades directed towards the same respective sector.
4. Define visual sensitivity as: $d' = z(\text{hit rate}) - z(\text{false alarm rate})$. Count clockwise responses to clockwise discrimination targets as hits and clockwise responses to counterclockwise discrimination targets as false alarms (and vice versa). Substitute discrimination performance values of 100% and 0% by values of 99% and 1%, respectively, before transforming them into d'. Transform discrimination performance values below the chance level (50% or d' = 0) into negative d' values.

Representative Results

Here, we only present some central, representative results. The entirety of results can be found in our recent publication[23]. Note that data were mainly analyzed irrespective of the duration of the saccade targets (i.e. transient and continuous cueing conditions were combined for the final analyses). For statistical comparisons, we drew 10,000 bootstrap samples (with replacement) from the distribution of single subject means and derived two-tailed p values from the distribution of differences between the bootstrapped samples.

The detection of saccade onsets and offsets was based on the velocity distribution of the gaze[24]. We used a moving average over 20 subsequent eye-position samples to determine saccade onsets/offsets whenever the velocity of the eye exceeded/fell below the median of the moving average by 3 SDs for at least 20 ms. Corrective saccades were defined as eye movements executed after the offline selected main saccade sequence and were only included in the respective corrective saccade analysis if they landed between 7° and 13° from the fixation target and were initiated within the first 500 ms following the main saccade sequence as well as before the participant's manual response.

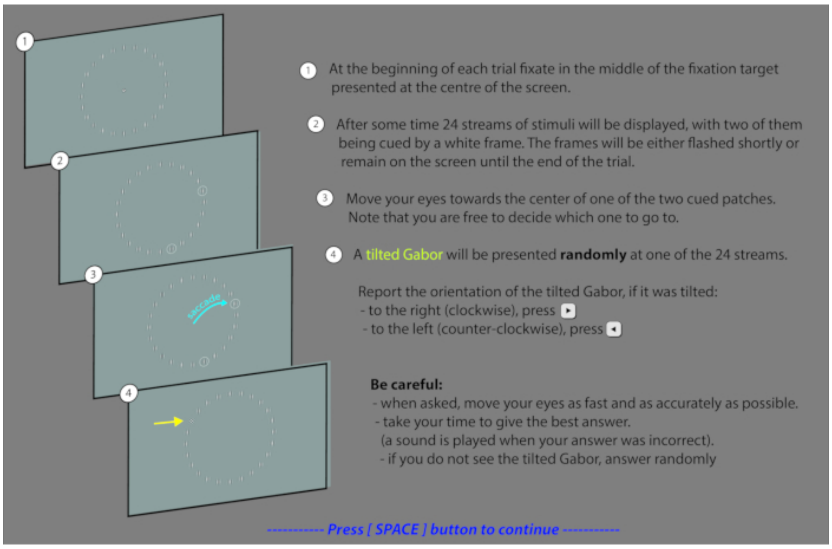
Before proceeding to final data analysis, data were rotated (see 6.2). Consequently, after data rotation, the most counterclockwise saccade target ST$_1$ was always represented at +45°/+15° (in the 90° and 30° conditions, respectively), the location BTW in between the saccade targets at 0° (in both the 90° and 30° conditions), and the most clockwise saccade target ST$_2$ at -45°/-15° (in the 90° and 30° conditions, respectively) relative to the angle 0. Locations other than ST$_1$, ST$_2$, and BTW were considered as control locations (CTRL) in both, the 90° and 30° conditions.

Our protocol allowed us to evaluate saccades in response to oculomotor competition among two saccade targets presented at different angular distances based on the recorded eye data. As expected, the saccade endpoint distributions associated with the 90° (**Figure 3A** and **3C**) and 30° (**Figure 3B** and **3D**) conditions differed substantially. We observed mostly accurate saccades towards one of the saccade targets in the 90 ° condition, where 41.0% ± 1.0% of saccades ended within the sector including the most counterclockwise saccade target ST$_1$ and 41.8% ± 1.9% within the sector including the most clockwise saccade target ST$_2$ (**Figure 3C**). In the 30° condition, in contrast, participants executed a substantial number of averaging saccades. Here, 33.6% ± 2.4% of the saccades ended within the sector in between the 2 saccade targets BTW, 29.95% ± 1.6% ended within the sector including ST$_1$, and 32.0% ± 1.8% within the sector including ST$_2$ (**Figure 3D**).

Furthermore, the assessment of visual sensitivity at all 24 locations distributed across the visual field allowed us to analyze the spatial deployment of attention during oculomotor programming in detail. Overall, taking into account saccades of all directions, we observed a selective facilitation of visual sensitivity at the two saccade targets relative to the control locations CTRL (corresponding to the average across all positions except for ST$_1$, ST$_2$, and BTW) in both the 90° (ST$_1$: d' = 2.2 ± 0.3 versus CTRL: d' = 0.3 ± 0.1, $p < 0.0001$; ST$_2$: d' = 2.2 ± 0.4 versus CTRL, $p < 0.0001$; ST$_1$ versus ST$_2$, $p = 0.8964$; **Figure 4A**) and 30 ° (ST$_1$: d' = 2.2 ± 0.3 versus CTRL: d' = 0.3 ± 0.1, $p < 0.0001$; ST$_2$: d' = 2.1 ± 0.3 versus CTRL, $p < 0.0001$; ST$_1$ versus ST$_2$, $p = 0.6026$; **Figure 4B**) conditions. While visual sensitivity at the intermediate location was significantly lower than at the saccade target locations (BTW: d' = 0.6 ± 0.2 versus ST$_1$, $p < 0.0001$; BTW versus ST$_2$, $p < 0.0001$; **Figure 4B**), it was, however, slightly increased relative to the control locations in the 30° condition (BTW versus CTRL, $p = 0.0010$).

In order to disentangle whether visual attention is obligatorily deployed at the endpoint of saccades, we analyzed visual sensitivity at all locations as a function of the saccade landing direction (see step 6.3 in the protocol). Crucially, the specific saccade landing distribution observed in the 30° condition of this protocol made it possible to analyze the deployment of visual attention before saccades associated with spatially distinct endpoints in response to identical visual input. More specifically, by analyzing visual sensitivity before averaging saccades, we could determine whether or not attention shifts towards the endpoint of saccades even when it does not spatially coincide with a saccade goal. We observed that visual sensitivity was significantly enhanced at the endpoint of accurate saccades in both the 90° (ST$_{1+2}$ saccaded: d' = 3.0 ± 0.4 versus ST$_{1+2}$ non-saccaded: d' = 1.7 ± 0.4, $p < 0.0001$; **Figure 4E**) and the 30° (ST$_{1+2}$ saccaded: d' = 2.7 ± 0.4 versus ST$_{1+2}$ non-saccaded: d' = 2.0 ± 0.3, $p = 0.0080$; **Figure 4F**) condition. In contrast, before averaging saccades, visual sensitivity was not enhanced at the saccade endpoint but slightly reduced (BTW saccaded: d' = 0.4 ± 0.2 versus BTW non-saccaded: d' = 0.7 ± 0.2, $p < 0.0001$; **Figure 4F**). Thus, visual attention was not obligatorily shifted towards the endpoint of the upcoming saccade. Interestingly, averaging saccades were associated with an equal enhancement of visual sensitivity at the two surrounding saccade targets (ST$_1$: d' = 2.2 ± 0.4 versus ST$_2$: d' = 2.2 ± 0.4, $p = 0.8402$; **Figure 4D**), suggesting that attentional selection among the saccade targets was not readily resolved before the onset of averaging saccades.

To further evaluate a potential correlate of attentional selection before averaging saccades, data were analyzed as a function of the landing direction of corrective saccades, which can be frequently observed upon the execution of averaging saccades. We did not observe a significant benefit at the endpoint of corrective saccades following an averaging saccade (corrective saccade directed towards ST$_{1+2}$: d' = 2.8 ± 0.5 versus corrective saccade not directed towards ST$_{1+2}$: d' = 2.5 ± 0.8, $p = 0.68300$; **Figure 5C**), which supports the interpretation that attentional selection was not resolved before averaging saccades.



1. At the beginning of each trial fixate in the middle of the fixation target presented at the centre of the screen.
2. After some time 24 streams of stimuli will be displayed, with two of them being cued by a white frame. The frames will be either flashed shortly or remain on the screen until the end of the trial.
3. Move your eyes towards the center of one of the two cued patches. Note that you are free to decide which one to go to.
4. A tilted Gabor will be presented **randomly** at one of the 24 streams.

Report the orientation of the tilted Gabor, if it was tilted:
- to the right (clockwise), press ▸
- to the left (counter-clockwise), press ◂

Be careful:
- when asked, move your eyes as fast and as accurately as possible.
- take your time to give the best answer.
(a sound is played when your answer was incorrect).
- if you do not see the tilted Gabor, answer randomly

----------- Press [SPACE] button to continue -----------

Figure 1: Instructions as presented to the participants. Visualization of the experimental instructions as presented to the participants at the beginning of each block. Please click here to view a larger version of this figure.

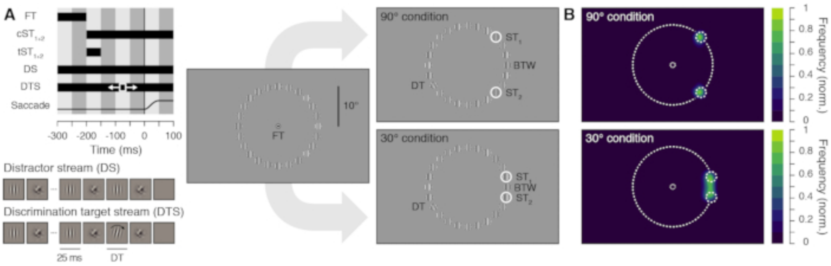


Figure 2: Experimental procedure and normalized saccade landing frequency maps. (**A**) Stimulus timing and display. Participants prepared a saccade from the fixation target (FT) to one of the two potential saccade targets (ST_1 and ST_2), presented simultaneously at two randomly chosen stimulus streams with an inter-target angular distance of either 90° (top panels) or 30° (bottom panels). The saccade targets were either shown continuously (cST_{1+2}) or transiently (tST_{1+2}). Stimulus streams could either be distractor streams (DS), composed of alternating vertical Gabors and masks (40 Hz) or discrimination target streams (DTS) which included the presentation of a brief discrimination target (DT, 25 ms), a clockwise or counterclockwise tilted Gabor, shown between 75 and 175 ms after the saccade targets onset. Participants saccaded towards one of the saccade targets and had to report the orientation of the discrimination target, appearing randomly at one of the 24 stimulus stream locations. Note that stimuli are sketched in order to increase their visibility. Actual stimuli match those shown in the stimulus streams depiction. (**B**) Normalized saccade landing frequency maps averaged across participants (n = 10) for the 90° (top) and 30° (bottom) conditions (collapsed across the transient and continuous ST presentation). This figure has been reprinted from Wollenberg et al. (2018)[23]. Please click here to view a larger version of this figure.

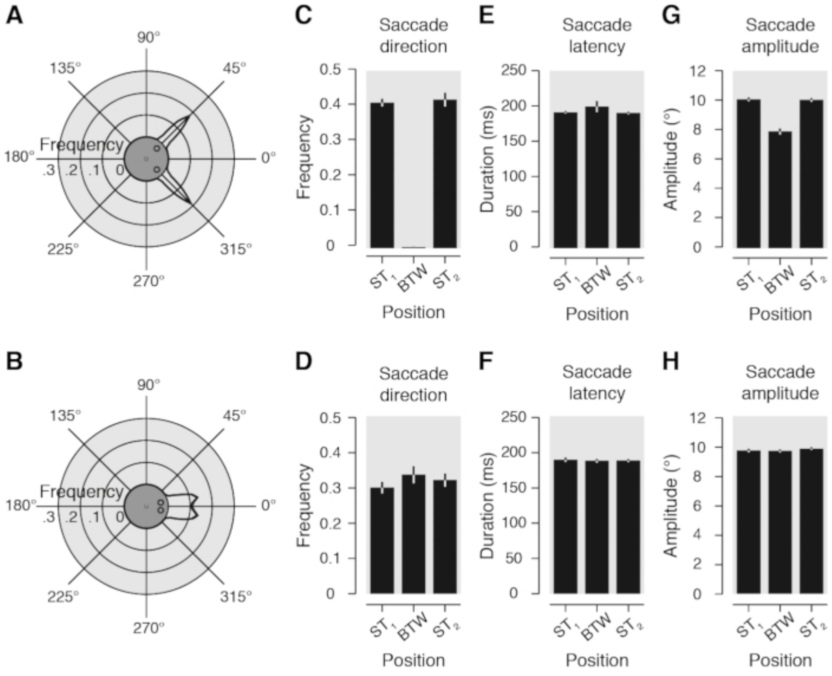


Figure 3: Saccade metrics. (**A-B**) Circular plots show the averaged frequency distribution of the saccade landing direction binned in evenly distributed angular sectors of 5°, in the 90° (A) and 30° conditions (B). Stimulus configuration is rotated as to align the two saccade targets symmetrically around the geometrical angle zero (see central insets). (**C-D**) Bar graphs illustrate averaged frequency of trials as a function of the saccade landing direction binned in 24 evenly distributed angular sectors of 15°. Data are shown for the three positions of interest (ST$_1$, BTW and ST$_2$) in the 90° (C) and 30° conditions (D). (**E-H**) Averaged saccade latency (E, F) and amplitude (G, H) observed for the same three positions of interest in the 90° (E, G) and 30° conditions (F, H). All data are shown irrespective of the duration (continuously or transiently) of the saccade targets. Light gray areas and error bars represent SEM. Polar plot black lines and corresponding light gray areas show linear interpolation between data points. This figure has been reprinted from Wollenberg et al. (2018)[23]. Please click here to view a larger version of this figure.

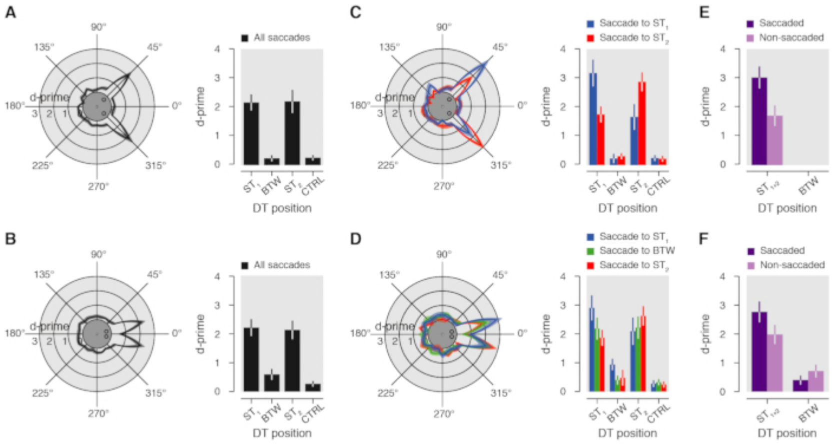


Figure 4: Visual sensitivity. (**A-B**). Circular plots show averaged visual sensitivity (d') as a function of the DT position in the 90° (A) and 30° conditions (B), irrespective of the duration of the saccade targets and across all saccade directions observed. Bar graphs illustrate visual sensitivity for four positions of interest (ST$_1$, BTW, ST$_2$, CTRL). (**C-D**) Visual sensitivity as a function of the DT position relative to the saccade landing direction in the 90° (C) and 30° conditions (D), irrespective of the duration of the saccade targets (blue: saccade to ST$_1$; green: saccade to BTW; red: saccade to ST$_2$). For each saccade direction, we took the average sensitivity for each discrimination target location. For example, the blue line plots visual sensitivity when saccades were made towards ST$_1$ and the discrimination target was either at ST$_1$ (+15° on the polar plot), BTW (15° counterclockwise to ST$_1$; 0° on the polar plot) or ST$_2$ (30° counterclockwise to ST$_1$; + 345° on the polar plot), and so on. (**E-F**) Bar graphs illustrate sensitivity observed for DT shown at the saccaded (purple: e.g., DT at ST$_1$ and saccade to ST$_1$) and the non-saccaded positions (light-purple: e.g. DT at ST$_1$ and saccade to ST$_2$ or BTW) in the 90° (E) and the 30° (F) conditions. Conventions are as in **Figure 3**. This figure has been reprinted from Wollenberg et al. (2018)[23]. Please click here to view a larger version of this figure.

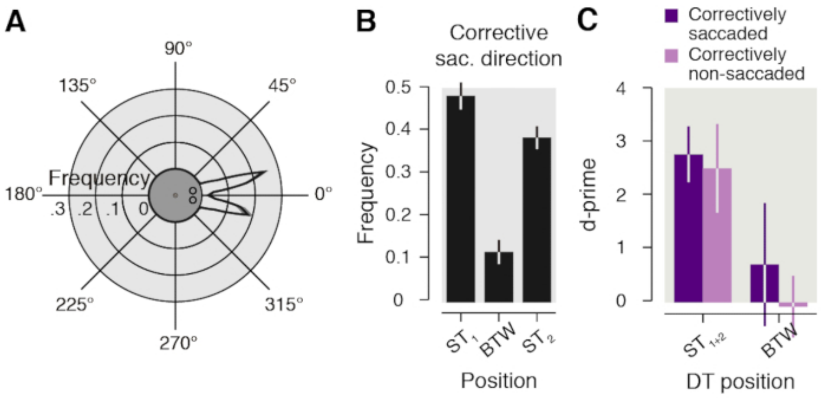


Figure 5: Corrective saccades. (**A**) Circular plot shows averaged frequency distribution of the corrective saccade landing direction following an averaging saccade. (**B**) The bar graph illustrates averaged frequency of trials as a function of the corrective saccade landing direction following an averaging saccade for three positions of interest (ST_1, BTW and ST_2). (**C**) The bar graph illustrates visual sensitivity as a function of the direction of the first corrective saccade for all trials in which an averaging saccade was executed. Purple bars show visual sensitivity for trials in which the corrective saccade was directed towards the location at which the DT appeared (e.g. DT at ST_1 and corrective saccade towards ST_1). Light purple bars show visual sensitivity for trials in which the corrective saccade was directed towards a different location than the location at which the DT appeared (e.g. DT at ST_1 and corrective saccade towards ST_2 or BTW). Conventions are as in **Figure 3-4**. This figure has been reprinted from Wollenberg et al. (2018)[23]. Please click here to view a larger version of this figure.

Discussion

This experimental protocol employed the concurrent assessment of gaze behavior and presaccadic visual sensitivity in a free choice saccade task. It allowed us to analyze whether visual attention is indeed obligatorily coupled to oculomotor programming at the behavioral level and therefore systematically deployed at the endpoint of saccades. Two saccade targets were presented in close proximity (30°) on half of the trials in which we observed a distinct global effect, reflected in a saccade landing distribution consisting of both, accurate and averaging saccades. To conclude on the spatial coupling between visual attention and the saccadic endpoint, visual sensitivity was analyzed and compared across different locations as a function of the saccade landing direction. While we observed a consistent and selective enhancement of visual sensitivity at the endpoint of accurate saccades, visual sensitivity was not enhanced at the endpoint of averaging saccades. Rather, visual sensitivity was equally facilitated at the two saccade targets before the execution of averaging saccades, suggesting that saccade averaging arises from unresolved attentional selection among the saccade targets. Our results, therefore, demonstrate that visual attention is not obligatorily deployed at the endpoint of the executed oculomotor program. A corrective saccade analysis, which demonstrated that the even deployment of visual sensitivity across the two saccade targets before averaging saccades did not systematically vary as a function the corrective saccade direction, further confirmed this interpretation. In this regard, our data are consistent with a recent model by Zirnsak et al.[25] which assumes a target selection process that gradually builds up over time.

Importantly, our protocol differs from other behavioral studies that reported evidence for a dissociation between attention and saccades in several aspects. While some studies based their conclusion on saccadic reaction times[14,15,16], we used a direct measure of visual spatial attention, namely visual sensitivity during saccade preparation. The specific parameters used throughout this protocol were effective in replicating the classical presaccadic shift of attention[8,9] as evident in the consistent enhancement of visual sensitivity at the endpoint of accurate saccades. Thus, the protocol allowed for reliable detection of systematic modulations of visual attention specific to saccade preparation. This is an important prerequisite to validly interpret presaccadic attentional effects, and in particular, the observed absence of attentional enhancement at the endpoint of averaging saccades.

A central and distinct aspect of this protocol was the random presentation of the discrimination target among various locations. Thereby, we could sample visual sensitivity across the entire visual field, which consequently allowed us to not only determine whether attention is facilitated at the endpoint of saccades but also to investigate the spread of attention around this area including adjacent locations. The discrete allocation of attention at the two saccade targets (limited to less than ~2.6°, the distance between two of our adjacent stimuli) we observed before averaging saccades contradicts an early account which suggested that averaging saccades may reflect a coarse processing of the visual scene[17] and argues for an enhancement of local rather than global visual information processing. Further, the random presentation of the discrimination target rendered its location completely unpredictable to participants. Thus, our protocol generally facilitated an even deployment of visual attention across the visual field with respect to the discrimination task. We consider this fact important with regard to any potential attentional effects and conclusions related to saccade preparation.

However, since eye movements are not typically performed while trying to discriminate stimuli across the entire visual field in natural vision, the results obtained in this protocol can not unrestrictedly account for oculomotor behavior in every day life. Furthermore, the oculomotor task did inevitably bias the deployment of attention via the saccade target cueing. The saccade targets did not only introduce relevant oculomotor goals but also salient exogenous cues that likely attracted attention. Thus, it is possible that visual discrimination performance at the intermediate location was generally deteriorated due to some masking elicited by the two surrounding saccade targets. In order to decrease the impact of the saccade targets with respect to discrimination performance at the intermediate location and to evaluate potential masking effects, we decided to present the saccade targets only transiently (for 50 ms) instead of continuously (until the trial end) on half of the trials. Consequently, even though both cueing conditions introduced visual onsets at the saccade target locations, the saccade targets had always disappeared before the onset of the discrimination target in the transient cueing condition. While the majority of results were very consistent across both cueing conditions and were therefore combined in the final analysis, we indeed observed an indication of a masking effect in the continuous cueing condition relative to the transient cueing condition. Overall, irrespective of the saccade direction, visual sensitivity at the intermediate location was slightly decreased in the continuous compared to the transient cueing condition. Given the notion that transient saccade target cueing apparently minimizes masking of the intermediate location while still being effective in eliciting averaging saccades, future studies using a protocol similar to ours should consider employing transient cueing of targets. However, despite our efforts to minimize masking effects via the transient cueing of targets, we can not rule out that the transient cueing still introduced a forward masking effect, which might potentially account for the poor discrimination performance at the intermediate location to some extent.

Taken together, our protocol allowed to directly address the coupling between visual attention and oculomotor programming, and to reveal a distinct spatial dissociation between attention and the endpoint of averaging saccades at the behavioral level. Our results argue against a mandatory coupling between visual attention and oculomotor programming suggested in the premotor theory of attention. Future studies should employ paradigms including concurrent neurophysiological recordings within areas such as the FEF and SC to further resolve the coupling between visual attention and oculomotor programming.

Disclosures

The authors have declared that no competing interests exist.

Acknowledgments

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Materials List for:

Investigating the Deployment of Visual Attention Before Accurate and Averaging Saccades via Eye Tracking and Assessment of Visual Sensitivity

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Materials

Name	Company	Catalog Number	Comments
Computer	Apple iMac (Cupertino, CA)		
CRT Screen	Sony GDM F900 (Tokyo, Japan)		24 inch screen with a spatial resolution of 1024 x 640 pixels and a vertical refresh rate of 120 Hz
Eye Tracker	EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada)		operating at a sampling rate of 1 kHz
Software	Matlab (The MathWorks, Natick, MA) / toolboxes: Psychophics, EyeLink		

3 General Discussion

3.1 Visuospatial attention and the endpoint of saccadic eye movements

3.1.1 Visual attention does not obligatorily shift to the saccade endpoint

The first study of this thesis *(Chapter 2.1)* combined a saccade task with a presaccadic visual discrimination task to examine the spatial relationship between shifts of visual attention and the endpoint of saccadic eye movements. Importantly, the presentation of two nearby, potential saccade targets induced a broad distribution of saccade endpoints, based upon which a subpopulation of target saccades could be distinguished from a subpopulation of averaging saccades. While target saccades landed accurately at either one of the two saccade targets (i.e., closest to one of the stimulus streams cued as a saccade target), averaging saccades landed in between the two saccade targets (i.e., closest to the stimulus stream located between the two saccade target streams). Consequently, it was possible to evaluate the spatial deployment of visual attention during movement preparation – assessed via the presaccadic visual discrimination task – depending on whether the subsequent saccade endpoint and the intended saccade target roughly coincided (target saccades) or were clearly dissociated from each other (averaging saccades).

This study revealed a striking dissociation between the attentional correlates of target saccades and averaging saccades. In line with the well-established presaccadic shift of attention (Deubel & Schneider, 1996; Kowler et al., 1995; Hoffman & Subramaniam, 1995), a consistent enhancement of visual sensitivity was observed at the endpoint of target saccades. Crucially, in contrast to target saccades, visual sensitivity was not enhanced at the endpoint of averaging saccades landing in between the adjacent saccade targets. This result was replicated in the second study of this thesis *(Chapter 2.2)* and likewise observed previously in a similar dual-task paradigm (Van der Stigchel & De Vries, 2015). Thus, contrary to the results of studies using saccadic adaptation to spatially dissociate the saccade endpoint from the intended saccade target (Doré-Mazars et al., 2004; Doré-Mazars & Collins, 2005; Collins & Doré-Mazars, 2006), the current data clearly demonstrate that shifts of visual attention are not obligatorily coupled to the endpoint of subsequently executed saccades. The observed dissociation between the locus of visual attention and the endpoint of averaging saccades challenges a central claim of the influential premotor theory of attention, which holds that shifts of visual attention are strictly contingent upon the operations of the motor system (Rizzolatti et al., 1987; Sheliga et al., 1994; Craighero et al., 1999). In fact, as highlighted by several neurophysiological studies, attentional and oculomotor signals are dissociable within central visuomotor integration structures of the monkey brain (Ignashchenkova et al., 2004; Thompson et al., 2005; Gregoriou et al., 2012). These studies could distinguish neurons preferentially responding to visual stimulation from neurons predictively encoding the execution of a saccade in the SC and FEF. Such a functional division may provide a potential neuronal basis for the behavioral decoupling between the locus of visual attention and the saccade endpoint in humans observed here.

3.1.2 Saccade accuracy is tightly linked to successful attentional selection

Apart from ruling out an obligatory coupling between presaccadic attentional shifts and the endpoint of saccades, the first study further demonstrated a systematic relationship between the accuracy of saccades and the spatial distribution of attentional resources prior to movement execution. Before the onset of target saccades, visual sensitivity was selectively enhanced at either one of the two saccade targets, with the largest sensitivity benefit observed at the the saccade target which subsequently became the saccade endpoint. Yet, as opposed to this effect, visual sensitivity was found to be equally enhanced at both of the neighboring saccade targets prior to the execution of averaging saccades, suggesting that saccade averaging was associated with unresolved attentional selection prior to movement onset. Accordingly, the deployment of attentional resources prior to movement execution appears to reflect the outcome of a perceptual target selection process which can account for systematic variability in saccade endpoints. These results are compatible with the view that visual attention establishes a perceptual selection mechanism which underlies the computation of motor commands for goal-directed actions (Schneider, 1995; Deubel & Schneider, 1996; Schneider & Deubel, 2002). Moreover, they support previous hypothetical considerations suggesting that averaging saccades reflect immature oculomotor responses which are triggered before a designated saccade target can be perceptually discriminated from competing salient objects (Ottes et al., 1985; Coëffe´ & O'Regan, 1987; Aitsebaomo & Bedell, 2000).

The behavioral data obtained in the first study can be linked to neuronal processing within retinotopically organized priority maps contained in brain areas such as the SC, FEF, and LIP (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Ptak, 2012; Zelinsky, & Bisley, 2015; Bisley & Mirpour, 2019). These maps are thought to establish common neuronal substrates for the control of saccades (as they project to the premotor brainstem circuitry; Fecteau & Munoz, 2006) and the guidance of visual attention (as they send feedback connections to early visual areas; Rolfs & Szinte, 2016). Indeed, subthreshold microstimulation in priority map structures can elicit selective and spatially corresponding enhancements of both visual sensitivity (Moore & Fallah, 2004; Müller et al., 2005) and neuronal activity in the extrastriate visual cortex (Moore & Armstrong, 2003; Ekstrom et al., 2008). The observed relationship between the presaccadic distribution of attentional resources and saccadic endpoints can therefore be theoretically explained in the following way. The appearance of the two potential saccade targets rapidly excites retinotopically corresponding neuronal populations within the priority maps in a bottom-up fashion (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010). Activity within these neuronal populations will therefore accumulate, leading to the formation of two local activity peaks in the priority maps. These peaks will subsequently compete for saccade target selection in a race-to-threshold during movement preparation (Hanes & Schall, 1996; Paré & Hanes, 2003; Boucher, Palmeri, Logan, & Schall, 2007). Over time, this race may be biased in favor of a particular target representation in the map via the arrival of top-down attentional signals from frontal brain areas (Godijn & Theeuwes, 2002; Meeter et al., 2010). Concurrently, sensory processing in early visual areas will be dynamically modulated via feedback connections from the priority maps (Moore & Armstrong, 2003; Ekstrom et al., 2008; Rolfs & Szinte, 2016). This means that the presaccadic enhancement of visual sensitivity at the two saccade targets roughly scales with the activity level of the competing peaks in the priority maps. Crucially, however, neurons in the priority maps interact with each other in a distance-dependent fashion (Van Opstal & Van Gisbergen, 1989; Munoz & Istvan, 1998; Trappenberg et al., 2001; Marino et al., 2012): While distant neuronal populations share inhibitory connections (long-range inhibition), adjacent populations mutually excite each other (local excitation). Thus, competition among distant potential saccade targets (i.e., two distant activity peaks) can be typically resolved in a winner-take-all fashion (Findlay & Walker, 1999; Marino et al., 2012). In this case only one of the activity peaks in the priority maps reaches saccadic threshold, and the brainstem premotor circuitry will trigger a precise saccade towards the selected saccade target (i.e., the target object encoded by the threshold-reaching peak in the map). Likewise, owing to the feedback connections from the priority maps to early visual areas, this successful selection will be reflected at the perceptual level: Around the moment of saccade onset, visual sensitivity will be enhanced at the selected saccade target relative to the remaining, unselected object (with the difference in visual sensitivity between the selected and unselected object being roughly proportional to the difference in the activity levels of the threshold-reaching peak and the remaining peak in the priority maps). Crucially, neuronal selection among two nearby, potential saccade targets may remain unresolved because corresponding activity peaks in the priority maps mutually excite each other (Marino et al., 2012). Accordingly, both peaks may occasionally reach saccadic threshold around the same time. In this case the subsequent saccade will land at an intermediate location between the potential targets represented by the adjacent activity peaks in the map (Robinson, 1972; Schiller & Sandell, 1983) – i.e., saccade averaging occurs. Again, this unresolved neuronal selection will be reflected – owing to the feedback connections to early visual areas – at the perceptual level around the time the saccade is executed: Visual sensitivity will be equally enhanced at the two potential saccade targets because the activity level of corresponding peaks in the priority maps is roughly the same.

Note, however, that these considerations do only provide a hypothetical and highly simplified description of the neuronal target selection process which is based on the insights of the first study, and may likewise be limited to the specific experimental conditions of this study. First, saccade endpoints likely vary gradually as a function of the overall population activity residing in the priority maps at the moment of saccade onset (Sparks et al., 1976; Van Gisbergen et al., 1987; Lee et al., 1988). Second, the results of the second study imply that saccade averaging can occur even when attentional resources are notably biased – yet generally less pronounced than observed for precise target saccades – to a saccade target rather than a nearby, task-irrelevant distractor of different color. This discrepancy is difficult to reconcile with the assumption of a common priority map underlying attentional and oculomotor control. One may therefore only speculate about the cause of the apparent discrepancy between the attentional correlates of saccade averaging observed in the first two studies. In theory, it could be argued that the color difference between the saccade target and the distractor in the second study allowed for a feature-selective modulation of early sensory processing via top-down mechanisms which bypass the priority maps. Such top-down mechanisms may potentially amplify the perceptual bias towards the saccade target and therefore lead to a mismatch between the deployment of attentional resources and the saccade endpoint. However, this proposal is purely speculative. Further psychophysical studies will be required to extend insights into the mapping between the presaccadic distribution attentional resources (i.e., perception) and the spatial parameters of saccadic eye movements (i.e., action). Such studies would particularly benefit from a simultaneous assessment of visual discrimination capacities at both of the competing objects. Moreover, it remains to be resolved whether saccade averaging is preceded by two competing activity peaks within priority map structures such as the SC (Edelman & Keller, 1998; Van der Stigchel & Nijboer, 2011), or whether these peaks in fact collapse into a single, intermediate activity peak (Glimcher & Sparks 1993; Vokoun et al., 2014).

3.1.3 How the study of visual attention can inform previous theories on saccade averaging

The insights into the attentional correlates of averaging saccades obtained in the first study lead to a refined understanding of the saccade averaging phenomenon. For instance, it has been suggested that saccade averaging reflects the operation of a global visual processing mode which is associated with a coarse representation of the visual scene (Findlay, 1982). The spatially specific and noncontiguous distribution of visual processing resources across the stimulus configuration observed here however clearly challenges this view. It was demonstrated that visual processing resources are precisely allocated at two adjacent target objects in parallel – but not in between them – prior to the execution of averaging saccades. Thus, contrary to the idea of a global visual processing mode, the visual system selectively processes salient local objects even when the eyes subsequently land at an intermediate location between these objects.

Moreover, the current data argue against the idea that the successive execution of an averaging saccade and a corrective saccade is to be considered a timesaving strategy of the oculomotor system (Coëffé & O'Regan 1987). The first study demonstrated that the average latency of saccades accurately landing at one of the two saccade targets was well below the overall latency of a saccadic sequence consisting of an initial averaging saccade followed by a small corrective saccade to one of the targets.

The results of the first study appear to be best explained in terms of spatial pooling. Various authors have suggested that saccade averaging is linked to the computation of a central reference point – the center of gravity – within extended stimulus configurations (Vishwanath & Kowler, 2003; Cohen, Schnitzer, Gersch, Singh, & Kowler, 2007). In this view, visual information is pooled over a given target area as to perceptually localize spatially extended objects and to determine the landing position of saccades. Such a spatial pooling mechanism may well account for the results of the first study: The endpoint of averaging saccades was located in between two objects represented as local attentional foci at the perceptual level. However, the absence of attentional enhancement at the endpoint of averaging saccades suggests that spatial pooling is implemented during the final stages of motor programming downstream from the level at which sensory (i.e., visual) and motor-related signals are integrated.

More generally, the novel insights obtained in the first study highlight that the assessment of visuospatial attention during episodes of competition among nearby, potential movement targets establishes a fruitful experimental framework to investigate both the preconditions for and the constraints of efficient visuomotor control.

3.2 Top-down eye movement control and the spatio-temporal dynamics of visual attention

3.2.1 Top-down control improves saccade accuracy

As highlighted by the phenomenon of saccade averaging (Findlay, 1982; Findlay & Walker, 1999; Vitu, 2008; Van der Stigchel & Nijboer, 2011), the competition between nearby, potential saccade targets can interfere with our capacity to precisely move our eyes in a goal-directed fashion. The first study demonstrated that this oculomotor interference is systematically reflected at the perceptual level and suggests that efficient eye movement control is contingent upon successful attentional target selection during movement preparation. Thus, the dynamics of visual attention seem to establish an explanatory framework for oculomotor control. These dynamics have been thoroughly described in various models on visual attention (Wolfe, 1994; Itti & Koch, 2001), and it has been suggested that, while salient objects automatically receive prioritized processing via the operation of bottom-up mechanisms, goal-directed attentional selection requires the operation of relatively slower top-down mechanisms (Nakayama & Mackeben, 1989; Carrasco, 2011). The second study therefore combined a saccade task with a presaccadic visual discrimination task to systematically examine the influence of top-down control on the interaction between visual attention and saccadic eye movements. In this dual-task participants had to move their eyes to a saccade target and ignore a nearby distractor of different color. Both of these cues were equisalient relative to the background, such that efficient saccade target selection required the resolution of bottom-up attentional competition among the saccade target and the distractor. Importantly, the extent of top-down control was manipulated in two ways. First, the predictability of target and distractor locations was varied across experimental blocks (using different pre-block instructions). Second, in order to systematically prolong visual processing time of the stimulus configuration prior to saccade onset, saccade execution was delayed via variable saccadic go-signals.

As revealed by the analysis of saccade endpoint distributions, spatial predictability allowed for improved top-down control over undelayed, short-latency saccades. When either the saccade target or the distractor location was predictable, these saccades more frequently landed at the instructed saccade target. Consequently, fast eye movement control was particularly constrained under spatial uncertainty. This observation is consistent with the results of previous studies (Coëffé & O'Regan 1987; He & Kowler, 1989) and further supports the idea that top-down mechanisms can effectively attenuate adverse effects of bottom-up competition on eye movement control in a rather fast fashion (Heeman, Theeuwes, & Van der Stigchel, 2014; Aagten-Murphy & Bays, 2017). Interestingly, despite improving movement accuracy, spatial predictability did not systematically modulate the deployment of visual attention prior to the execution of short-latency saccades. This indicates that the signals underlying fast top-down eye movement control do not necessarily transfer to perception. Further psychophysical and neurophysiological research will be required to elucidate this apparent dissociation between perception and action, which implies at least partially separable attentional and oculomotor control mechanisms.

Moreover, in line with the previously reported latency dependence of saccade averaging (Findlay, 1982; Ottes et al., 1985; Coëffé & O'Regan 1987; Edelman & Keller, 1998; Chou et al., 1999), the second study demonstrated that saccade accuracy systematically improved as movement execution was delayed. A saccadic go-signal delay of 100 ms yielded a particularly large increase in the proportion of precise target saccades when target and distractor locations were unpredictable. This pronounced improvement in saccade accuracy was accompanied by a reduction of attentional competition between the saccade target and the distractor. Indeed, a 100 ms saccadic go-signal delay significantly increased the visual discrimination benefit at the saccade target relative to the distractor when both locations were unpredictable, but not when either one of them was predictable. As a result, saccade accuracy became comparable across the different spatial predictability conditions only after a 100 ms go-signal delay. In sum, these results demonstrate that a short prolongation of visual processing time can reduce bottom-up attentional competition and compensate for the adverse effect of spatial uncertainty on saccade accuracy. Longer saccadic go-signal delays (i.e., beyond 100 ms) did not further increase saccade accuracy, which suggests that the capacity to exert voluntary control over saccadic eye movements in response to oculomotor competition reaches optimal efficiency within a rather short time window.

3.2.2 Bottom-up attentional competition between nearby objects is resolved over time

As mentioned before, top-down attentional mechanisms are generally believed to emerge slower than automatic bottom-up attentional mechanisms (Nakayama & Mackeben, 1989; Carrasco, 2011). By systematically delaying movement execution, the second study allowed to directly assess – via the presaccadic visual discrimination task – how these mechanisms affect the saccade target selection process over time.

The appearance of the saccade target and the distractor elicited fast and automatic bottom-up attentional orienting responses, which were reflected by selective visual discrimination benefits at corresponding locations. These initial bottom-up attentional effects however decayed over time. Importantly, while a discernible discrimination enhancement was sustained at the saccade target even 400 ms after the appearance of the saccade target and the distractor, the discrimination benefit at the distractor vanished (i.e., discrimination performance approached chance level) after 200 ms. These dynamics support the idea that bottom-up and top-down mechanisms influence saccade target selection at different temporal scales (Van Zoest, Donk, & Theeuwes, 2004; Van Zoest & Donk, 2005; Van Zoest & Donk, 2006; Van Zoest & Donk, 2008) – see **Figure 5** for a schematic illustration. Early during movement preparation, attentional resources are mainly deployed in a bottom-up fashion, such that salient objects receive prioritized processing relatively independent of whether they represent a designated target or a task-irrelevant distractor. Yet, owing to an increasing influence of top-down mechanisms over time, attentional resources can be more selectively deployed to the designated target object, which can thereby be better distinguished from irrelevant objects in the visual field and likewise protrudes as the effective target for an upcoming saccade. In line with this idea, several authors have suggested that visual attention can be transiently allocated at two separate locations, whereas the attentional locus narrows down on a single location with time (Dubois, Hamker, & Van Rullen, 2009; Zirnsak, Beuth, & Hamker, 2011). Indeed, it was demonstrated that distractor-related activity in the monkey FEF starts to decay after an initial buildup period (Bichot & Schall, 2002). Yet, further neurophysiological research will be needed to resolve whether the declining attentional capture by the distractor observed in the second study reflects a passive decay or an active inhibition mechanism.

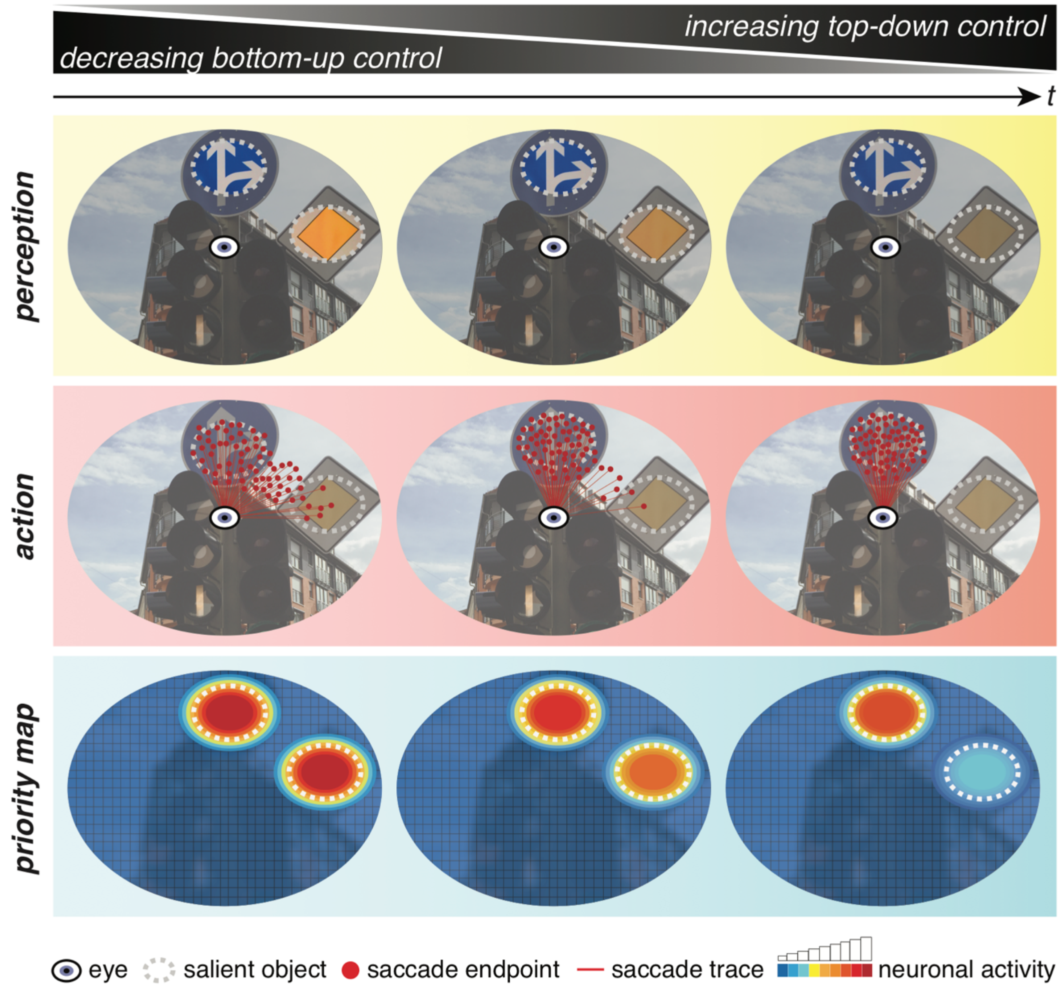

Figure 5. Visual attention and oculomotor control.
Schematic illustration depicting the dynamics of bottom-up competition and top-down selection at the perceptual (*perception*; top row highlighted in light yellow), oculomotor (*action*; middle row highlighted in light red), and neuronal (*priority map*; bottom row highlighted in light blue) level. This illustration outlines a situation in which an observing agent aims (i.e., top-down) to evaluate whether he/she is allowed to turn right by moving the eyes towards the appropriate street sign (i.e., the blue one). However, the simultaneous presence of nearby, salient objects (i.e., the blue and yellow street signs) initially leads to strong and automatic bottom-up excitation of corresponding neuronal populations within the priority map, respectively increasing visual object representations at the perceptual level. These bottom-up effects elicit neuronal and perceptual competition interfering with efficient oculomotor control (leftmost columns), leading to a substantial proportion of saccades erroneously landing in between the competing objects (i.e., saccade averaging) or even at the inappropriate street sign (i.e., the yellow one). Yet, with increasing influence of top-down mechanisms (middle and rightmost columns) which counteract automatic bottom-up effects, neuronal and perceptual competition can be resolved (i.e., biased towards the intended target object) more efficiently. These top-down effects originate from frontal brain areas and entail the operation of selective attention. Consequently, saccade accuracy improves, as reflected in the decrease of saccades landing at locations different from the intended target object (i.e., the blue street sign). While this figure illustrates the influence of increasing visual processing time (i.e., movement preparation time), informative prior information such as spatial predictability or knowledge about visual features of the target object can additionally accelerate the operation of top-down control mechanisms. Note: The *perception* and *priority map* visualizations are highly simplified for the sake of illustration.

3.3 Movement target selection and voluntary attentional control

3.3.1 Separate attentional systems for the selection of eye and hand movement targets

The third study *(Chapter 2.3)* assessed the deployment of visual attention in a dual-task which required participants to execute combined eye and hand movements while concurrently attempting to voluntarily attend to a movement-irrelevant location. This experimental design allowed to systematically investigate the interaction among attentional mechanisms underlying the selection of eye and hand movement targets, and how these premotor attentional mechanisms influence voluntary attentional control.

The first main result of this study decisively contradicts the idea that the brain generally recruits a common mechanism for the selection of eye and hand movement targets (Khan et al., 2011). When participants concurrently prepared eye and hand movements to distinct locations, visual attention was allocated in parallel to both movement targets. Importantly, this parallel selection occurred without a cost: The visual discrimination benefits at the effector-specific targets was comparable to conditions in which only an eye or a hand movement had to be prepared. This demonstrates that movement target selection in one effector was unaffected by additional motor preparation in the other effector. Thus, in line with previous studies (Jonikaitis & Deubel, 2011; Hanning et al., 2018), the current data clearly imply that the selection of eye and hand movement targets was implemented by separate, effector-specific attentional systems and resources (see **Figure 6** for a schematic illustration). This does however not preclude the possibility that attentional mechanisms underlying eye and hand movement target selection are coupled when both effectors operate synergistically under natural conditions.

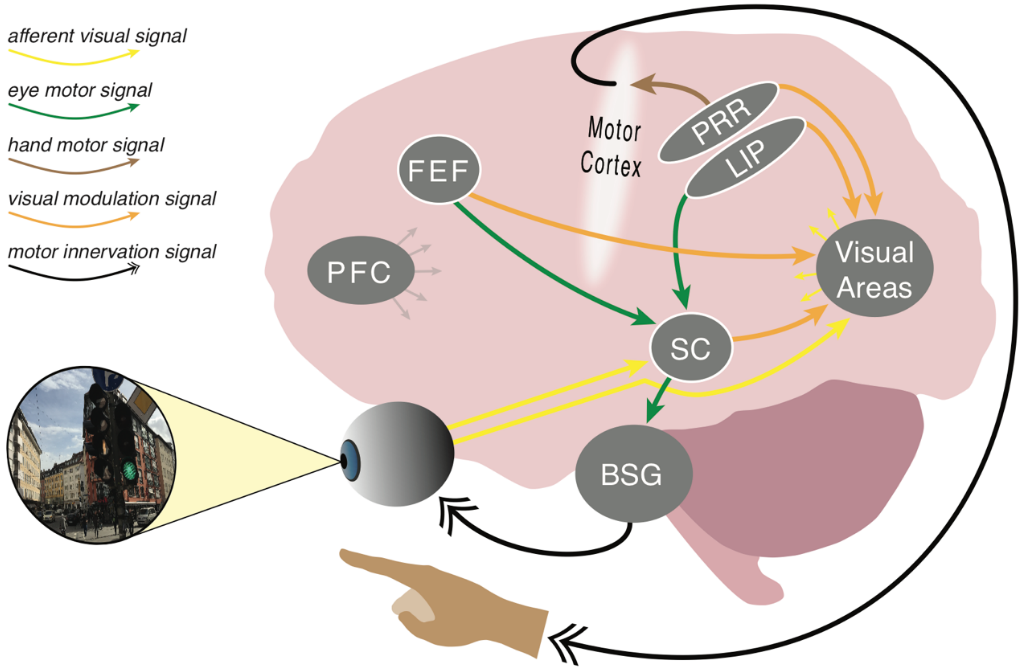

Figure 6. Visually guided actions and effector-specific modulations of visual attention. Schematic depiction illustrating a potential circuitry which can account for effector-specific movement target selection systems in the human brain (lateral view). Visual information entering the eyes spreads out through the brain upon initial bottom-up processing in early visual areas. Areas of the prefrontal cortex (PFC) can provide top-down signals which modulate processing in various brain areas according to the current behavioral goals of the observer. Structures (framed in white) such as the frontal eye fields (FEF), the lateral intraparietal area (LIP), the subcortical superior colliculus (SC), and a putative parietal reach region (PRR) integrate bottom-up and top-down signals and establish effector-specific priority maps. On the one hand, these priority maps send distinct eye and hand motor signals to corresponding motor areas in the brain, i.e., the brainstem saccade generator (BSG) controlling saccadic eye movements and the motor cortex controlling hand movements. On the other hand, they may effectively modulate sensory processing via feedback connections to early visual areas. These recurrent visual modulation signals are thought to elicit selective perceptual enhancements (i.e., premotor attentional benefits) at the upcoming targets of both eye and hand movements.

The independence of premotor attentional mechanisms observed here is consistent with fMRI studies in humans which demonstrated effector-specific activations in separable areas within the parietal lobe (Tosoni, Galati, Romani, & Corbetta, 2008; Van der Werf, Jensen, Fries, & Medendorp, 2010). Moreover, distinct brain areas have been consistently linked to the generation of eye and hand movements in macaques (Snyder et al., 1997; Snyder et al., 2000; Andersen & Buneo, 2002; Calton et al., 2002). Areas such as the SC (Dorris et al., 1997), FEF (Bruce & Goldberg, 1985), and LIP (Gnadt & Andersen, 1988) play a crucial role for saccadic eye movements, whereas the PRR provides a specialized neuronal substrate for manual reaching movements (Snyder et al., 1997; Batista & Andersen, 2001; Scherberger & Andersen, 2007; Baldauf et al., 2008). Some authors have even argued for the existence of effector-specific priority maps (Snyder et al., 1997; Lawrence &

Snyder, 2009). Accordingly, premotor attentional shifts may arise from dissociable neuronal substrates specialized for the transformation of behaviorally relevant visual signals into corresponding motor programs for a given effector system. A critical test of this hypothesis will be to assess whether simultaneous microstimulation in effector-specific priority maps (e.g., in FEF and PRR, or in LIP and PRR) can produce spatially distinct attentional benefits, i.e., selective enhancements in the activity of retinotopically corresponding neurons in the visual cortices (which can be assessed via single-cell recordings) or local improvements of visual sensitivity at corresponding locations in the visual field (which can be assessed psychophysically). In fact, while it is known that central oculomotor structures such as the FEF can effectively enhance neuronal activity in the visual cortex (Moore & Armstrong, 2003; Ekstrom et al., 2008), the influence of specialized hand movement substrates such as the PRR on neuronal activity in the visual cortex has not been investigated so far.

Interestingly, despite the independence observed at the perceptual level, eye and hand movement preparation systematically interacted at the motor level. Eye movement execution slowed down when a hand movement was concurrently programmed. Likewise, concurrent eye movement preparation slowed down the execution of hand movements. Similar interactions among the motor parameters of the two effectors were observed in previous studies (Bekkering, Adam, Van den Aarssen, Kingma, & Whiting, 1995; Neggers & Bekkering, 2000; Song & McPeek, 2009). While such motor interactions have led to the proposal of a common selection mechanism for both effectors, the perceptual independence observed here leads to a refined view on the frequently observed coupling between eye and hand movements (Land et al., 1999; Neggers & Bekkering, 2000; Johansson et al., 2001; Land & Hayhoe, 2001; Neggers & Bekkering, 2001; Mennie et al., 2007). Separate attentional mechanisms may select effector-specific movement targets during an early phase of movement preparation, which is however followed by a coupling between both effectors at later motor processing stages (see also: Hanning et al., 2018). Some authors have suggested, for instance, that the SC may be involved in the selection of targets for both eye and hand movements (Song, Rafal, & McPeek, 2011; Song & McPeek, 2015). This idea could in principal account for a crosstalk between the two effectors, which was, however, only observed at the motor level in the third study.

A central challenge for future neurophysiological work will be to disentangle the neuronal mechanisms giving rise to efficient, parallel selection of eye and hand movement targets via visual attention on the one hand, and the motor-specific interaction between both effectors on the other hand.

3.3.2 Movement preparation interferes with voluntary attentional control

The second main result of third study relates to the interaction of premotor attentional mechanisms and the voluntary deployment of visual attention for the purpose of perceptual selection. Various studies showed that the preparation of saccadic eye movements interferes with voluntary attentional control (Deubel & Schneider, 1996; Kowler et al., 1995; Hoffman & Subramaniam, 1995). The third study demonstrated that this interference is not only constrained to oculomotor programming. Both eye and hand movement preparation were found to heavily deteriorate the ability to voluntarily attend to a movement-irrelevant, yet perceptually important object in the visual field. This was evident in the observation that visual discrimination performance significantly decreased at voluntarily attended objects whenever an eye or hand movement had to be prepared to a different location in the visual field. Interestingly, this effect became even more pronounced during the simultaneous preparation of eye and hand movements, suggesting that voluntary attentional control progressively suffers as the number of distinct action plans accumulates.

As highlighted by these findings, premotor shifts of visual attention appear to establish a mandatory prerequisite for efficient planning of visually guided actions. In light of the adverse effects of such premotor attentional mechanism on voluntary attention, action-driven selection likely occupies a superordinate role in the attentional control system (Allport, 1987; Neumann, 1990). In this context, an exciting endeavor for future research will be to elucidate how premotor attentional mechanisms interact with the mechanisms underlying attentional selection for merely perceptual purposes at the neuronal level.

3.4 Conclusions

The insights of this thesis imply that the control of visually guided actions is tightly linked to the spatio-temporal dynamics of visual attention. Both goal-directed eye and hand movements are preceded by selective shifts visual attention. Importantly, these premotor attentional shifts are not obligatorily coupled to the endpoint of subsequent movements, which challenges the common idea that the signals underlying the guidance of visual attention are strictly derived from neuronal activity in the motor system. Attentional mechanisms appear to subserve the selection of targets for upcoming movements, and thus play a functional role for goal-directed visuomotor control. Indeed, the spatial distribution of attentional resources may account for the accuracy of saccadic eye movements when multiple potential target objects compete for oculomotor selection. Under such conditions precise movement execution typically requires that attention can be selectively deployed to a designated target object, which can therefore be accurately located and perceptually distinguished from other objects in the visual field. The efficiency of this target selection process tends to be contingent on the emergence of top-down signals which can bias bottom-up attentional competition among conspicuous objects in favor of the current behavioral goals over time. Conversely, movement accuracy appears to systematically deteriorate if attentional selection among potential target objects remains unresolved until movement onset. The visuomotor control benefits associated with premotor attentional selection however come at a cost. Both eye and hand movement preparation heavily interfere with the ability to attend at movement-irrelevant locations in the visual field, supporting the idea that attentional selection establishes a crucial prerequisite for the precise programming of visually guided movements. Action selection therefore likely occupies a superordinate role in the attentional control system. Yet, despite interfering with voluntary attentional control, premotor attentional mechanisms can operate in an effector-specific fashion as to allow for efficient, parallel selection of spatially distinct eye and hand movement targets. This notion of independent, effector-specific attentional resources may account for a rather flexible and adaptive coordination of eye and hand movements.

To conclude, the results of the current thesis emphasize that selective visual attention is to be considered a fundamental perceptual selection mechanism which is finely tuned to cope with the challenge of efficient visuomotor control in the face of a highly complex environment. However, even though the premotor attentional effects observed in the experiments of this thesis clearly imply that visual attention effectively guides subsequent actions as to achieve certain behavioral goals, it should be acknowledged that a merely correlational relationship among perception and action can not be ultimately refuted on the basis of the current data alone.

Finally, complementary neurophysiological approaches will be required to explore the neuronal underpinnings (especially at the level of the so-called priority maps in the brain) of the particular interactions among visual attention, movement preparation, and movement control reported in this thesis. First, it remains to be resolved which neuronal substrates can account for the effector-specificity of attentional mechanisms involved in eye and hand movement target selection, and how these substrates interact with the circuitry underlying voluntary attentional control. Moreover, a central challenge will be to assess how exactly the accuracy of saccadic eye movements relates to the distribution of activity across neuronal populations which encode competing, potential movement targets in visuomotor nodes such as the superior colliculus. Both single-cell and microstimulation protocols appear to provide promising tools to tackle these questions in the future.

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