Are premotor attention shifts a mere by-product of motor programming?

Investigating the role of habitual processes in the attention-action coupling

Inaugural-Dissertation

zur Erlangung des Doktorgrades der Philosophie

an der Ludwig-Maximilians-Universität München

vorgelegt von

# **Christof Elias Topfstedt**

aus

Wiesbaden-Dotzheim

Erstgutachter/-in:	Prof. Dr. Thomas Schenk
Zweitgutachter/-in:	Prof. Dr. Markus Conci
Drittgutachter/-in:	Prof. Dr. Simone Schütz-Bosbach
Tag der mündlichen Prüfung:	17.06.2024

# Acknowledgments

First and foremost, I would like to thank my supervisor Thomas Schenk, who made this whole project possible and who supported me tirelessly throughout the doctorate. Thank you for your relaxed and cordial manner, for all the time and effort you put in, for all the valuable discussions, and for all the elegant solutions you came up with whenever we encountered challenges in the project. I truly appreciated working with you and learned a lot from it.

I am also very grateful to Luca Wollenberg, with whom I invested a lot of time in the two experimental studies of this dissertation, which was not only highly productive but also a lot of fun, including the moments of extreme silliness. I really enjoyed this time.

Many thanks also to Jakob Thomsen and Andreas Häußler, who put a lot of effort into laying the technical foundations for this research project and with whom it was always a pleasure to work with.

Finally, I would like to thank Frederic Göhringer, Miriam Löhr-Limpens, Doris Schmid, Karin Ludwig, Inara Mahkamova, Theresa Halder, Paul Fisher, Franz Schwarzacher, Lisa Beckmann, Eva Lechner, Johanna Funk, Sigrid Seiler, Silvia Jakobi and Maria Vorbeck. You all contributed to creating a familiar and supportive atmosphere that immensely enriched the entire time of this research trip.

# Abstract

Influential models of visuo-spatial attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Schneider, 1995) postulate that the programming of goal-directed motor actions is inevitably accompanied by a spatially congruent shift of attention toward the target of the upcoming movement (premotor shift of attention). This presumed obligatory attentional selection of motor targets has been attributed to motor programming itself, either as a by-product of motor programming (Rizzolatti et al., 1987; Rizzolatti et al., 1994) or as a prerequisite for motor programming to enable the extraction of the target's spatial information (Allport, 1987; Neumann, 1987; Schneider, 1995). Although the linkage of spatial attention and motor programming is well established in different types of goal-directed motor actions, there is mixed evidence regarding the proposed obligatory nature of the attentionaction coupling. This raises the possibility that the premotor attention shift phenomenon is mediated by mechanisms unrelated to motor programming. In this dissertation, two experimental studies are presented that both investigated whether attentional selection of the target of an upcoming motor action can also be attributed to a habitual expectation that motor target locations contain visual information of high behavioral relevance. To this end, participants in both studies performed a psychophysical dual-task in which they had to identify a task-relevant visual stimulus (an attention probe) while concurrently preparing a pointing movement (first study) or saccadic eye movement (second study) toward a motor target. In a training phase, the position of the attention probe was manipulated so that participants learned to expect either spatial congruence or incongruence between the attention probe and the motor target. In a subsequent test phase with randomized attention probe position, possible training effects on attention allocation were assessed. Overall, both studies yielded similar results. Spatial attention allocation was markedly biased toward the expected position of the attention probe, regardless of whether this position matched the motor target or not. The observation that attentional resources can be shifted to a position other than the target of an upcoming motor action indicates that the link between spatial attention and motor programming is more flexible than generally assumed. It further suggests a crucial role of habitual top-down modulations of spatial attention in the generation of premotor attention shifts.

# Zusammenfassung

Einflussreiche Modelle der visuell-räumlichen Aufmerksamkeit (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Schneider, 1995) postulieren, dass die Programmierung zielgerichteter motorischer Handlungen zwangsläufig mit einer räumlich kongruenten Verlagerung der Aufmerksamkeit auf das Ziel der bevorstehenden Bewegung einhergeht (prämotorische Aufmerksamkeitsverschiebung). Diese angenommene obligatorische Aufmerksamkeitsselektion motorischer Ziele wurde der motorischen Programmierung selbst zugeschrieben, entweder als Nebenprodukt der motorischen Programmierung (Rizzolatti et al., 1987; Rizzolatti et al., 1994) oder als Voraussetzung der motorischen Programmierung, um die räumlichen Informationen des Ziels extrahieren zu können (Allport, 1987; Neumann, 1987; Schneider, 1995). Obwohl die Verknüpfung von räumlicher Aufmerksamkeit und motorischer Programmierung bei verschiedenen Arten zielgerichteter motorischer Handlungen gut belegt ist, ist die Evidenz bezüglich der angenommenen obligatorischen Natur der Aufmerksamkeits-Handlungs-Kopplung uneinheitlich. Daraus ergibt sich die Möglichkeit, dass das Phänomen der prämotorischen Aufmerksamkeitsverschiebung durch Mechanismen vermittelt wird, die nicht mit der motorischen Programmierung zusammenhängen. In dieser Dissertation werden zwei experimentelle Studien vorgestellt, in denen untersucht wurde, ob die Aufmerksamkeitsselektion des Ziels einer bevorstehenden motorischen Handlung auch auf eine habituelle Erwartung zurückgeführt werden kann, dass motorische Zielorte visuelle Informationen von hoher Verhaltensrelevanz enthalten. Zu diesem Zweck führten die Probanden und Probandinnen beider Studien eine psychophysische Doppelaufgabe durch, bei der sie einen aufgabenrelevanten visuellen Stimulus (einen Aufmerksamkeitsreiz) identifizieren mussten, während sie gleichzeitig eine Zeigebewegung (erste Studie) oder eine sakkadische Augenbewegung (zweite Studie) in Richtung eines motorischen Ziels vorbereiteten. In einer Trainingsphase wurde die Position des Aufmerksamkeitsreizes so manipuliert, dass die Probanden und Probandinnen lernten, entweder eine räumliche Kongruenz oder Inkongruenz zwischen dem Aufmerksamkeitsreiz und dem motorischen Ziel zu erwarten. In einer anschließenden Testphase mit randomisierter Position des Aufmerksamkeitsreizes wurden mögliche Trainingseffekte auf die Aufmerksamkeitsallokation erfasst. Insgesamt lieferten beide Studien ähnliche Ergebnisse. Die räumliche Aufmerksamkeitsallokation war deutlich in Richtung der erwarteten Position des Aufmerksamkeitsreizes verschoben, unabhängig davon, ob diese Position mit dem motorischen Ziel übereinstimmte oder nicht. Die Beobachtung, dass Aufmerksamkeitsressourcen auf eine andere Position als das Ziel einer bevorstehenden motorischen Handlung verlagert werden können, deutet darauf hin, dass die Verbindung zwischen räumlicher Aufmerksamkeit und motorischer

Programmierung flexibler ist als allgemein angenommen. Sie weist zudem auf eine zentrale Rolle habitueller Top-down-Modulationen der räumlichen Aufmerksamkeit bei der Generierung prämotorischer Aufmerksamkeitsverschiebungen hin.

# Table of Contents

A	cknowl	edgmentsiii
A	bstract	iv
Zı	usamm	enfassungv
1	Intr	oduction1
	1.1	Attentional selection: key mechanism for efficient visual processing1
	1.2	Spatial attention and goal-directed motor actions2
	1.2	.1 Evidence for and against an obligatory attention-action coupling
	1.3	Objectives of the dissertation6
2	Exp	erimental studies9
	2.1	The role of habitual learning in premotor attention allocation10
	2.2	Training enables substantial decoupling of visual attention and saccade preparation36
3	Ger	neral discussion
	3.1	Summary of studies62
	3.2	Evidence for a habitual attention-action coupling hypothesis64
	3.3	No evidence for a spatial reference hypothesis68
	3.4	Training is important to divert attention from motor targets69
	3.5	Top-down processes at least facilitate motor target selection70
	3.6	Implications for attention models and our understanding of covert attentional orienting71
4	Cor	nclusions
5	Ref	erences74

## 1 Introduction

## 1.1 Attentional selection: key mechanism for efficient visual processing

The world around us contains a vast amount of visual information. When this information enters our eyes, it is continuously transmitted to our visual cortex. However, neural processing of information is costly. Each cortical computation consumes a large amount of metabolic energy, while the total amount of available energy resources in the brain is limited and must be shared among neurons at any given time (Attwell & Laughlin, 2001). Under these conditions, processing every single piece of incoming information is infeasible. Yet it would also not be necessary, given the fact that only a fraction of the visual input is relevant to behavior (Treue, 2001). The capped energy budget of the nervous system rather demands regulation of the flow of sensory signals so that processing resources can be selectively allocated only to potentially significant elements of the scene (Lennie, 2003).

One of the powerful tools that has evolved to address the need for information selection in visual processing is the combined use of the fovea (i.e., part of the eye providing the highest visual acuity) with the ability to perform saccades (i.e., rapid, ballistic eye movements) (Moore & Zirnsak, 2017; Treue, 2001). In fact, we use this mechanism extensively, typically executing several saccades per second to bring potentially relevant parts of the scene into the range of foveal vision (Findlay & Gilchrist, 2003). However, in order to process information, it is not sufficient to just look at something. Although we intuitively experience a complete and detailed representation of our visual surroundings, studies on perceptual phenomena such as those of *inattentional blindness* (Mack & Rock, 2000) or *change blindness* (Rensink et al., 1997) have demonstrated that observers often fail to detect unexpected stimuli or changes in unattended parts of a scene, despite the fact that all relevant information is visually available. This suggests that it is the selection of information by attentional processes that plays the decisive role in determining what receives precedence in visual processing and what does not. Consequently, it is also the joint orientation of gaze and the locus of spatial attention through which 'looking' is turned into 'seeing' (Carrasco, 2011).

Importantly, besides these so-called *overt* shifts of spatial attention, information selection can also be accomplished via *covert* attention shifts, i.e. shifts of attention in the absence of concurrent eye movements (Posner, 1980; von Helmholtz, 1867). Moreover, it is generally assumed that spatial attention can be oriented either goal-driven via top-down processes (*endogenous* attention) or stimulus-driven via bottom-up processes (*exogenous* attention) (James, 1890; Posner, 1980). The typical effects of attentional selection are perceptual benefits, such as enhancements of

contrast sensitivity (Cameron et al., 2002) and spatial resolution (Yeshurun & Carrasco, 1998) of attended items, as well as an increase in the speed of stimulus detection at covertly attended locations (Posner, 1980). Spatial attention thus allows to prioritize the processing of selected parts in the visual scene while neglecting other irrelevant information (Carrasco, 2011). This makes it an efficient mechanism for coping with limited neural processing capacity (Lennie, 2003).

## 1.2 Spatial attention and goal-directed motor actions

The very fact that we typically explore our visual environment by aligning gaze and locus of attention through overt shifts of spatial attention already suggests a close relationship between motor actions and attentional selection. However, despite early calls in modern psychology to consider attention as a central mechanism guiding the coordination of sensory and motor processes (Dewey, 1896), research on spatial attention was (and still is) dominated by studies of its effects on perception in the absence of motor actions (Pratt & Gozli, 2015).

In the 1980s, however, a new subfield in attention research emerged that emphasized the critical role of spatial attention in motor actions (Pratt & Gozli, 2015). For example, Allport (1987) argued that, from an evolutionary perspective, the central function of attentional selection is not to support perception per se, but rather to enable the planning of goal-directed movements – such as saccadic eye or manual movements – through a selective coupling of sensory information to motor action control (*selection-for-action*). In particular, he pointed out that the visual scene typically contains multiple potential motor targets, but that effector systems are usually limited to performing only one action at a given time (Allport, 1987). For this reason, attentional selection has been claimed to be a prerequisite for motor programming, as it enables information of the upcoming motor target to be separated from that of competing objects in the visual scene (Allport, 1987) and can provide the motor system with the spatial parameters of the target (Neumann, 1987).

Around the same time, Rizzolatti et al. (1987) published the influential but controversial premotor theory of attention, which suggests a very tight link between spatial attention and motor actions. The premotor theory of attention rejected the prevailing notion that spatial attention is controlled by an anatomically and functionally independent neural system (Craighero & Rizzolatti, 2005). Instead, Rizzolatti et al. (1987) proposed that spatial attention derives directly from activity in the same neural circuits that generate saccadic eye movements. Specifically, covert shifts of spatial attention were considered to be merely a by-product of the processes involved in the motor programming of (unexecuted) saccadic eye movements (Rizzolatti et al., 1987), an assumption that was later extended to other goal-directed movements (Rizzolatti et al., 1994).

Another prominent theory highlighting a close relationship between spatial attention and goal-directed movements is the visual attention model by Schneider (1995). This theory postulates that spatial attention operates at an early stage of visual processing and provides a common mechanism underlying perception and action. Based on the assumption that the primate visual system is organized in two processing streams (Goodale & Milner, 1992; Mishkin et al., 1983), the visual attention model states that attentional selection of a particular object representation leads to simultaneous and prioritized processing of this information in both the ventral "what"-pathway for object recognition and the dorsal "where"-pathway for generating motor programs directed toward the object. Thus, in line with the viewpoints of Allport (1987) and Neumann (1987), but in contrast to the premotor theory of attention (Rizzolatti et al., 1987), the visual attention model assumes that spatial attention is a prerequisite for motor programming, not its cause (Schneider & Deubel, 2002).

Despite the different assumptions of the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994) and the visual attention model (Schneider, 1995; Schneider & Deubel, 2002) regarding the mechanism underlying the link between spatial attention and motor actions, both theories make the same prediction at the behavioral level: The programming of a goal-directed movement by the motor system is inevitably accompanied by a shift of spatial attention toward the upcoming motor target (premotor shift of attention). Furthermore, both theories agree that this assumed obligatory coupling between spatial attention and motor programming should not only be observed in saccadic eye movements, but also in other goal-directed motor actions (Rizzolatti et al., 1994; Schneider, 1995). In fact, the prediction of an obligatory attention-action coupling has been investigated primarily in saccadic eye movements and, albeit to a lesser extent, in manual movements (e.g., pointing and grasping movements). The following chapter (Chapter 1.2.1) provides an overview of this research and adressess both evidence in favor of a mandatory linkage of spatial attention and motor programming and research findings that challenge the obligatory nature of this coupling.

# 1.2.1 Evidence for and against an obligatory attention-action coupling

Several lines of research have examined the coupling between spatial attention and motor actions. For instance, electrophysiological studies have shown that event-related potentials (ERPs) indicative of covert attention shifts are triggered when irrelevant visual probes are presented at motor-relevant positions within the programming phase of saccades (Eimer et al., 2006) and manual movements (Baldauf & Deubel, 2009; Eimer et al., 2006), consistent with the notion of a common neural mechanism for spatial attention and motor programming. Similarly, lateralized attentionassociated ERP components have only been observed when manual responses and spatial attention

were directed to the same hemifield, but not when the task required to shift attention and gaze to different hemifields (Gherri & Eimer, 2010), which indicates that planning a motor action toward one location disrupts the capacity to attend to a position other than the upcoming motor target. The idea that attentional orienting and motor programming rely on the same neural process is also supported by neuroimaging and electrical microstimulation studies. It has been shown that covert and overt attention shifts are associated with a considerable overlap of brain activity in a network of frontal and parietal cortical areas (Beauchamp et al., 2001; Corbetta et al., 1998; de Haan et al., 2008; Nobre et al., 2000; Perry & Zeki, 2000). In line with these findings, studies in non-human primates have demonstrated that subthreshold microstimulation of oculomotor brain regions like the superior colliculus (SC) (Müller et al., 2005) and frontal eye field (FEF) (Moore & Fallah, 2001, 2004) leads to enhanced perceptual performance at the location to which a saccade would have been evoked at a higher stimulation strength. At first glance, the involvement of the FEF and SC in both covert and overt attention is consistent with the assumption that the two processes are controlled by the same neural mechanism. However, there is also evidence that contradicts this assumption. Studies examining the FEF and SC at high spatial resolution have shown that both brain regions contain distinct populations of neurons, with some (visual and visuomotor neurons) being active and others (motor neurons) being unresponsive or inhibited during covert attention shifts (Gregoriou et al., 2012; Ignashchenkova et al., 2004; Thompson et al., 2005). This can be interpreted as evidence that covert attentional orienting is not dependent on oculomotor programming. In line with this, transcranial magnetic stimulation over the human FEF has been used to demonstrate that covert shifts of attention and oculomotor programming occur at different time points and therefore represent dissociable processes (Juan et al., 2008).

At the behavioral level, the attention-action coupling has typically been studied by means of a psychophysical dual-task paradigm (e.g., Deubel & Schneider, 1996). Note that this paradigm has also been employed in the studies included in this dissertation (Chapter 2.1 and 2.2). In these experiments, participants are asked to prepare a goal-directed movement toward one of several peripherally presented placeholder objects, with the specific motor target typically indicated by an endogenous cue (e.g., a central arrow pointing toward one of the placeholder objects). Prior to movement execution, an attention probe in the form of a to-be-discriminated visual stimulus (e.g., the character E or ∃, or a clockwise or counterclockwise tilted line) is flashed either at the motor target or at one of the remaining, movement-irrelevant placeholder positions. Once the movement has been executed, the identity of the probe has to be indicated by participants via button press. By comparison of discrimination performance at different probe positions (e.g., between the motor target and movement-irrelevant positions) across multiple trials, the dual-task paradigm thus allows the measurement of spatial attention allocation prior to movement onset (e.g., while motor

programming is still in progress). For both saccadic eye movements (Deubel, 2008; Deubel & Schneider, 1996; Hanning et al., 2022; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011; Khan et al., 2011; Kowler et al., 1995) and manual movements (Deubel et al., 1998; Hanning et al., 2022; Jonikaitis & Deubel, 2011; Khan et al., 2011; Schiegg et al., 2003), these psychophysical dualtask studies have consistently provided evidence for a premotor shift of attention toward the upcoming motor target: discrimination performance is best for attention probes presented at the motor target compared to other positions. This spatial congruency effect is observed even when participants are instructed to direct attention to a position other than the imminent target of saccades (Deubel, 2008; Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler et al., 1995) and manual movements (Deubel et al., 1998; Schiegg et al., 2003), which is usually taken as evidence for the notion that premotor attention shifts are indeed mandatory. Notably, premotor attention shifts also occur when sequences of saccades (Baldauf & Deubel, 2008; Godijn & Theeuwes, 2003) or manual movements (Baldauf et al., 2006) are planned, with attentional resources being shifted to all upcoming motor targets in parallel. In line with the aforementioned evidence in favor of an obligatory attention-action coupling, other behavioral studies have further shown that the deployment of attention at a movement-irrelevant location affects the trajectory of saccadic eye movements (Moehler & Fiehler, 2014; Sheliga et al., 1994; Van der Stigchel & Theeuwes, 2007), an observation that is often interpreted in terms of an interdependency of the spatial attention and oculomotor system.

However, there is also behavioral evidence that contradicts the idea that spatial attention is strictly linked to motor programming. First, the results of several psychophysical dual-task studies indicate that the programming of a motor action is not always accompanied by a spatially congruent shift of attention. For example, premotor attention shifts to saccade targets are only observed when the saccadic program is subsequently executed, but not when motor execution is successfully inhibited (Born et al., 2014). Moreover, it has been shown that so-called averaging saccades (i.e., saccades that land between competing stimuli) are not preceded by a premotor shift of attention to the endpoint of the saccadic eye movement (Van der Stigchel & de Vries, 2015; Wollenberg et al., 2018, 2019; Wollenberg et al., 2020), demonstrating that covert attention is not strictly linked to the directionality of oculomotor programs. Second, it has been shown that some attentional resources can be diverted from saccade targets during motor programming (Born et al., 2013; Kowler et al., 1995; Moehler & Fiehler, 2014; Montagnini & Castet, 2007), rendering it difficult to consider covert attention shifts as a mere by-product of motor programming, as proposed by the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994). Third, studies in both neuropsychological patients and healthy participants have shown that endogenous but not exogenous attention can be directed to positions beyond the range of eye movements (Gabay et al., 2010; Smith et al., 2004;

Smith et al., 2012; but see Hanning & Deubel, 2019). This indicates that endogenous attentional control in particular is not dependent on motor programming.

In sum, studies on the relationship between covert shifts of attention and motor programming have demonstrated that the two processes are tightly linked, whereas there is mixed evidence as to whether this linkage is mandatory.

# 1.3 Objectives of the dissertation

As outlined above, the proposed obligatory attentional selection of future motor targets (as reflected in the premotor attention shift phenomenon) has been explained either as an epiphenomenon of motor programming (Rizzolatti et al., 1987; Rizzolatti et al., 1994) or as a prerequisite for motor programming to enable the extraction of movement-relevant information related to the target (Allport, 1987; Neumann, 1987; Schneider, 1995). However, the contradictory evidence regarding the obligatory nature of the attention-action coupling (see Section 1.2.1) raises the possibility that the attentional selection of future motor targets is mediated by a mechanism other than motor programming itself. In particular, it should be noted that motor targets are generally not chosen at random, but for a specific reason, either because something potentially relevant has appeared or is expected to appear at that location (and we want to explore that location with our eyes), or because the location contains a relevant object (that we intend to manipulate). With this in mind, it seems plausible to assume that attentional selection of the target location of an upcoming movement results from an anticipation that this location contains interesting information (Posner et al., 1980), rather than being the product of a strict link between spatial attention and motor programming. Put differently, the selection of future motor target locations by spatial attention might be guided by a learned habitual expectation that these locations contain information of high behavioral relevance (habitual attention-action coupling hypothesis). If the habitual attentionaction coupling hypothesis is correct, one might expect that if this habitual expectation is altered by learning to expect relevant information at a position other than the target of an upcoming movement, it should be possible to shift attention away from the motor target position and toward this (movement-irrelevant, yet perceptually relevant) position.

Using the common psychophysical dual-task paradigm (see Chapter 1.2.1), Dignath et al. (2019) recently attempted to test this assumption. To this end, different groups of participants were trained to expect an attention probe to always appear either at a cued target of an upcoming pointing movement, at a position opposite the pointing target, or at an unpredictable position. In a subsequent test phase with randomized probe position, they found that attention probes were best identified at the expected (i.e., trained) probe position, regardless of whether this position matched

the pointing target position or not. The observation of superior attentional performance at a position irrelevant to the upcoming pointing movement was taken as evidence against the notion of an obligatory attention-action link. However, this decoupling effect was demonstrated in a delayed pointing task (Dignath et al., 2019), which may have allowed motor programming to be completed before attention was diverted from the pointing target (cf. Deubel & Schneider, 2003). It is therefore unclear, whether the findings of Dignath et al. (2019) also apply to the motor programming phase. In addition, Dignath et al. (2019) used an attention task (i.e., discrimination task) that included only two positions at which the attention probe could appear (i.e., at or opposite the pointing target). This made the attention task relatively simple, presumably resulting in a task sensitivity being too low to still ensure reliable measurements of attention allocation. This view is supported by the fact that Dignath et al. (2019) found high task performance at all task-relevant positions (rather than evidence for a typical premotor attention shift) in a control group in which participants had not been trained to expect the attention probe at a specific position. It is therefore likely that the decoupling effect reported by Dignath et al. (2019) does not reflect a training-induced modulation of attention allocation, but is rather due to a low task difficulty that allowed the task to be performed without high attentional demands. Overall, it is therefore still unclear whether a training to anticipate a taskrelevant stimulus at a motor-irrelevant position enables a decoupling of the attention-action link and, if so, whether such a top-down modulation of spatial attention is possible concurrently with motor programming.

The first experimental study of this dissertation (Chapter 2.1) addressed these open questions. In particular, we aimed to replicate the decoupling effect observed by Dignath et al. (2019) and, more importantly, to test whether such a decoupling of attention from the target of an upcoming movement is also possible while motor programming is still in progress. In fact, only a decoupling effect observed during ongoing motor programming would demonstrate that motor target selection is not induced by motor-related processes, thus providing evidence in favor of the habitual attention-action coupling hypothesis. To this end, we conducted an adapted version of the experimental design used by Dignath et al. (2019). In two experiments, participants were asked to perform the common psychophysical dual-task consisting of an attention task and a pointing task. In a training phase, we manipulated the position of the attention probe so that participants learned to always expect the probe at a cued pointing target (Experiment 1), opposite the pointing target (Experiment 1 and 2), or at an unpredictable position (Experiment 1 and 2). In a subsequent test phase, the position of the attention probe was randomized to allow measurements of traininginduced top-down modulations of spatial attention allocation. To test whether potential training effects on attention allocation do not rely on the completion of motor programming, but can also occur concurrently with motor programming, we varied the time of movement delays (i.e., stimulus

onset asynchrony between a movement cue and a movement go-signal) so that attention allocation could be determined both within (Experiment 1 and 2) and after (Experiment 1) the assumed motor programming phase. In addition, we doubled the number of task positions compared to the study by Dignath et al. (2019). This had two advantages. First, it increased the difficulty of the attention task compared to the task used by Dignath et al. (2019). Second, it allowed us to introduce task-irrelevant control positions, which enabled an assessment of the sensitivity of our attention task to measure relative differences in spatial attention allocation.

Although the first experimental study (Chapter 2.1) allowed us to investigate whether a learned expectation of spatial incongruence between visual and motor targets enables a decoupling of the attention-action link in manual movements, it is unclear whether the obtained findings can be generalized to saccadic eye movements. However, given the intricate link between ocular and attentional orienting and the long-standing dominance of studies of saccadic eye movements in research on spatial attention, the more critical test of the habitual attention-action coupling hypothesis would be to examine the possibility of an attentional decoupling in saccades (i.e., during oculomotor programming). The second experimental study (Chapter 2.2) addressed this open question. Using a dual-task paradigm similar to that of the first study, participants were asked to perform an attention task in parallel with a saccade task with variable movement delays, allowing the measurement of attention allocation at different time points (i.e., during and after the assumed motor programming phase) prior to movement execution. In a training phase, we manipulated the position of the attention probe to elicit either an expectation of spatial congruence or incongruence between the position of the probe and the saccade target. In a subsequent test phase, possible training-induced effects on premotor attention allocation were investigated by presenting the attention probe at a randomized position. As in the study of Dignath et al. (2019) and the first study of this dissertation, we established an expectation of spatial incongruence between positions by presenting an attention probe at the saccade target in all trials of the training phase. However, in contrast to previous studies (Dignath et al., 2019; first study of this dissertation), we had two different training groups to establish an expectation of spatial incongruence between positions: one in which the attention probe was always presented at a position defined relative to the varying saccade target (e.g., opposite the saccade target), and another one in which the attention probe was always presented at a fixed position not varying with the saccade target. The purpose of using two different spatial incongruence conditions (as discussed in more detail in the following chapters) was to additionally explore whether a possible expectancy-driven decoupling of attentional resources from motor targets is related to a specific spatial relationship between the position of the motor target and the anticipated probe position.

# 2 Experimental studies

The following chapter contains two peer-reviewed published studies.

# 2.1 The role of habitual learning in premotor attention allocation

## The following study has been published as:

Topfstedt, C. E., Wollenberg, L., & Schenk, T. (2023). The role of habitual learning in premotor attention allocation. *Journal of Vision*, *23*(5), 1-18. <u>https://doi.org/10.1167/jov.23.5.19</u>

### **Author Contributions:**

Christof E. Topfstedt: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Project administration. Luca Wollenberg: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing -Review & Editing, Project administration.

Thomas Schenk: Conceptualization, Methodology, Writing - Review & Editing, Funding acquisition.

# The role of habitual learning in premotor attention allocation

**Christof Elias Topfstedt** 

# Luca Wollenberg

Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany

Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany

Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany



 $\searrow$ 

1

# Thomas Schenk

Dual-task studies have demonstrated that goal-directed actions are typically preceded by a premotor shift of visual attention toward the movement goal location. This finding is often taken as evidence for an obligatory coupling between attention and motor preparation. Here, we examined whether this coupling entails a habitual component relating to an expectation of spatial congruence between visual and motor targets. In two experiments, participants had to identify a visual discrimination target (DT) while preparing variably delayed pointing movements to a motor target (MT). To induce distinct expectations regarding the DT position, different groups of participants performed a training phase in which the DT either always appeared at MT, opposite to MT, or at an unpredictable position. In a subsequent test phase, the DT position was randomized to assess the impact of learned expectancy on premotor attention allocation. Although we applied individually determined DT presentation times in the test phase of Experiment 1, a fixed DT presentation time was used in Experiment 2. Both experiments yielded evidence for attentional enhancement at the expected DT position. Although interpretability of this effect was limited in Experiment 1 because of between-group differences in DT presentation time, results of Experiment 2 were much clearer. Specifically, a marked discrimination benefit was observed at the position opposite to MT in participants anticipating the DT at this position, whereas no statistically significant benefit was found at MT. Crucially, this was observed at short movement delays, demonstrating that expectation of spatial incongruence between visual and motor targets allows for decoupling of attentional resources from ongoing motor preparation. Based on our findings, we suggest that premotor attention shifts entail a considerable habitual component rather than being the sole result of motor programming.

# Introduction

Visual attention is the mechanism that enables our visual system to cope with its limited capacity to process the vast amount of available visual information in our environment. It allows us to select behaviorally relevant aspects or locations of the visual scene for prioritized processing while other information is ignored (Carrasco, 2011). Attentional selection is not only assumed as crucial for optimal processing of visual input information (selection-for-perception) but also to provide the motor system with visuospatial information required to generate goal-directed movements such as reaches, grasps, or saccadic eye movements (selection-for-action; Allport, 1987). More specifically, a goal-directed action is typically directed toward only one of several available targets in our visual surroundings. For this reason, information selection has been claimed to be a prerequisite for movement planning to supply the motor system with the spatial parameters of the target (Neumann, 1987) and to inhibit signals from competing movement goals (Allport, 1987).

Several theories of visual attention emphasize the close link between visual attention shifts and goal-directed actions and further suggest that the two processes are mandatorily coupled to one another. For instance, the Visual Attention Model (VAM; Schneider, 1995; Schneider & Deubel, 2002) states that selection-for-perception and selection-for-action are bound together by a common attentional mechanism. More precisely, VAM assumes that attentional selection of an object in the visual scene leads to prioritized processing of this information in both the ventral stream for object recognition and the dorsal stream for

Citation: Topfstedt, C. E., Wollenberg, L., & Schenk, T. (2023). The role of habitual learning in premotor attention allocation. *Journal of Vision*, *23*(5):19, 1–18, https://doi.org/10.1167/jov.23.5.19.

https://doi.org/10.1167/jov.23.5.19

Received August 30, 2022; published May 25, 2023

ISSN 1534-7362 Copyright 2023 The Authors

This work is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License.

setting up motor programs towards the selected target. In contrast, the authors of the Premotor Theory of Attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994) argued against the notion of separate processing mechanisms for movement preparation and visual attention. Rather, the theory states that both endogenous (i.e., top-down) and exogenous (i.e., bottom-up) attention shifts are the direct consequence of motor programming activity. However, despite these different views on the neural underpinnings of the attention-action link, both theories propose a similar behavioral consequence of this coupling: Planning a goal-directed movement is mandatorily accompanied by a covert attention shift towards the movement goal, and vice versa (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994; Schneider, 1995; Schneider & Deubel, 2002).

Support for the claim of an obligatory coupling between motor planning and attention shifts came from several studies using a dual-task paradigm in which participants prepare a goal-directed movement toward an endogenously cued location whereas attention allocation is probed by presenting a discrimination target (DT) either at the movement target (MT) or at a different location. These studies consistently showed that single saccades (Deubel, 2008; Deubel & Schneider, 1996; Deubel & Schneider, 2003; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011) and single pointing movements (Deubel, Schneider, & Paprotta, 1998; Jonikaitis & Deubel, 2011; Hanning, Wollenberg, Jonikaitis, & Deubel, 2022) are preceded by a premotor shift of attention toward the movement goal location, as indicated by enhanced discrimination performance at the MT compared to other locations. Similarly, attentional facilitation was found at the to-be-grasped parts of the target object of an upcoming grasping movement (Schiegg, Deubel, & Schneider, 2003). Moreover, these premotor attention shifts are not restricted to the preparation of single goal-directed movements. When sequences of saccades or reaches are planned, separate foci of attention are deployed to all target locations in parallel (Baldauf & Deubel, 2008; Baldauf, Wolf, & Deubel, 2006; Godijn & Theeuwes, 2003). Importantly, attentional facilitation at the movement goal location persists even in conditions in which participants are encouraged to direct attention away from the MT (Deubel, 2008; Deubel & Schneider, 1996; Deubel et al., 1998; Hanning et al., 2022; Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1995; Schiegg et al., 2003), suggesting that the link between motor planning and visual attention is mandatory.

Consistent with these findings, other behavioral studies have shown that covert attention allocation leads to deviations in saccade trajectories when the attended location and the target of an oculomotor program diverge (Moehler & Fiehler, 2014; Sheliga, Riggio, &

Rizzolatti, 1994; Sheliga, Riggio, & Rizzolatti, 1995; Van der Stigchel & Theeuwes, 2007). Furthermore, electrophysiological studies provided evidence in support of the notion of an obligatory attention-action coupling. For example, studies of nonhuman primates have shown that subthreshold microstimulation of brain regions involved in the generation of saccades, such as the frontal eye field (FEF) and the superior colliculus (SC), leads to attentional facilitation at the motor field location of the stimulated neurons (Moore & Fallah, 2001, 2004; Müller, Philiastides, & Newsome, 2005). Correspondingly, it was found that attention-associated components of event-related potentials (ERPs) are enhanced in human participants when visual stimuli are presented at movement-relevant locations during the preparation phase of saccades and manual movements (Baldauf & Deubel, 2009; Eimer, Forster, Van Velzen, & Prabhu, 2005; Eimer, Van Velzen, Gherri, & Press, 2006; Gherri & Eimer, 2010).

Although a close link between movement programming and covert attention has been widely demonstrated, the obligatory nature of this coupling remains controversial (for a review, see Smith & Schenk, 2012). For instance, physiological studies have shown that overt and covert orienting are controlled by distinct neuronal populations within the FEF (Sato & Schall, 2003; Thompson, Biscoe, & Sato, 2005) and that both processes are temporally dissociated (Juan et al., 2008; Juan, Shorter-Jacobi, & Schall, 2004). Consistent with this finding, behavioral dual-task studies demonstrated a spatial dissociation between the endpoint of so-called averaging saccades and the locus of visual attention (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018, 2019; Wollenberg, Hanning, & Deubel, 2020). Furthermore, there is evidence that endogenous attentional control in particular does not depend on motor preparation. Studies with neuropsychological patients have shown that an impairment in executing goal-directed eye movements is associated with deficits in exogenous attention but that the ability to shift attention endogenously in space is unaffected (Gabay, Henik, & Gradstein, 2010; Smith, Rorden, & Jackson, 2004). Likewise, exogenous but not endogenous attention shifts of healthy participants were found to be limited to areas in the visual field within the range of eye movements (Smith, Schenk, & Rorden, 2012; but see Hanning & Deubel, 2020). In addition, studies using a dual-task paradigm have shown that top-down processes can modulate the attention-action coupling. Kowler et al. (1995, Experiment 4), for example, observed that when following the instruction to avoid a prioritization of either the perceptual or the saccade task, participants were capable of withdrawing some attentional resources from the movement goal without costs in saccade latency or accuracy. Similarly, Montagnini and Castet (2007) showed that attention can be deployed endogenously to locations other than a saccade target, but that this ability diminished shortly before movement onset.

One way to account for the contradictory evidence regarding the nature of the attention-action link would be to consider the typical premotor attention shift towards a movement goal location as a merely habitual process (Posner, Snyder, & Davidson, 1980), because the target of a goal-directed movement is of highest behavioral relevance in most everyday situations. If so, a prerequisite to decouple covert attention from the target of an upcoming goal-directed movement might be extensive training (Reeves & McLellan, 2020). To date, very few studies have investigated how training to shift attention toward a non-movement target affects the attention-action coupling. Song and Bédard (2013) found that participants directed attentional resources equally well to both a visual and a reach target when they had learned to spatially dissociate both target locations through visuomotor adaptation. Also, Reeves and McLellan (2020) showed that learning affects covert attentional deployment. Specifically, they observed that the majority of their participants were capable of executing a simultaneous shift of gaze and of attention in opposite directions, but that learning this skill required up to 10 hours of practice. However, both studies (Reeves & McLellan, 2020; Song & Bédard, 2013) used a Rapid Serial Visual Presentation (RSVP) task to measure attention allocation, which has several weaknesses when studying top-down modulations of premotor attention shifts compared to the more commonly used discrimination task (Deubel & Schneider, 1996). First, participants are aware of the spatial position of the attention test (i.e., the RSVP stream), which facilitates the use of explicit strategies to solve the task. Second, the task requires sustained maintenance of attention at the position of the RSVP stream, making it difficult to test attention allocation at varying time points relative to the onset of the movement. This would be crucial, however, to examine at which stage of movement preparation attentional resources can be decoupled from the movement goal location. Third, an RSVP stream is a highly salient event and thus does not allow us to distinguish whether attentional facilitation at that position is caused by attentional capture of the stream itself (exogenous attention) or by top-down modulations of attention (endogenous attention).

In contrast, Dignath, Herbort, Pieczykolan, Huestegge, and Kiesel (2019) recently used a discrimination task to test whether the learned anticipation of spatial congruence or incongruence of a visual and a motor target modulates the link between visual attention and motor preparation. Specifically, they asked participants to accomplish training in which a DT was presented either at the target of a pointing movement or at a position opposite to this target. Results showed that attention is strictly tied to the movement goal location when participants had learned that a DT position always coincides with the MT. In contrast, learning to expect the DT at the position opposite the MT caused participants to shift attentional resources only towards that location, suggesting that it is possible to overcome the attention-action link through practice. However, there are reasons to be cautious in taking these results as evidence against an obligatory coupling between covert attention shifts and processes of motor preparation. First, the pointing task of Dignath et al. (2019) contained a movement delay (i.e., stimulus onset asynchrony [SOA] between a movement cue and a go-signal for movement initiation) that was relatively long (i.e., 612-799 ms). Thus it is possible that those participants, who had learned to decouple the locus of attention from the movement goal location, did so only after the movement had been fully programmed. This would be in line with the findings of Deubel and Schneider (2003), who showed that attention can be withdrawn from a reach target but only if the movement is delayed by more than 300 ms, indicating that these movements can be "performed 'off-line,' that is, without attention" (p. 295). Second, the discrimination task of Dignath et al. (2019) consisted of only two placeholder positions at which the DT could appear (i.e., at or opposite the MT). However, the use of only two placeholders makes the discrimination task relatively simple, which could lead to insufficient sensitivity of the attention test (i.e., attention is no longer necessary for DT identification). In such a case, certain outcomes of the discrimination task do not permit unambiguous conclusions to be drawn, particularly when no task-irrelevant control position is available as a baseline condition. For instance, if discrimination performance is observed to be equally well at both positions, it is not possible to tell whether attention was directed towards both positions or whether the task allowed probe identification without attention. Dignath et al. (2019) reported exactly such a pattern of equivalent performance at both available positions for one control group in which participants had not learned to anticipate the DT at a specific position. It is in this case possible that the sensitivity of the discrimination task of Dignath et al. (2019) was actually too low to still serve as a reliable measure of attention allocation. This means that it cannot be determined whether the training effects reported by Dignath et al. (2019) were driven by processes of attentional selection or whether they were rather a consequence of a low difficulty of the discrimination task. In summary, it is still unclear (1) whether the anticipation of spatial incongruence of a visual target and a movement goal location can modulate the attention-action coupling and, if so, (2) whether these top-down effects on attention allocation can occur even when the critical movement programming phase is still in progress.

In the current study, we aimed to address these open questions by conducting two experiments (Experiments 1 and 2) with a modified version of the dual-task paradigm used by Deubel and Schneider (2003) and Dignath et al. (2019). Similar to these previous studies, the dual-task in both experiments consisted of a delayed pointing task, in which participants had to prepare a pointing movement toward an endogenously cued MT, and a discrimination task, in which they had to indicate the identity of a DT that was presented before movement execution. However, we doubled the number of placeholder positions compared to the study by Dignath et al. (2019). This allowed us, on the one hand, to increase the difficulty of the discrimination task and, on the other hand, to measure discrimination performance at task-irrelevant control positions. By introducing this baseline condition, we were able to directly test whether the sensitivity of our attention test was sufficiently high to reliably measure relative differences in the spatial allocation of attention.

In Experiment 1, we asked participants to perform a training session that was similar to the one of the study of Dignath et al. (2019). Participants either learned that a DT always appears at the same position as a MT, always at a position opposite a MT, or at a randomly chosen position. As in the study of Dignath et al. (2019), we adjusted presentation times of the DT for each participant over the course of the training phase to account for interindividual differences in discrimination performance. In a subsequent test phase, putative training effects on the attention-action coupling were examined by presenting the DT with equal probability at one of the placeholder positions. To test whether the previously found effects of learned spatial congruence and incongruence (Dignath et al., 2019) can be generalized to the movement preparation phase, we varied the time between the presentation of the movement cue and go-signal to initiate the pointing movement (movement delay). If learning can modulate the attention-action link both before and after the completion of movement preparation, similar effects on attention allocation should be found for short and long movement delays.

Experiment 1 revealed differences between training conditions in the length of adjusted presentation times of the attention probe (DT). Although these differences offered insights into the difficulty of establishing a learned spatial congruence or incongruence between positions during the training phase, they made it difficult to compare training effects on attention allocation between training conditions in the subsequent test phase. We therefore conducted a second experiment (Experiment 2) that was similar to Experiment 1, except that we used a fixed probe presentation time in the discrimination task. This allowed for improved intergroup comparison of results and additional examination of whether training effects observed in Experiment 1 were modulated by probe presentation time.

### **Experiment 1**

#### Methods

#### Participants

Sixty-nine healthy participants (45 females; 10 left-handed; average age: 24.1 years; age range 19–37 years) took part in Experiment 1, including one author (C.E.T.). All participants had normal or corrected-to-normal vision and normal motor behavior. Except C.E.T., participants were naïve to the purpose of the experiment. Two of them had participated in a previous study on attention allocation. Participants gave informed consent to participate in the study. The experiment was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki.

#### Apparatus

Figure 1 depicts the experimental setup. Participants were seated in front of a one-way mirror with their head positioned on a chin rest. A computer monitor (Acer XB271HUA; Acer, New Taipei City, Taiwan) at the top of the setup presented visual stimuli at a frame rate of 120 Hz and a resolution of 1600  $\times$ 1440 pixels (size of the used screen area:  $37.3 \times 33.6$ cm). The opposite inclination of the monitor and the mirror allowed the projection of visual stimuli onto a virtual pointing plane beneath the mirror. Thereby, participants were able to execute pointing movements toward visually presented movement targets without seeing their reaching hand. The viewing distance to the center of the monitor was 56.4 cm. Gaze fixation was controlled by tracking participants' right eye at 1000 Hz using an EyeLink 1000 Plus eye tracking system (SR Research Ltd., Mississauga, Ontario, Canada). Pointing movements were recorded by a robotic haptic device (Phantom Premium 1.5.; 3D Systems, Rock Hill, SC, USA) with a temporal resolution of 1000 Hz. Participants positioned the tip of their right index finger in a thimble attachment mounted at the end effector of haptic device. To ensure that participants were not able to move their index finger through the pointing plane, a haptic feedback in the form of a resisting force was applied at the pointing plane's position. A cursor (red bar) was presented before and after movement execution to provide visual feedback of the current finger position. Because of technical constraints of the experimental setup, the cursor was displayed with a constant vertical offset of approximately 3.0° beneath

#### Topfstedt, Wollenberg, & Schenk



Figure 1. Sketch of the experimental setup. Participants positioned their head on a chin rest (marked in blue) facing towards a one-way mirror (depicted transparently for illustration only). A monitor (marked in dark green) projected movement targets on a virtual pointing plane (marked in bright green). The index finger of the reaching hand was positioned in a thimble attachment at the end effector (illustrated as a black sphere) of a haptic device. Thereby, participants were able to perform pointing movements toward visually presented movement targets without seeing their reaching hand.

the tip of the index finger (please note that vertical deviations between the endpoint of the pointing movements and the motor target's position were close to zero in each part of the experiment [i.e., all  $M < 0.13^\circ$ , all  $SD < 0.40^\circ$ ], indicating that participants adapted the pointing movements right from the start of the experiment).

#### Design and procedure

The time course of a typical trial is depicted in Figure 2. At the beginning of each trial, a white circular button (radius  $0.75^{\circ}$ ) consisting of a black frame and a central black fixation cross (size  $0.5^{\circ} \times$  $0.5^{\circ}$ ) was presented on a uniform grey background. The button was surrounded by four black premask characters (seven-segment character "8"; size  $0.9^{\circ} \times$  $1.4^{\circ}$ ) presented at a distance of 7.2° from fixation. At this stage, the cursor was visible. Participants were instructed to position the cursor on the white button while fixating the central fixation cross with their eyes. They were asked to maintain gaze fixation throughout the trial. By touching the white button with the cursor, the background color of the button changed to a

uniform gray, and, simultaneously, the cursor was turned off. After a delay of 500 to 800 ms, the button was replaced by a movement cue (black arrow) that pointed with equal probability toward one of the four premask characters. After an SOA of 100 or 800 ms (movement delay), a tone (440 Hz) was presented for 50 ms serving as a go-signal to point as quickly and accurately as possible toward the cued MT. To perform the movement, participants were instructed to lift their finger off the pointing plane. With go-signal offset, one of the four premask characters was replaced by a DT (seven-segment character "E" or "3"), while distractors (seven-segment character "2" or "5") were presented at the three remaining placeholder positions. After an individual presentation time (see section Staircase procedure), the DT and the distractors were masked again. Feedback of pointing accuracy was given by presenting the cursor again after movement execution. At the end of a trial, participants reported the identity of the DT by pressing one of two buttons on a keyboard with their left hand. Participants received acoustical feedback about the discrimination performance after each trial of the training phase but not of the test phase (see next paragraph).

The experiment consisted of a training and a test session, which took place on two consecutive days. In the training session, participants were assigned to one of four training groups. Training conditions differed from each other in the adjustment of individual probe presentation times (see section Staircase procedure) and the relative positions of the DT and MT. In the Training Same group, the DT was always presented at the location of the MT. In the Training Opposite group, the DT always appeared at the location opposite to the MT. We had two control groups (Control Same and Control Opposite). The reason for using two control groups will be explained in the next section (Staircase procedure). In both control groups, the DT was presented with equal probability at one of the four placeholder positions. Participants were not informed about the relative positions of the DT and MT in any of the four conditions. The training session started with two blocks of 32 practice trials of the pointing task only (latency training). In these trials, participants were informed by a visual feedback signal (red [indicates an error] vs. green [indicates an acceptable movement] circle) whether the movement had been initiated too early (i.e., before go-signal onset), too late (>350 ms), or sufficiently fast ( $\leq$ 350 ms). Participants then completed two blocks of 32 practice trials of the dual-task in which they performed the pointing task and the discrimination task in parallel (dual-task training). In these trials, participants received acoustical feedback about discrimination performance after each trial. The probe display was presented for 408 ms. The subsequent training phase consisted of 12 blocks of 32 trials.



Figure 2. Time course of a typical trial. Participants positioned a red cursor on a central white button with their right index finger. Eye fixation was maintained throughout the trial. An arrow cue indicated the pointing target. After presentation of a go-signal, participants executed a pointing movement toward the cued location. At 50 ms after go-signal onset, a probe display was presented consisting of a DT (seven-segment character "E" or "3") and three distractors (seven-segment character "2" or "5"). Participants reported the identity of the DT after movement execution.

	Training same	Training opposite	Control same	Control opposite
Training phase				
Performance feedback	Yes	Yes	Yes	Yes
DT position	MT	Opposite MT	Random	Random
DT condition used for individual presentation time adjustments	MT	Opposite MT	MT	Opposite MT
Number of trials	384	384	384	384
Test phase				
Performance feedback	No	No	No	No
DT position	Random	Random	Random	Random
DT presentation time	Individually adjusted	Individually adjusted	Individually adjusted	Individually adjusted
Number of trials	512	512	512	512

Table 1. Main differences in experimental conditions between training groups and between the training phase and test phase.

In the test session, participants first performed two blocks of 32 trials of the latency training and two blocks of 32 trials of the dual-task training. The procedure of the practice trials was similar to the training session, except that individual presentation times of the probe display (see section Staircase procedure) were used in the dual-task training. Then, each participant performed 16 blocks of 32 experimental trials in which the DT was presented with equal probability at one of the four placeholder positions (test phase). To discourage quick unlearning of potential attentional biases acquired during training, no feedback about discrimination performance was given during the test phase. Table 1 summarizes the most important differences between the training groups and between the training phase and test phase.

17

#### Staircase procedure

Similar to Dignath et al. (2019), the presentation time of the probe display was adjusted individually over the course of the training phase. We applied a 3-down 1-up staircase procedure, which converges to a 79.4%performance level. At the beginning of the training phase, the DT presentation time was set to 250 ms. The step size of adjustments after each direction reversal varied across the training phase: 66.67 ms for reversals 1-3, 33.33 ms for reversals 4-6, 16.67 ms for reversals 7–9, and 8.33 ms for the remaining reversals. The minimum presentation time was 8.33 ms. Trials were not included in the staircase calculations if an eve fixation violation (see section Data analysis) was detected or if the pointing movement was not initiated within 350 ms after go-signal onset. After completion of the training phase, individual presentation times were determined by averaging presentation times calculated at the last four reversals.

The type of trials included in the computations of the threshold (i.e., adjusted probe presentation time) differed between training groups (see Table 1). In Training Same and Training Opposite, all training phase trials could potentially be included in the threshold calculations, since the probe was consistently presented at only one specific position (Training Same: MT position; Training Opposite: opposite position) in the training phase of these two groups. However, the question of which trials to use to calculate the threshold in control conditions with varying probe positions was less straightforward, since inclusion of all trials (regardless of probe position) would likely lead to a ceiling effect, making the task no longer sensitive enough to measure attention allocation in the subsequent test phase. For this reason, we also restricted threshold calculations in control conditions to one specific probe position. In addition, we aimed at consistency between threshold calculations in Training Same and Training Opposite and threshold calculations in control conditions. To this end, we used two control groups. In Control Same, only trials in which the DT was presented at the MT position were included in the threshold computations. In Control Opposite, only trials in which the DT was presented opposite the MT position were used to calculate the threshold. Given that this approach resulted in a group difference in the number of potential trials (Training Same and Training Opposite: 100% of training phase trials; Control Same and Control Opposite: 25% of training phase trials) included in the threshold computations, we set a minimum number of staircase reversals (i.e., 14 reversals) that had to be reached in the training phase to proceed with the experiment (see also section Data analysis). This ensured that the threshold was calculated with sufficient accuracy in all training groups.

#### Data analysis

Recordings of pointing movements and gaze behavior were analyzed with MATLAB R2021b (MathWorks, Inc., Natick, MA, USA). We defined the onset of pointing movements as the first point in time when velocity exceeded a threshold of 0.02 m/s for a duration of at least 150 ms. Because participants were instructed to lift the finger to perform the movement, movement offset was measured as the first point in time the pointing plane was touched again. Pointing movement duration was defined as the time between movement onset and movement offset.

Three participants of the Control Same group and one participant of the Control Opposite reached less than 14 reversals in the staircase procedure and did not take part in the test session. We excluded participants when their adjusted probe presentation time deviated from the median of their training group by more than three times the median absolute deviation (Levs. Ley, Klein, Bernard, & Licata, 2013). This was true for four participants of the Training Opposite group and four participants of the Control Same group. For offline analyses of the test phase data of the remaining sample (N = 57 out of a total of 69), we discarded trials if one of the following exclusion criteria was met. Regarding gaze behavior, trials were excluded if gaze was not maintained within 2.5° from fixation (for a similar approach, see Hanning, Aagten-Murphy, & Deubel, 2018) between movement cue onset and mask onset (Fixation violation) or if a blink occurred within the same time interval (Blink violation). Regarding pointing behavior, we excluded trials if no pointing movement onset or offset was detected (No movement). if the movement was initiated before go-signal onset (Movement too early), or if the movement endpoint deviated from the center of the MT by more than 2.5° (Movement inaccurate; for a similar approach, see Hanning et al., 2018). Moreover, trials were discarded as an outlier if movement latencies differed from the participant's median by more than three times the median absolute deviation (Movement latency outlier). After applying the exclusion criteria for erroneous trials, we additionally discarded the data sets of participants when more than 45% of trials (for a similar approach, see Arkesteijn, Belopolsky, Smeets, & Donk, 2019) of the test phase were rejected. This was the case for one participant of the Training Same group, one participant of the Training Opposite group, one participant of the Control Same group, and two participants of the Control Opposite group. The final sample (N = 52) consisted of 14 participants in the Training Same group, 14 participants in the Training Opposite group, 11 participants in the Control Same group, and 13 participants in the Control Opposite group. Supplementary Table S1 provides a detailed overview of the proportion of trials rejected because

of the aforementioned exclusion criteria for the final sample of each group.

Statistical analyses were performed in JASP version 0.16.1 (JASP Team). To examine the movement parameters, we conducted mixed analyses of variance (ANOVAs) with within-participants factor SOA condition (100 ms vs. 800 ms) and between-participants factor training group. Adjusted presentation times were analyzed with a one-way ANOVA with factor training group or, in case of unequal variances, with a corresponding Welch ANOVA. Performance in the discrimination task was expressed as the percentage of correct decisions regarding the identity of the DT. For analyses of discrimination performance, we employed a repeated measures ANOVA with factors SOA condition and DT position (DT at MT vs. DT at neutral positions vs. DT at opposite position) separately for each training group. Greenhouse-Geisser corrections were applied when sphericity was violated. Unless stated otherwise, post hoc pairwise comparisons were Bonferroni corrected.

#### Results

We performed two analyses of the experimental data obtained in Experiment 1. The first data analysis included all experimental data after applying the exclusion criteria described in the Methods section. The results of this data analysis are presented in the following section (First analysis). However, the first analysis revealed that adjusted presentation times of the discrimination target (DT) were relatively long for some of the participants, so that in some trials the DT was not yet masked at the time of movement onset. Thus it is possible that some of the effects observed in our first data analysis emerged only after movement onset. To rule out that post-onset probes confounded our results, we performed a second data analysis after discarding all trials from the dataset where the DT was still present after movement onset. The findings of the second analysis are presented in section Second analysis.

#### First analysis

*Movement parameters*: Regarding movement latencies (Table 2), we examined whether our manipulation

of movement delays was successful in that motor preparation was still in progress after an SOA of 100 ms but completed after an SOA of 800 ms. If so, movement latencies should be longer in trials with an SOA of 100 ms than in trials with an SOA of 800 ms. As expected, a mixed ANOVA with factors training group and SOA condition revealed a significant main effect of SOA condition, F(1, 48) = 159.55, p < 0.001,  $\eta_p^2$ = 0.77, suggesting that participants initiated pointing movements faster in trials with an SOA of 800 ms (M = 275 ms, SD = 43 ms) compared to trials with an SOA of 100 ms (M = 308 ms, SD = 41 ms). Neither the main effect of training group, F(3, 48) = 0.99, p = 0.404,  $\eta_p^2 = 0.06$ , nor the interaction, F(3, 48) = 1.17, p = 0.332,  $\eta_p^2 = 0.07$ , was significant. This indicates that an SOA of 100 ms required participants to first finalize motor preparation, whereas 800 ms were sufficient to release a completed motor program directly. However, pre-programming of the movement led to an average reduction in movement latencies of only 33 ms. Presumably, trials with an SOA of 800 ms required participants to initially suppress movement execution on movement cue presentation, resulting in the unexpectedly long movement latencies that were observed relative to the go-signal.

Movement duration across training groups was 325 ms (SD = 96 ms) in trials with an SOA of 100 ms and 330 ms (SD = 92 ms) in trials with an SOA of 800 ms. Moreover, Table 2 indicates that the difference in movement durations between an SOA of 800 ms and an SOA of 100 ms was larger in the Control Same group (M = 21 ms) compared to the remaining groups (Training Same: M = -6 ms; Training Opposite: M = 0ms; Control Opposite: M = 10 ms). A mixed ANOVA with factors training group and SOA condition revealed a significant interaction between SOA and training group, F(3, 48) = 2.88, p = 0.046,  $\eta_p^2 = 0.15$ ; however, neither the two main effects (main effect of SOA condition:  $F(1, 48) = 3.70, p = 0.060, \eta_p^2 = 0.07$ ; main effect of training group:  $F(3, 48) = 0.84, p = 0.477, \eta_{p}^{2}$ = 0.05) nor any post hoc comparisons of the data cells involved in the interaction reached significance (all p >0.169).

*Presentation times*: As mentioned in the Methods section, presentation times of the DT were adjusted individually over the course of the training phase. To compute the threshold values for presentation times,

	Training same $M\pm SD$	Training opposite M $\pm$ SD	Control same M $\pm$ SD	Control opposite M $\pm$ SD
Latency: SOA 100	$308 \pm 57$	$315\pm38$	290 ± 24	$315\pm32$
Latency: SOA 800	$269\pm62$	$288 \pm 41$	$260 \pm 33$	$280\pm24$
Duration: SOA 100	$343\pm79$	$318\pm86$	345 $\pm$ 157	$295\pm43$
Duration: SOA 800	$337\pm63$	$318\pm83$	$366\pm158$	$305\pm43$

Table 2. Movement latencies and movement durations for each training group and SOA (100 ms vs. 800 ms) in Experiment 1. *Note:* Values in ms.

#### Journal of Vision (2023) 23(5):19, 1-18

only the discrimination responses of a specific DT position were used within each of the training groups (Training Same, Control Same: MT position; Training Opposite, Control Opposite: opposite position). A side-effect of this method was that we were able to take the adjusted presentation times as a measure of how consistently participants of each training group allocated attention towards this DT position during the training phase. In particular, the comparison of presentation times between the Training Same and Training Opposite group was of high relevance for the analysis of training effects, because a group difference in presentation times would indicate a varying difficulty in establishing the implicitly learned spatial congruence (Training Same) or incongruence (Training Opposite) during the training phase. Moreover, a comparison of presentation times between the Training Same and Control Same group allowed to assess the contribution of learning in the allocation of attention at the MT position. Whereas shorter presentation times in the Training Same compared to the Control Same group would indicate that learning plays a crucial role in premotor attention allocation at the movement goal location, similar presentation times would suggest that premotor attention shifts towards this position are solely induced by processes of motor preparation.

Results of a Welch ANOVA revealed that presentation times (Figure 3A) differed considerably between training groups, F(3, 24.56) = 8.20, p < 0.001,  $\eta_{\rm p}^{2} = 0.45$ . Games-Howell post hoc comparisons showed that presentation times were shorter in the Training Same (M = 90 ms; SD = 87 ms) compared to the Training Opposite group (M = 188 ms, SD= 44 ms, p = 0.007), indicating that participants of the Training Same group directed attention more consistently toward the anticipated DT position (MT position) than participants of the Training Opposite group (opposite position). In other words, shifting attention toward the movement goal location (Training Same) was easier than learning to shift attention towards a non-movement target (Training Opposite). However, presentation times of the Training Same group were also shorter than those in the Control Same group (M = 173 ms, SD = 57 ms, p = 0.891). This shows that the expectation of spatial congruence between the DT and MT position in the Training Same group indeed facilitated attention shifts toward the MT position, which indicates that the attention-action coupling within this group was indeed modulated by top-down processes. Moreover, there was no difference in presentation times between the Training Opposite and Control Same group (p = 0.891), implying that task difficulty was comparable in these conditions. Furthermore, presentation times of the Control Opposite group (M = 342 ms, SD = 178 ms) were longer compared to the ones of the remaining training



Figure 3. Adjusted presentation times of the DT of each training condition (A) in the first data analysis of Experiment 1. Mean discrimination performance of training and DT conditions in trials with a 100 ms (B) and 800 ms (C) SOA between movement cue onset and go-signal onset. Error bars indicate within-participants *SEM*.

groups (Control Opposite vs. Training Same: p = 0.001; Control Opposite vs. Training Opposite: p = 0.040; Control Opposite vs. Control Same: p = 0.025). This is not surprising because participants of this control condition were unaware of the DT's position, and thus there was no incentive to direct attention toward the opposite position. Presumably, an average presentation time of 342 ms may therefore reflect the time required to discriminate a probe stimulus at a position that is currently unattended. Moreover, presentation times in our experiments were longer than those reported by (Dignath et al., 2019; they reported a mean presentation time of 95 ms), indicating that our four-placeholder task was more difficult than the two-placeholder task used by Dignath and colleagues (2019). Discrimination performance: Because of the group differences in presentation times (for DT), we examined discrimination performance (Figures 3B, 3C) separately for each training group. For the Training Same group, a repeated measures ANOVA with factors DT position

and SOA condition revealed a large effect of DT position, F(1.16, 15.07) = 25.56, p < 0.001,  $\eta_p^2 = 0.66$ , on accuracy in the discrimination task. The main effect of SOA condition, F(1, 13) = 1.39, p = 0.259,  $\eta_p^2 =$ 0.10, and the interaction, F(2, 26) = 1.72, p = 0.198,  $\eta_{\rm p}^{2} = 0.12$ , was not significant. Post hoc comparisons showed that participants were significantly better in discriminating the DT at the MT (M = 74.8%, SD =15.0%) compared to the neutral positions (M = 52.2%, SD = 5.0%, p < 0.001) and the opposite position (M = 51.2%, SD = 5.1%, p < 0.001). No differences in discrimination performance were found between the opposite and neutral positions (p > 0.999). These results indicate that the learned expectation of spatial congruence between a task-relevant stimulus and the movement goal locations caused participants to direct attention only toward the movement goal position, regardless of the length of movement delays.

In the Training Opposite group, average discrimination performance across SOA conditions was 82.2% (*SD* = 8.2%) at the MT, 78.3% (*SD* = 9.7%) at neutral positions, and 81.9% (SD = 8.1) at the opposite position. A repeated measures ANOVA indicated that discrimination performance differed between DT positions, F(2, 26) = 4.63, p = 0.019,  $\eta_{p}^{2}$ = 0.26, but not between SOA conditions, F(1, 13) <0.01, p = 0.995,  $\eta_p^2 < 0.01$ . Importantly, the interaction was also non-significant, F(2, 26) = 1.50, p = 0.241,  $\eta_p^2$ = 0.10, suggesting that the length of SOAs was of no relevance for the deployment of attentional resources at DT positions. Post hoc comparisons revealed that overall discrimination performance was enhanced at the opposite position compared to the neutral positions (p = 0.041), but that performance did not differ between the MT and the opposite position (p > 0.999). This indicates that the learned expectation of spatial incongruence between positions allowed participants to direct some but not all attentional resources towards the opposite position. However, the difference in performance between the MT position and neutral DT positions did not reach significance (p = 0.080), suggesting a higher variation in performance differences than between the opposite and neutral positions.

Surprisingly, in the Control Same group, ANOVA results revealed that performance in the discrimination task was comparable irrespective of DT position, F(1.15, 11.45) = 1.03, p = 0.344,  $\eta_p^2 = 0.09$ , suggesting that there was no clear pattern of a premotor attention shift towards the movement goal location. The main effect of SOA was also not significant, F(1, 10) = 0.12, p = 0.736,  $\eta_p^2 = 0.01$ , but results showed a significant interaction, F(2, 20) = 4.76, p = 0.020,  $\eta_p^2 = 0.32$ . To examine this interaction, we employed a repeated measures ANOVA with factor DT position separately for each SOA condition. As Figure 3 suggests, performance differences between positions were more pronounced in trials with an SOA of 100 ms compared

to trials with an SOA of 800 ms. Nonetheless, there was neither a significant main effect of DT position for the SOA of 100 ms, F(1.24, 12.39) = 2.78, p = 0.116,  $\eta_p^2 = 0.22$ , nor for the SOA of 800 ms, F(2, 20) = 0.09, p = 0.918,  $\eta_p^2 = 0.01$ .

For the Control Opposite group, results showed a significant main effect of DT position, F(2, 24) = 3.64, p = 0.042,  $\eta_p^2 = 0.23$ , a significant interaction SOA condition × DT position, F(1.28, 15.35) = 4.54, p = 0.0420.042,  $\eta_p^2 = 0.27$ , but a nonsignificant main effect of SOA condition, F(1, 12) = 0.28, p = 0.607,  $\eta_p^2$ = 0.02. In contrast to the Control Same group, we found a significant effect of DT position in trials with an SOA of 100 ms, F(2, 24) = 5.10, p = 0.014,  $\eta_p^2 =$ 0.30. However, although Figure 3B suggests a trend towards enhanced discrimination performance at the MT and the opposite position compared to neutral DT positions, none of the post hoc pairwise comparisons reached significance (DT at MT vs. DT at neutral positions: p = 0.064; DT at neutral positions vs. DT at opposite position: p = 0.096; DT at MT vs. DT at opposite position: p = 0.830). For trials with an SOA of 800 ms, there was also no significant effect of DT position on discrimination performance, F(2, 24) = $0.77, p = 0.474, \eta_p^2 = 0.06.$ 

#### Second analysis

The results of discrimination performance in our first analysis should be interpreted with caution because the duration of adjusted presentation times led to trials in which the DT was still present after movement onset. However, because it is assumed that the premotor shift of attention is linked to motor preparation and since one might expect that motor preparation is completed at the time of movement onset, one might also expect that after movement onset, attention is released again and might now be free to be allocated also to other positions. Given these assumptions, attentional effects that cannot be clearly assigned to the pre-motion-onset interval should be excluded from an analysis focused on the examination of premotor shifts of attention. For this reason, we conducted a second data analysis. Before this second data analysis, all trials were excluded for which the DT was not yet masked at the time of movement onset (Movement before probe offset). Furthermore and similar to our first analysis, we excluded all participants from the analyses for whom more than 45% of the test phase trials had to be rejected after applying all the relevant exclusion criteria (including the new one). On this basis, we had to exclude one further participant of the Training Same group, one further participant of the Training Opposite group, three further participants of the Control Same group, and ten further participants of the Control Opposite group. Given that the remaining sample of the Control Opposite group consisted of only three

21

participants, we dropped the Control Opposite group from the analysis and only analyzed the data of the Training Same group (n = 13), Training Opposite group (n = 13), and Control Same group (n = 8). A summary of the proportion of trials rejected according to our exclusion criteria prior to the second analysis is shown for each of the included groups in Supplementary Table S2.

The second analysis of the Training Same, Training Opposite and Control Same group revealed an overall pattern of results similar to that of our first analysis in terms of movement parameters (Supplementary Table S3), presentation times (Supplementary Figure S1A), and discrimination performance (Supplementary Figure S1B, Supplementary Figure S1C). A detailed description of statistical results of our second analysis is therefore reported in Supplementary Materials. Yet, the results of discrimination performance of the Training Opposite group revealed a clearer picture regarding attention allocation compared to our first analysis. As in the first analysis, there was a significant main effect of DT positions, F(2, 24) = 5.39, p = 0.012,  $\eta_p^2 = 0.31$ , a non-significant effect of SOA, F(1, 12) = 0.04, p = 0.848,  $\eta_p^2 < 0.01$ , and a nonsignificant interaction, F(2, 24) = 0.79, p = 0.467,  $\eta_p^2 = 0.06$ . However, in contrast to our first analysis past has a sum in contrast to our first analysis, post hoc comparisons indicated that performance was not only enhanced at the opposite position (M = 82.1%, SD = 9.0%, p =0.036) but also at the MT position (M = 83.4%, SD =8.8%, p = 0.024) compared to neutral DT positions (M = 77.9%, SD = 10.2%), although there was no difference in discrimination performance between the MT and the opposite position (p > 0.999). These results suggest that, irrespective of the time available for motor preparation, participants of the Training Opposite group directed more attentional resources to the anticipated probe position and the movement goal location than to neutral positions.

Overall, the similarity of results of our two data analyses suggests that our findings in the Training Same, Training Opposite, and Control Same group were not caused by shifts of attention that occurred with or after movement initiation.

#### Discussion

The results of Experiment 1 indicate that attention allocation was biased towards the expected position of the attention probe in the Training Same group and, to a lesser degree, in the Training Opposite group. Surprisingly, we did not observe a premotor attention shift in the control groups (Control Same, Control Opposite), which is at odds with previous evidence suggesting a strict attention-action coupling in pointing movements (Deubel, Schneider, & Paprotta, 1998; Jonikaitis & Deubel, 2011). The results further suggest that the training-induced effects on attention allocation did not require pre-programming of movements or (as confirmed by our second analysis) occur only with or after movement onset, but rather emerged during ongoing motor preparation.

Nonetheless, Experiment 1 revealed betweengroup differences in adjusted probe presentation times, rendering it difficult to compare results of discrimination performance between training groups. Moreover, relative differences in discrimination performance between probe positions were less pronounced with longer (Training Opposite, Control Same, Control Opposite) compared to shorter presentation times (Training Same). Thus we cannot rule out that the length of adjusted presentation times confounded performance in the discrimination task of Experiment 1. To examine this possibility and to allow better comparison of results of the discrimination task between training groups, we ran a second experiment (Experiment 2) similar to Experiment 1 but with a fixed probe presentation time that was identical in all training groups.

# **Experiment 2**

#### Methods

#### Participants

Twenty-one naïve participants (16 female; 1 left-handed; mean age 23.8 years; age range 18–35 years) with normal or corrected-to-normal vision and normal motor behavior took part in Experiment 2. None of them had participated in the first experiment. Participants gave informed consent to participate in the study. The experiment was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki.

#### Apparatus

The experimental setup was identical to the one used in Experiment 1.

#### Design and procedure

Experiment 2 was similar to Experiment 1, except for the following modifications. First, we used a fixed presentation time for the DT of 83.33 ms in each part of the experiment that included the discrimination task. The fixed DT presentation time was identical for all training groups.

Second, Experiment 2 included only two training conditions. As in Experiment 1, we had a Training Opposite group in which the DT was presented in all

22

trials of the training phase at the location opposite the MT position. In a Control group, the DT was presented with equal probability at one of the four placeholder positions. However, since average adjusted presentation times (first analysis: 90 ms; second data analysis: 76 ms) of the Training Same group in Experiment 1 were similar to the fixed DT presentation time of Experiment 2, we did not include this training condition in Experiment 2.

Third, in Experiment 2, we focused on traininginduced effects on attention allocation within the critical movement preparation phase. To this end, we only included a movement delay (i.e., SOA between movement cue and go-signal onset) of 100 ms in the discrimination task.

Fourth, it is possible that implicit learning of the spatial relationship between the DT and MT in the training phase of Experiment 1 was limited due to the enhanced difficulty of the discrimination task compared to the study of Dignath et al. (2019). To rule out this possibility, we thus explicitly informed participants in Experiment 2 about the spatial relationship of the MT and DT prior to the training phase. Yet, as in Experiment 1, participants were not informed about the position of the DT before the test phase.

Fifth, we conducted a screening phase before Experiment 2 to ensure that each participant was able to reliably discriminate the DT at a presentation time of 83.33 ms at a covertly attended position in the subsequent experiment. The screening phase consisted of eight blocks of 30 trials of the discrimination task without concurrent pointing movement. The DT was presented in 80% of the trials at a placeholder position (likely probe position) that was known to the participants and which was held constant over a trial block. In the remaining 20% of trials, the probe appeared with equal probability at one of the three remaining placeholder positions. Participants continued with the experiment only if their discrimination performance for DTs at the likely probe position exceeded a value of 75% in the last two trial blocks of the screening phase.

Finally, to ensure that participants were sufficiently familiar with the dual-task, they had to complete four blocks of the dual-task training (instead of only two blocks as in Experiment 1) prior to the training phase and the test phase of Experiment 2.

#### Data analysis

Six participants were excluded from the experiment because they did not reach the threshold of discrimination performance in the screening phase. Before the data analyses of Experiment 2, we discarded trials of the remaining sample (N = 15 out of a total of 21) if one of the following exclusion criteria was met: Fixation violation, Blink violation, No movement, Movement too early, Movement inaccurate, Movement latency outlier, Movement before probe offset (cf., Experiment 1). None of the participants had to be excluded due to exceeding the maximum percentage of excluded test phase trials (>45%; cf., Experiment 1). However, we excluded one further participant of the Training Opposite group because discrimination performance in the test phase was below chance level at each probe position, presumably because of confusing the mapping between DT identity and response button. The final sample consisted of seven participants in the Training Opposite group and seven participants in the Control group. A summary of the proportion of trials rejected according to the applied exclusion criteria is shown for each group in Supplementary Table S4.

To examine the movement parameters, we employed independent samples *t* tests with movement latency and movement duration as the dependent variables. For analyses of discrimination performance, we conducted repeated measures ANOVAs with factors DT position (DT at MT vs. DT at neutral positions vs. DT at opposite position) for each training group (Training Opposite, Control). Greenhouse-Geisser corrections were applied when sphericity was violated. Post hoc pairwise comparisons were Bonferroni corrected.

#### Results

#### **Movement parameters**

Movement parameters of each training group are shown in Table 3. Results showed that neither movement latency, t(12) = -0.23, p = 0.826, d = 0.54, nor movement durations, t(12) = -0.62, p = 0.549, d = 0.54, differed between the Training Opposite and the Control group.

Interestingly, descriptive results indicate that movement latencies for trials with an SOA of 100 ms were shorter in Experiment 2 than in Experiment 1. This presumably reflects an effect of the applied movement delays. Experiment 2 contained only a short movement delay of 100 ms, likely allowing participants to consistently execute movements rapidly after the movement cue appeared. In contrast, movement delays were varied between 100 ms and 800 ms across trials of Experiment 1, which possibly increased uncertainty and thereby generally slowed down movement initiation.

	Training opposite M $\pm$ SD	Control M $\pm$ SD	
Latency	$231\pm48$	$237\pm49$	
Duration	$344~\pm~109$	$374\pm63$	

Table 3. Movement latencies and movement durations for each training group in Experiment 2. *Note:* Values in ms.

Journal of Vision (2023) 23(5):19, 1-18

#### Discrimination performance

Figure 4 shows the results of the discrimination task for each training condition in the test phase of Experiment 2. For the Control group, discrimination performance significantly differed between probe positions, F(1.13, 6.76) = 17.39, p < 0.001,  $\eta_p^2 =$ 0.74. Post-hoc pairwise comparisons showed that discrimination performance was significantly enhanced at the MT position compared to both the opposite position (p = 0.019) and neutral positions (p =0.013), although there was no significant difference in discrimination performance between the opposite position and neutral positions (p > 0.999). This indicates that attention was strictly linked to the movement goal location in the Control group.

For the Training Opposite group, ANOVA results showed a significant effect of DT position on discrimination performance, F(1.09, 6.55) =49.28, p < 0.001,  $\eta_p^2 = 0.89$ . Post-hoc pairwise comparisons revealed that discrimination performance was significantly enhanced at the opposite position compared to both the MT position (p = 0.004) and neutral positions (p < 0.001), indicating that participants of the Training Opposite group directed most attentional resources towards the expected DT position. However, for the difference in discrimination performance between the MT position and neutral positions we only found a marginally significant effect (p = 0.060). To explore whether this nonsignificant benefit in discrimination performance at the MT position was less pronounced compared to the one found in the Control group, we conducted an additional independent samples t test with the discrimination performance at the MT position as the dependent variable. Results showed that discrimination performance was indeed higher at the MT position in the Control group than in the Training Opposite group, t(12) = -7.19, p < 0.001, d = -3.84, suggesting that shifting attentional resources



Figure 4. Discrimination performance of each DT and training condition in Experiment 2. Error bars indicate within-participants *SEM*.

to the anticipated DT position (opposite position) came at the expense of attentional performance at the MT position in the Training Opposite group.

#### Discussion

In line with previous evidence for a strict attentionaction coupling in pointing movements (Deubel, Schneider, & Paprotta, 1998; Jonikaitis & Deubel, 2011), we now observed a clear premotor shift of attention towards the movement goal location in a control condition (Control) with unpredictable DT position. Importantly, the findings of the Training Opposite group in Experiment 2 demonstrate that participants were capable of guiding most attentional resources towards a non-movement target at which they had learned to anticipate the attention probe, indicating a crucial role of habitual top-down processes in premotor attention allocation. Moreover, since we only used a short SOA of 100 ms between the movement cue and movement go-signal in Experiment 2, the results suggest that the observed attentional effects emerged during ongoing movement preparation.

# **General discussion**

The current study investigated whether the commonly observed coupling between visual attention and motor preparation is associated with a habitual expectation of spatial congruence between objects of interest and targets of motor actions. In particular, we addressed the question of whether attentional resources can be decoupled from ongoing motor preparation based on a learned expectation of spatial incongruence between visual and motor targets. To this end, we conducted two experiments in which we combined a visual discrimination task with a pointing task. To examine attention allocation at different stages of the motor preparation phase, pointing movements had to be executed upon a variable movement delay of either 100 ms or 800 ms in Experiment 1. In Experiment 2, only a fixed movement delay of 100 ms was applied. Both experiments comprised a training phase and a subsequent test phase. The training phase served to establish distinct top-down expectations regarding the spatial relationship between the discrimination target (DT) and the motor target (MT). This was realized via systematically varying the likelihood of the DT to appear at a specific position. For different groups in Experiment 1, the DT either always appeared at the position of the current MT (Training Same), at the position opposite to the current MT (Training Opposite), or at a randomly selected position (Control Same and Control Opposite) throughout the training phase. In Experiment 2, we focused on eliciting an

expectation of spatial incongruence between DT and MT positions and included only a Training Opposite group in addition to a Control group with unpredictable DT position. After the training phase, participants of all groups completed a test phase in which the DT position was randomized, allowing us to assess training-induced, expectancy-driven biases in premotor attention allocation on the basis of discrimination performance data. The test phase differed between the experiments only regarding the DT presentation time. While DT presentation times were determined individually for each participant in Experiment 1 (based on a thresholding procedure in the training phase), a fixed DT presentation time was used in Experiment 2.

The data obtained in Experiment 2 provide strong evidence that habitual top-down processes play a crucial role in the emergence of the attention-action coupling. Consistent with previous findings (Deubel, Schneider, & Paprotta, 1998; Jonikaitis & Deubel, 2011; Hanning et al., 2022), we observed a premotor shift of attention in the Control group in which participants had not learned to expect the DT at a particular position. In contrast, the results of the Training Opposite group revealed that attentional resources were selectively allocated to a movement-irrelevant, yet task-relevant, visual target when participants anticipated spatial incongruence between the DT and MT positions. This evidence for a decoupling of attentional resources from the movement goal is difficult to reconcile with the assumption of functional equivalence of motor preparation and visual attention as proposed by the Premotor Theory of Attention (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994). In fact, we observed that the attentional enhancement at the expected DT position was substantially larger than at the MT position in the Training Opposite group. This implies that, contrary to earlier findings on saccadic eye movements (Kowler et al., 1995; Montagnini & Castet, 2007), participants were able to divert most attentional resources from the target of upcoming movements. Importantly, this effect was observed in movements that were delayed by only 100 ms, contradicting previous evidence that attention can only be decoupled from a reach target when there is sufficient time available to complete movement preparation (Deubel & Schneider, 2003). In other words, the results of Experiment 2 suggest that the observed top-down modulations of attention occurred during ongoing movement preparation. A similar effect has been previously reported only in pointing movements that were substantially delayed and therefore presumably allowed for motor pre-programming (Dignath et al., 2019). Our findings thus complement previous studies on saccades, which have demonstrated that endogenous attentional control can operate independently of movement planning processes (Gabay et al., 2010; Smith et al., 2004; Smith et al., 2012). However, it

is conceivable that the decoupling of attentional resources from motor preparation processes was achieved only through tradeoffs in other aspects of task performance. However, our results do not support this assumption. Training groups did not differ in terms of movement latency or movement duration, suggesting that participants did not adopt a strategy to decouple attention from the movement goal at the expense of movement performance. Despite the absence of significant between-group differences at the motor level, we cannot rule out that motor behavior was generally affected, at least to some extent, by dual-task costs in the current study. Thus the attentional effects observed here may be specific to dual-task conditions.

Experiment 2 suggested that expectancy-driven allocation of attentional resources toward a movementirrelevant position interfered with shifting attention toward the upcoming movement goal. We observed that discrimination performance at the MT position was significantly reduced in the Training Opposite group (in which participants expected the DT to appear at the position opposite to the MT) relative to the Control group (in which participants had no particular expectation about the DT position). Interestingly, in a recent dual-task study, Hanning et al. (2022) reported a different pattern of results. In this study, the preparation of both eye and pointing movements was found to deteriorate voluntary attention allocation toward a movement-irrelevant position likely to contain a discrimination target. However, contrary to the current study, participants had to perform several different experimental conditions, and there was no designated initial training phase. Thus it is possible that the precedence of motor-based attention shifting over top-down expectancy-driven attention allocation (as observed by Hanning et al., 2022) reflects a default mode, which (as implied by the present results) can only be reversed through sufficient training. Accordingly, an interesting endeavor for future studies will be to more systematically examine tradeoffs between action-driven and expectancy-driven attentional selection as a function of training duration.

In line with the idea that the attention-action coupling is influenced by habitual top-down processes, we also observed a small benefit in discrimination performance at the anticipated DT position compared to neutral control positions in the Training Opposite group in Experiment 1. However, although our results suggest that this effect did not require preprogramming of movements or emerged only with or after movement onset, the differences between training groups in adjusted DT presentation times combined with the lack of evidence for a premotor attention shift in the Control Same group limited the explanatory power of the discrimination task results in this experiment. Nonetheless, the between-group differences in presentation times provided insights into the varying difficulties in guiding attention to the anticipated DT position during the training phase, thereby complementing our findings in Experiment 2. In particular, the finding of prolonged DT presentation times in the Training Opposite group compared to the Training Same group demonstrates an increased difficulty in directing attentional resources to a position that deviates from the target of an upcoming movement. This suggests a stubborn, yet not necessarily obligatory, nature of the attention-action coupling. Furthermore, it shows that training may play an essential role in overcoming this default mode of shifting attention to the target of imminent goal-directed movements. However, in contrast to Experiment 2, we did not explicitly inform participants about the spatial relationship between the DT and MT prior to the training phase in Experiment 1, which might have rendered predictability of the DT position more difficult. Nonetheless, previous studies in which participants were explicitly informed about the position of the attention probe did not observe a substantial disengagement of attention from movement targets (Deubel, 2008; Deubel & Schneider, 1996; Deubel et al., 1998; Hanning et al., 2022; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Schiegg et al., 2003). This suggests that training is indeed critical for effective top-down modulations of premotor attention allocation.

The results of Experiment 1 also revealed that DT presentation times were longer in the Control Same group than in the Training Same group. Since presentation times in these two groups were adjusted only on the basis of trials in which the DT was presented at the MT position and incorrect responses resulted in an increase in presentation time, this finding implies that participants of the latter group directed attention more consistently towards the MT position over the course of the training phase. Considering that the training of the two groups differed only in the position at which the DT was presented (Training Same: MT position; Control Same: random DT position), the shorter presentation times in Training Same might therefore suggest that the expectation of spatial congruence between DT and MT facilitated attention shifts to the MT position. Indeed, if visual attention shifts were a mere by-product of motor preparation processes, no group differences in presentation times should be found. However, it is possible that participants in the Control Same group became aware of the fact that the DT did not always appear at the MT position and therefore attempted to divert attention away from the MT position to detect DTs at other positions as well. Because of the unpredictability of the DT position in this control condition, this would have led to a prolongation of the adjusted presentation times, which would explain the difference in DT presentation times between the Training Same group and the Control Same group.

Surprisingly, in Experiment 2, the results of the Training Opposite group revealed no significant difference in discrimination performance between the MT position and neutral control positions, which suggests that the commonly observed premotor shift of attention towards the upcoming movement goal reflects the expectation that a relevant visual target appears at the MT position and is not just a simple by-product of motor preparation. Otherwise it would be hard to explain why the Training Opposite condition should abolish the typical MT-superiority. Yet, as can be seen in Figure 4, discrimination performance was slightly enhanced at the MT position compared to neutral positions. Although this benefit was only marginally significant, it is possible that such an effect would become apparent with a larger sample size. However, it is important to note that even if we had observed significant attentional facilitation at the MT position, it would have remained unclear whether this effect could be attributed to processes of motor preparation or to the fact that the expected DT position was defined relative to the MT position (i.e., opposite to it) in the Training Opposite group. In other words, the MT position was needed as a spatial reference or landmark to determine the DT position in this training group. Accordingly, a plausible alternative explanation for an observation of attentional facilitation at the MT position would be that participants first focused their attention on the MT before they could allocate attention to the (opposite) location where the DT was expected to appear. Future research is therefore needed to determine the precise extent to which attentional processes are truly required for planning goal-directed movements (e.g., by using a stationary position, unrelated to the MT, to induce an expectation of spatial incongruence between the DT and MT positions).

Nevertheless, the present study demonstrates that attention and action can be decoupled to a considerable extent by training. In contrast to previous research (Dignath et al, 2019), this effect was demonstrated in a dual-task paradigm in which the task did not provide an opportunity to complete motor preparation before attention was probed, but in which attention allocation was assessed during ongoing movement planning. Overall, our results thus suggest that the premotor attention shift phenomenon is not solely attributable to processes of motor preparation, but involves a hitherto largely neglected habitual top-down component that is linked to an anticipation of spatial congruence between behaviorally relevant visual and motor targets.

# Conclusions

The present study provided evidence for the notion that the close link between visual attention and the 26

preparation of goal-directed actions is related to a habitual expectation of spatial congruence between objects of interest and targets of upcoming movements. We demonstrated that a training-induced anticipation of spatial incongruence between positions of a motor target and a task-relevant visual target allowed for a marked decoupling of attentional resources from targets of upcoming pointing movements. Importantly, this effect emerged while motor programming was still in progress and without impairment of movement performance. This suggests that the link between attentional deployment and motor preparation is less strict than typically assumed. In light of these findings, we suggest that the commonly observed premotor shift of attention is not a sole consequence of motor preparation per se, but that habitual top-down processes play a relevant role in its formation.

*Keywords: visual attention, reaching movements, motor planning, learning, dual-task* 

# Acknowledgments

Supported by grants from the German Research Foundation (Deutsche Forschungsgemeinschaft: DFG-SCHE-735/4-1, DFG-SCHE 735/2-2 and DFG-SCHE 735/3-2).

Commercial relationships: none. Corresponding author: Thomas Schenk. Email: thomas.schenk@psy.lmu.de. Address: Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany.

## References

- Allport, A. (1987). Selection for Action: Some Behavioral and Neurophysiological Considerations of Attention and Action In H. Heuer, & A. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 395–419): Oxfordshire: Routledge.
- Arkesteijn, K., Belopolsky, A. V., Smeets, J. B. J., & Donk, M. (2019). The limits of predictive remapping of attention across eye movements. *Frontiers in Psychology*, 10, 1146, https: //doi.org/10.3389/fpsyg.2019.01146.
- Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research*, 184(3), 411–425, https://doi.org/10.1007/ s00221-007-1114-x.
- Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand

movement sequences: An event-related potential study. *Journal of Cognitive Neuroscience*, 21(1), 18–29, https://doi.org/10.1162/jocn.2008.21021.

- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research*, 46(26), 4355– 4374, https://doi.org/10.1016/j.visres.2006.08.021.
- Bonfiglioli, C., Duncan, J., Rorden, C., & Kennett, S. (2002). Action and perception: Evidence against converging selection processes. *Visual Cognition*, 9(4-5), 458–476, https: //doi.org/10.1080/13506280143000539.
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484–1525, https://doi.org/10.1016/j.visres.2011.04.012.
- Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, 72(6), 630–640, https://doi.org/10.1007/s00426-008-0165-3.
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827–1837, https://doi.org/10.1016/0042-6989(95)00294-4.
- Deubel, H., & Schneider, W. X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals* of the New York Academy of Sciences, 1004(1), 289–296, https://doi.org/10.1196/annals.1303.026.
- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: Evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, 5(1-2), 81–107, https://doi.org/10.1080/713756776.
- Dignath, D., Herbort, O., Pieczykolan, A., Huestegge, L., & Kiesel, A. (2019). Flexible coupling of covert spatial attention and motor planning based on learned spatial contingencies. *Psychological Research*, 83(3), 476–484, https://doi.org/10.1007/s00426-018-1134-0.
- Eimer, M., Forster, B., Van Velzen, J., & Prabhu, G. (2005). Covert manual response preparation triggers attentional shifts: ERP evidence for the premotor theory of attention. *Neuropsychologia*, 43(6), 957– 966, https://doi.org/10.1016/j.neuropsychologia. 2004.08.011.
- Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2006). Manual response preparation and saccade programming are linked to attention shifts: ERP evidence for covert attentional orienting and spatially specific modulations of visual processing. *Brain Research*, 1105(1), 7–19, https://doi.org/10.1016/j.brainres.2005.10.060.
- Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention

Journal of Vision (2023) 23(5):19, 1-18

in patients with duane retraction syndrome. *Neuropsychologia*, 48(10), 3102–3109, https://doi.org/10.1016/j.neuropsychologia. 2010.06.022.

- Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: An electrophysiological investigation of links between action and attention. *Neuropsychologia*, 48(4), 961– 969, https://doi.org/10.1016/j.neuropsychologia. 2009.11.017.
- Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance, 29*(5), 882–896, https://doi.org/10.1037/0096-1523.29.5. 882.
- Hanning, N. M., Aagten-Murphy, D., & Deubel, H. (2018). Independent selection of eye and hand targets suggests effector-specific attentional mechanisms. *Scientific Reports*, 8(1), 1–8, https://doi.org/10.1038/s41598-018-27723-4.
- Hanning, N. M., & Deubel, H. (2020). Attention capture outside the oculomotor range. *Current Biology*, 30(22), R1353–R1355, https://doi.org/10.1016/j.cub.2020.09.054.
- Hanning, N. M., Wollenberg, L., Jonikaitis, D., & Deubel, H. (2022). Eye and hand movements disrupt attentional control. *Plos One*, 17(1), e0262567, https://doi.org/10.1371/journal.pone.0262567.
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787–795, https://doi.org/10.3758/BF03206794.
- Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, 22(3), 339–347, https: //doi.org/10.1177/0956797610397666.
- Juan, C.-H., Muggleton, N. G., Tzeng, O. J. L., Hung, D. L., Cowey, A., & Walsh, V. (2008). Segregation of visual selection and saccades in human frontal eye fields. *Cerebral Cortex*, 18(10), 2410–2415, https://doi.org/10.1093/cercor/bhn001.
- Juan, C.-H., Shorter-Jacobi, S. M., & Schall, J. D. (2004). Dissociation of spatial attention and saccade preparation. *Proceedings of the National Academy of Sciences*, 101(43), 15541–15544, https://doi.org/10.1073/pnas.0403507101.
- Khan, A. Z., Song, J.-H., & McPeek, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, 11(1), 9–9, https://doi.org/10.1167/11.1.9.
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming

of saccades. *Vision Research*, 35(13), 1897–1916, https://doi.org/10.1016/0042-6989(94)00279-U.

- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 49(4), 764–766, https://doi.org/10.1016/j.jesp.2013.03.013.
- Moehler, T., & Fiehler, K. (2014). Effects of spatial congruency on saccade and visual discrimination performance in a dual-task paradigm. *Vision Research*, 105, 100–111, https://doi.org/10.1016/j.visres.2014.10.001.
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*(14), 8–8, https://doi.org/10.1167/7.14.8.
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, 98(3), 1273–1276, https://doi.org/10.1073/pnas.98.3.1273.
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, *91*(1), 152–162, https://doi.org/10.1152/jn.00741.2002.
- Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences, 102*(3), 524–529, https://doi.org/10.1073/ pnas.0408311101.
- Neumann, O. (1987). Beyond capacity: A functional view of attention. In H. Heuer, & A. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 361–394): Oxfordshire: Routledge.
- Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal* of Experimental Psychology: General, 109(2), 160–174, https://doi.org/10.1037/0096-3445.109.2. 160.
- Reeves, A., & McLellan, J. S. (2020). The 'anti-shift': Shifting attention opposite to a saccade. *Vision Research*, *167*, 31–38, https://doi.org/10.1016/j.visres.2019.06.009.
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1), 31–40, https://doi.org/10.1016/0028-3932(87) 90041-8.
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà, & M. Moscovitch (Eds.), *Attention and performance*

Journal of Vision (2023) 23(5):19, 1-18

*XV: Conscious and nonconscious information processing* (pp. 232–265): Cambridge, MA: The MIT Press.

Sato, T. R., & Schall, J. D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron*, 38(4), 637–648, https://doi.org/10.1016/S0896-6273(03)00237-X.

Schiegg, A., Deubel, H., & Schneider, W. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*, *10*(4), 409–431, https://doi.org/10.1080/ 13506280244000140.

Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Visual Cognition*, 2(2-3), 331–376, https://doi.org/10.1080/13506289508401737.

Schneider, W. X., & Deubel, H. (1995). Visual attention and saccadic eye movements: Evidence for obligatory and selective spatial coupling. *Studies in Visual Information Processing*, 6, 317–324.

Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In W. Prinz, & B. Hommel (Eds.), Attention and performance XIX: Common mechanisms in perception and action (pp. 609–627): Oxford University Press.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*(3), 507–522, https://doi.org/10.1007/BF00233988.

Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye movements. *Experimental Brain Research*, 105(2), 261–275, https://doi.org/10.1007/BF00240962.

Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, 14(9), 792–795, https://doi.org/10.1016/j.cub.2004.04.035. Smith, D. T., & Schenk, T. (2012). The premotor theory of attention: Time to move on? *Neuropsychologia*, 50(6), 1104–1114, https://doi.org/10.1016/j.neuropsychologia.2012.01. 025.

Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology: Human Perception and Performance, 38*(6), 1438–1447, https://doi.org/10.1037/a0027794.

Song, J.-H., & Bédard, P. (2013). Allocation of attention for dissociated visual and motor goals. *Experimental Brain Research*, 226(2), 209–219, https://doi.org/10.1007/s00221-013-3426-3.

Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *The Journal of Neuroscience*, *25*(41), 9479–9487, https://doi.org/10.1523/jneurosci.0741-05.2005.

Van der Stigchel, S., & Theeuwes, J. (2007). The relationship between covert and overt attention in endogenous cuing. *Perception & Psychophysics*, 69(5), 719–731.

Van der Stigchel, S., & de Vries, J. P. (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. *Journal of Vision, 15*(15), 17–17, https: //doi.org/10.1167/15.15.17.

Wollenberg, L., Deubel, H., & Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. *PLOS Biology*, 16(6), e2006548, https://doi.org/10.1371/journal.pbio.2006548.

Wollenberg, L., Deubel, H., & Szinte, M. (2019). Investigating the deployment of visual attention before accurate and averaging saccades via eye tracking and assessment of visual sensitivity. *JoVE*,(145), e59162, https://doi.org/10.3791/59162.

Wollenberg, L., Hanning, N. M., & Deubel, H. (2020). Visual attention and eye movement control during oculomotor competition. *Journal of Vision*, 20(9), 16–16, https://doi.org/10.1167/jov.20.9.16.



**Figure S1**. Probe presentation times (A) and discrimination performance (B, C) in trials used in the second data analysis of Experiment 1. Error bars indicate within-participants standard error of the mean (*SEM*).
Exclusion criteria	Training Same	Training Opposite	Control Same	Control Opposite
Fixation violation	4.2	2.4	2.2	5.5
Blink violation	1.0	1.1	0.9	2.3
No movement	0.5	1.4	0.1	0.3
Movement too early	2.1	0.3	0.5	0.6
Movement inaccurate	7.0	7.5	5.4	3.9
Movement latency outlier	4.6	2.9	2.2	3.2
Total excluded trials	15.2	13.4	9.0	12.0

**Table S1**. Percentages of excluded trials for first analysis of the test phase data in Experiment 1. Note that the different exclusion criteria percentages do not add up to the total percentage of excluded trials, since multiple criteria could apply for a single trial.

Exclusion criteria	Training Same	Training Opposite	Control Same
Fixation violation	4.5	2.5	2.5
Blink violation	1.1	1.2	1.1
No movement	0.5	1.5	0.0
Movement too early	2.1	0.3	0.2
Movement inaccurate	7.1	5.0	3.9
Movement latency outlier	4.8	2.9	1.5
Movement before probe offset	5.0	10.5	10.1
Total excluded trials	17.7	20.2	16.5

**Table S2**. Percentages of excluded trials for second analysis of the test phase data inExperiment 1.

	Training Same	Training Opposite	Control Same	
	M ± SD	M ± SD	M ± SD	
Latency: SOA 100	311 ± 59	318 ± 41	297 ± 27	
Latency: SOA 800	274 ± 64	300 ± 45	274 ± 40	
Duration: SOA 100	347 ± 79	327 ± 84	315 ± 55	
Duration: SOA 800	340 ± 64	328 ± 82	344 ± 66	

**Table S3**. Movement latencies and movement durations of trials used in the second dataanalysis of Experiment 1. Values in ms.

Exclusion criteria	Training Opposite	Control
Fixation violation	0.2	1.2
Blink violation	0.1	0.7
No movement	0.1	0.3
Movement too early	0.1	0.1
Movement inaccurate	4.4	1.5
Movement latency outlier	2.7	2.5
Movement before probe offset	1.9	3.8
Total excluded trials	8.4	8.7

**Table S4**. Percentages of excluded trials for analysis of the test phasedata in Experiment 2.

#### **Supplementary Results**

#### Detailed report of statistical results of second analysis of Experiment 1

Movement parameters. In the second data analysis of Experiment 1, we first investigated whether the additional exclusion of trials led to differences between training conditions with respect to movement parameters (Table S3). Results were similar overall compared to our first analysis. A mixed ANOVA with factors SOA condition and training group indicated that movement latencies across groups were longer in trials with an SOA of 100 ms (M = 311 ms, SD = 46 ms) compared to trials with an SOA of 800 ms (M = 284 ms, SD = 52 ms), F(1, 31) = 83.47, p < .001,  $\eta_p^2 = 0.73$ . The main effect of training group was not significant, F(2, 31) = 0.69, p = .511,  $\eta_p^2 = 0.04$ . In contrast to the previous analysis, we found a significant interaction, F(2, 31) = 4.86, p = .015,  $\eta_p^2 = 0.24$ . However, post hoc comparisons indicated a similar pattern of results within each of the training groups. Movement latencies were longer in trials with an SOA of 100 ms compared to trials with an SOA of 800 ms in the Training Same (p < .001), Training Opposite (p = .005), and Control Same group (p = .006). None of the remaining post hoc comparisons was significant (all p > .407). For movement duration, a similar mixed ANOVA showed a non-significant main effect of SOA condition, F(1, 31) = 2.33, p = .137,  $\eta_p^2 = 0.07$ , a non-significant main effect of training group, F(2, 31) = 0.18, p = .839,  $\eta_p^2 = 0.01$ , but a significant interaction, F(2, 31) = 3.64, p = .038,  $\eta_p^2 = 0.19$ . As in our first analysis, none of the post hoc comparisons of this interaction was significant (all p > .145).

**Presentation times**. Also, the results of DT presentation times were similar to the ones of our first analysis. A significant one-way ANOVA indicated that adjusted probe presentation times (Figure S1A) differed between training groups, F(2, 31) = 11.49, p < .001,  $\eta_p^2 = 0.43$ . Post hoc comparisons showed that presentation times were shorter in the *Training Same* group compared to the *Training Opposite* (p < .001) and *Control Same* group (p = .012), but not between the *Training Opposite* and *Control Same* group (p > .999).

**Discrimination performance**. In addition, we examined whether the results of the discrimination task (Figure S1) differed from the ones of our first analysis. Regarding the *Training Same* group, results were similar in comparison to our first analysis. A repeated measures ANOVA revealed a significant main effect of DT position, F(1.19, 14.27) = 22.37, p < .001,  $\eta_p^2 = 0.65$ , but a non-significant main effect of SOA condition, F(1, 12) = 1.26, p = .283,  $\eta_p^2 = 0.10$ , and a non-significant interaction, F(2, 24) = 1.01, p = .379,  $\eta_p^2 = 0.08$ . Post hoc comparisons confirmed that discrimination performance across SOAs was enhanced at the MT (M = 73.3%, SD = 14.3%) compared to the neutral positions (M = 52.1%, SD = 5.7%, p < .001) and the opposite position (M = 51.5%, SD = 4.7%, p = .002) but not between neutral positions and the position opposite the MT (p > .999). In the *Training Opposite* group, discrimination performance differed between DT positions,

 $F(2, 24) = 5.39, p = .012, \eta_p^2 = 0.31$ . The main effect of SOA,  $F(1, 12) = 0.04, p = .848, \eta_p^2 < 0.01$ , and the interaction,  $F(2, 24) = 0.79, p = .467, \eta_p^2 = 0.06$ , was not significant. Post hoc comparisons of the effect of DT position revealed a clearer pattern of results compared to our first analysis. Performance was better at the opposite position (M = 82.1%, SD = 9.0%) compared to the neutral DT positions (M = 77.9%, SD = 10.2%, p = .036). However, performance at the MT (M = 83.4%, SD = 8.8%) was also better compared to neutral positions (p = .024). There was no performance difference between the MT and the opposite position (p > .999). These results indicate that participants shifted attentional resources to the movement goal location but also towards the opposite position,  $F(1.12, 7.82) = 0.63, p = .470, \eta_p^2 = 0.08$ , and no significant main effect of SOA position,  $F(1, 7) = 0.01, p = .930, \eta_p^2 < 0.01$ . In contrast to our first statistical analysis, the interaction was also not significant,  $F(2, 14) = 1.95, p = .179, \eta_p^2 = 0.22$ . These results suggest that there was no evidence of a premotor attention shift towards the movement goal location in the *Control Same* group.

# 2.2 Training enables substantial decoupling of visual attention and saccade preparation

## The following study has been published as:

Topfstedt, C. E., Wollenberg, L., & Schenk, T. (2024). Training enables substantial decoupling of visual attention and saccade preparation. *Vision Research*, *221*, 1-13, Article 108424. <u>https://doi.org/10.1016/j.visres.2024.108424</u>

## **Author Contributions:**

Christof E. Topfstedt: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data Curation, Writing - Original Draft, Writing - Review & Editing, Visualization, Project administration. Luca Wollenberg: Conceptualization, Methodology, Investigation, Writing - Original Draft, Writing -Review & Editing, Project administration, Funding acquisition.

Thomas Schenk: Conceptualization, Methodology, Writing - Review & Editing, Funding acquisition.

Vision Research 221 (2024) 108424

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

## Training enables substantial decoupling of visual attention and saccade preparation



Klinische Neuropsychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Leopoldstraße 13, 80802 Munich, Germany

ARTICLE INFO	A B S T R A C T
Keywords: Visual attention Saccade Motor programming Premotor theory of attention Visual attention model	Visual attention is typically shifted toward the targets of upcoming saccadic eye movements. This observation is commonly interpreted in terms of an obligatory coupling between attentional selection and oculomotor pro- gramming. Here, we investigated whether this coupling is facilitated by a habitual expectation of spatial congruence between visual and motor targets. To this end, we conducted a dual-task (i.e., concurrent saccade task and visual discrimination task) experiment in which male and female participants were trained to either anticipate spatial congruence or incongruence between a saccade target and an attention probe stimulus. To assess training-induced effects of expectation on premotor attention allocation, participants subsequently completed a test phase in which the attention probe position was randomized. Results revealed that discrimination performance was systematically biased toward the expected attention probe position, irrespective of whether this position matched the saccade target or not. Overall, our findings demonstrate that visual attention can be substantially decoupled from ongoing oculomotor programming and suggest an important role of habitual

expectations in the attention-action coupling.

#### 1. Introduction

The visual information falling on our retinae at any given moment by far exceeds the limited processing capacity of our brain. Efficient visual perception is therefore contingent on selective processing. A means to this end are saccadic eye movements. We typically execute three to four saccades per second (Findlay & Gilchrist, 2003), allowing us to sequentially foveate locations or objects of interest and thereby process their content at highest visual acuity. However, perceptual selection can also be achieved through another mechanism, namely via covert shifts of visual attention. By shifting attention covertly in space, relevant visual information can be selected and processed in detail without concurrent movement of the eyes. Influential theories of visual attention postulate a tight and obligatory link between the mechanisms underlying the deployment of visual attention and the programming of motor actions. The premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994) states that covert attention shifts originate directly from activity in the motor system and are merely a by-product of programming goal-directed actions. The visual attention model (Schneider, 1995; Schneider & Deubel, 2002) assumes that attentional selection is a prerequisite for motor preparation, with covert attention shifts being linked to the selection of targets for upcoming actions. Although there is disagreement about the causal relationship of the attention-action link, both theories postulate that the programming of goal-directed actions, such as saccades or manual movements, is inevitably accompanied by an attention shift toward the motor target.

Indeed, a large number of studies have provided evidence for the assumption that processes of attentional selection and motor preparation are closely intertwined. For instance, neurophysiological studies have shown that saccade programming and covert attention shifting elicit largely overlapping neural activation in frontal and parietal regions of the human brain (Corbetta et al., 1998; de Haan, Morgan, & Rorden, 2008). Also, subthreshold stimulation of oculomotor brain regions of non-human primates, such as the frontal eye fields (FEF) and the superior colliculus (SC), has been found to improve visual performance at the position to which gaze would have been shifted at a higher stimulation level (Moore & Fallah, 2004; Müller, Philiastides, & Newsome, 2005). At the behavioral level, evidence in favor of an obligatory attention-action coupling has come primarily from psychophysical dualtask studies requiring participants to perform goal-directed actions

\* Corresponding author.

Received 13 November 2023; Received in revised form 29 April 2024; Accepted 29 April 2024 Available online 13 May 2024

0042-6989/© 2024 The Author(s). Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).





VISION

E-mail address: thomas.schenk@psy.lmu.de (T. Schenk).

<sup>&</sup>lt;sup>1</sup> These authors share first authorship.

https://doi.org/10.1016/j.visres.2024.108424

toward cued placeholder stimuli, while premotor attention allocation is probed by flashing a discrimination target either at the motor target or at a different position. A consistent finding of these studies was that discrimination performance is selectively enhanced when the attention probe and the target of a saccade (Deubel, 2008; Deubel & Schneider, 1996, 2003; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011) or manual movement (Deubel, Schneider, & Paprotta, 1998; Jonikaitis & Deubel, 2011; Schiegg, Deubel, & Schneider, 2003) spatially coincide compared to when they diverge. Notably, this spatial congruency effect was still observed when experimental conditions provided an incentive to withdraw attention from the motor target (Deubel, 2008; Deubel & Schneider, 1996; Deubel, Schneider, & Paprotta, 1998; Schiegg, Deubel, & Schneider, 2003), indicating that attention allocation toward targets of upcoming goal-directed movements is mandatory. Indeed, a very recent dual-task study (Hanning et al., 2022) affirmed these earlier observations by demonstrating that attention can be deployed to distinct eye and hand movement targets in parallel and without cost, whereas the preparation of these movements cumulatively deteriorates the capacity to attend to movementirrelevant, yet highly task-relevant, objects.

Even though the evidence for an obligatory attention-action link is compelling, there are also findings that cast doubt on the notion that visual attention shifts are inextricably coupled to processes of motor preparation (see Smith & Schenk, 2012, for an overview). For example, studies in non-human primates have shown that only the activity of visually responsive subpopulations of FEF neurons, but not the activity of saccade-related movement neurons, is modulated by covert attention (Gregoriou, Gotts, & Desimone, 2012; Thompson, Biscoe, & Sato, 2005), suggesting that oculomotor preparation and shifts of visual attention rely on distinct mechanisms. Consistent with this observation, a temporal dissociation between covert attention and saccade preparation has been demonstrated for the human FEF using transcranial magnetic stimulation (Juan et al., 2008). Moreover, there is evidence from psychophysical dual-task studies suggesting a less strict attention-action link. For instance, it has been found that some attentional resources can be diverted from the target of an upcoming saccade (Born, Ansorge, & Kerzel, 2013; Kowler et al., 1995; Moehler & Fiehler, 2014; Montagnini & Castet, 2007), a finding that is difficult to reconcile with the assumption that covert attention is merely a by-product of motor programming activity (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994). Likewise, it was recently demonstrated that visual discrimination performance is not enhanced at the endpoint of imminent averaging saccades landing in between two competing stimuli (Van der Stigchel & de Vries, 2015; Wollenberg, Deubel, & Szinte, 2018, 2019; Wollenberg, Hanning, & Deubel, 2020), arguing against a strict dependence of attention allocation on the spatial parameters of subsequently executed saccades. Also, there is evidence that unexecuted saccadic programs are not accompanied by an attention shift to the motor target (Born, Mottet, & Kerzel, 2014), which shows that saccade preparation does not always entail a spatially congruent allocation of attentional resources.

Given the conflicting evidence regarding the link between attention and action, it is important to point out that under natural conditions, goal-directed movements are generally directed toward targets of high behavioral relevance, and thus shifting attention to the target of an upcoming movement is beneficial in most situations. Accordingly, the commonly observed shift of attention toward motor targets might not necessarily reflect an inherent property of motor programming, but potentially a stubborn habit-driven phenomenon (Posner, Snyder, & Davidson, 1980) that is difficult to overcome without sufficient training (Dignath et al., 2019; Reeves & McLellan, 2020). This assumption was recently examined by Reeves and McLellan (2020) in a rapid serial visual presentation (RSVP) task requiring participants to shift attention from a letter stream to a proximal numeral stream from which the first items had to be reported. Importantly, participants were trained to perform this attention shift either while simultaneously saccading from the letter stream to the numeral stream (pro-shift) or vice versa (antishift). Results showed that after several hours of training, the majority of participants achieved similar levels of task performance (in terms of reaction time and numeral report measures) in anti-shift and pro-shift trials, suggesting that attentional selection can operate independently of saccade preparation. However, some caution should be exercised in interpreting these findings as evidence against an obligatory attention-action coupling, since participants foveated the numeral stream in anti-shift trials before saccade execution. Thus, it is possible that successful performance of anti-shift trials did not result from decoupling of attention and saccade preparation, but instead from strategic exploitation of high-acuity foveal vision.

Furthermore, to investigate the role of habitual processes in the attention-action link, it is crucial to determine to what extent and at what stage within the motor preparation phase attentional resources can be decoupled from the motor target. Therefore, the more commonly used discrimination task (e.g., Deubel & Schneider, 1996) appears to be a more suitable tool to study the attention-action link than an RSVP task, as it allows attention allocation to be probed at different positions competing for attentional resources and at different time points relative to movement execution. Using a discrimination task, Dignath et al. (2019) recently demonstrated for pointing movements that a learned expectation of spatial congruence or incongruence between a discrimination and a motor target can modulate the attention-action link. Specifically, they showed that after training, participants directed attention toward an anticipated discrimination target position, regardless of whether it matched or diverged from the motor target. However, this was only shown in a delayed pointing task that potentially allowed for pre-programming of movements (cf. Deubel & Schneider, 2003), rendering it unclear whether these findings also hold for the critical stage of motor preparation. To answer this question, we recently conducted an adapted version of the experiment of Dignath et al. (2019) in which participants completed a training of a concurrent attention probing and pointing task (Topfstedt, Wollenberg, & Schenk, 2023). By manipulating the attention probe position, participants learned to expect the probe at the same or opposite position of a cued pointing target. In addition, we varied the time of movement delays (i.e., time between a movement cue and a movement go-signal) to examine potential training effects on attention allocation at different stages of the motor preparation phase. Results of a subsequent test phase showed that attention was markedly biased toward the anticipated probe position, even when it diverged from the motor target position. Moreover, these findings were not affected by the time available for movement preparation, suggesting that decoupling attentional resources from the motor target is not limited to pre-programmed movements, but can be achieved during ongoing movement programming. These results imply that, at least for manual movements, habitual processes may play a more important role regarding the attention-action coupling than previously assumed.

Although our previous findings in pointing movements suggest that the attention-action link is substantially modulated by habitual topdown processes (Topfstedt, Wollenberg, & Schenk, 2023), it remains unclear whether this also applies to saccadic eye movements. For instance, it has been shown that attention can be diverted from a reach target, but not from a saccade target, when sufficient time (>300 ms) is available for motor preparation (Deubel & Schneider, 2003), suggesting that the nature of the attention-action link might differ depending on the type of goal-directed movement. The present study was designed to address this open question. Similar to previous studies involving manual pointing movements (Dignath et al., 2019; Topfstedt, Wollenberg, & Schenk, 2023), we investigated whether and, if so, to what extent, habitual processes contribute to the commonly observed presaccadic shift of attention. To this end, we conducted an experiment that allowed us to test the possibility of a decoupling of visual attention from saccade programming. Please note that we use the term *decoupling* to refer to an instance in which attentional resources are allocated to positions other than the target a of concurrently programmed saccade, without

necessarily implying the complete absence of attentional facilitation at the saccade target. We asked participants to complete a training and a test session of a dual-task consisting of an attention probing and a saccade task. The initial training session (Attention Training) included a manipulation of the attention probe position. Participants learned anticipating that the probe will always appear either at the saccade target position (Training Same), at a position defined relative to the saccade target (Training Relative), or at a fixed position independent of the saccade target (Training Fixed). In the subsequent test session (Test Phase), however, the attention probe appeared equally likely at one out of several placeholder positions. Thus, based on probe discrimination data obtained in the Test Phase, it was possible to examine whether the expectation of spatial congruence or incongruence of attention probe and saccade target positions modulates presaccadic attention allocation. If the attention-action link is mainly the result of habitual processes, we should find that participants shift attention only toward the anticipated probe position, regardless of whether this position corresponds to the saccade target or not. In contrast, if visual attention is a mere by-product of processes of motor preparation (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994), attention should only be shifted to the saccade target, regardless of an expectation of spatial congruence or incongruence of positions. However, a third possibility would be that an anticipation of spatial incongruence leads to attentional facilitation at both the saccade target and the expected probe position. At first glance, such a finding would be in line with the assumption that the preparation of a goal-directed movement requires attentional selection of its target (Schneider, 1995; Schneider & Deubel, 2002). However, in previous studies (Dignath et al., 2019; Topfstedt, Wollenberg, & Schenk, 2023), participants were trained to expect an attention probe at a spatial position defined relative to the motor target (i.e., the position opposite the motor target). In this case, an observation of a retention of attentional resources at the motor target position could also be explained by the fact that attention was (initially) shifted to the motor target because it served as a spatial reference to identify the position of the attention probe (in the current study, we refer to this as the "spatial reference hypothesis"). Our study design allowed us to test this hypothesis by comparing presaccadic attention allocation in a training condition in which the attention probe was anticipated to appear at a position relative to the saccade target (Training Relative) to a training condition in which the probe was expected at a position not defined relative to the saccade target (Training Fixed). In addition, we wanted to examine whether potential top-down modulations of attention depend on the time available for motor preparation. Similar to our previous study (Topfstedt, Wollenberg, & Schenk, 2023), we thus varied the time of movement delays (i.e., stimulus onset asynchrony, SOA, between a movement cue and a movement go-signal of either 0 ms or 1000 ms) in the saccade task so that attention allocation was probed either within or after the assumed phase of motor programming. If the attention-action coupling is at least in part the result of habitual processes, prior training should affect attention allocation in a later task and the effect of this training should not be limited to long movement delays (i.e., delays during which movement pre-programming becomes possible).

#### 2. Methods

#### 2.1. Participants

Forty-one healthy students (aged 18–42 years; 28 females) with normal or corrected-to-normal vision gave written informed consent and participated in the experiment for monetary compensation or course credits. All participants were unaware of the purpose of the experiment. The experiment was approved by the local ethics committee and conducted in accordance with the Declaration of Helsinki.

The present study aimed to test whether it is possible to decouple attentional resources from the targets of imminent saccades. Evidence for such a decoupling was recently reported in a very similar dual-task study on pointing movements (Topfstedt, Wollenberg, & Schenk, 2023). More specifically, this study demonstrated a significant advantage in discrimination performance at a movement-irrelevant position where participants were trained to expect an attention probe compared to the upcoming motor target position. This performance benefit had an effect size of  $d_z = 4.72$  (calculated on the basis of the original data, but not reported in Topfstedt, Wollenberg, & Schenk, 2023). However, as mentioned in the Introduction, it is conceivable that the decoupling of attention and action is more difficult to overcome in saccades (Deubel & Schneider, 2003), so that the effect might be less pronounced in saccades compared to pointing movements. Accordingly, in the current study, we aimed for a final sample size (see Section 2.4.) of at least ten participants per condition, as this allows us to detect effects with a size of  $d_z \ge 1.00$  with an a priori power of 80 % (calculated using G\*Power for a matched pairs two-tailed *t* test with  $\alpha = .05$ ).

#### 2.2. Apparatus

Participants sat in a dimly illuminated room viewing a one-way mirror with their head positioned on a chin rest. The mirror reflected the image of a downward facing computer monitor (Acer XB271HUA; 120 Hz;  $2560 \times 1440$  pixels; screen size:  $59.67 \times 33.57$  cm) mounted at the top of the experimental setup. The distance between participants' eyes and the center of the stimulus presentation was 56.0 cm. We recorded the gaze position of participants' right eye with a temporal resolution of 1000 Hz using an EyeLink 1000 Plus eye-tracking system (SR Research Ltd., Ottawa, Ontario, Canada). To ensure high tracking accuracy throughout the experiment, the eye-tracker was calibrated prior to each experimental session (see Section 2.3.) and whenever necessary due to participants taking a short break or noticeable head movement. Manual responses were recorded with a standard numeric keypad.

#### 2.3. Design and procedure

Fig. 1 illustrates the time course of a typical trial. Stimuli were displayed on a uniform grey background. Each trial began with the presentation of a central black fixation cross (size:  $0.5^\circ$   $\times$   $0.5^\circ)$  and four black premask characters (seven-segment "8"; size:  $0.9^{\circ} \times 1.4^{\circ}$ ) positioned equidistant from each other at an eccentricity of  $7.2^{\circ}$  relative to the fixation cross. To start a trial, participants had to maintain gaze within a  $2.0^{\circ}$  radius around the fixation cross. After 1000–1300 ms (randomly selected in steps of 25 ms), the fixation cross was replaced by an arrow cue (size:  $1.5^{\circ} \times 1.5^{\circ}$ ) that indicated the saccade target (ST) by pointing in the direction of one of the premask characters with equal probability. After a stimulus onset asynchrony (SOA) of 0 ms (SOA-0 condition) or 1000 ms (SOA-1000 condition), an acoustical go-signal (440 Hz tone) was presented. Note that an SOA of 0 ms required immediate saccade preparation while an SOA of 1000 ms allowed for extended movement preparation time and thus the possibility for movement pre-programming. Participants were instructed to make a rapid and accurate saccade to the indicated ST as soon as the go-signal tone was played. They were also asked to avoid blinking throughout the trial. After a delay of 100-150 ms (randomly selected in steps of 25 ms) relative to go-signal onset, the premask characters were replaced by an attention probe (seven-segment "3" or "E") and three distractors (seven-segment "2" or "5"). Accordingly, depending on the movement delay, the attention probe appeared either during ongoing motor programming (SOA-0) or once the programming phase was presumably complete (SOA-1000). The probe display was shown for 83 ms and then masked again. After movement execution, participants reported the identity of the attention probe ("3" vs. "E") in a non-speeded manner by manually pressing one of two buttons (left vs. right) on the keypad. They received acoustical feedback about discrimination performance after each trial of the Discrimination Only task and Attention Training but not on trials of the Test Phase (see further below).



**Fig. 1.** Typical trial sequence. Participants started a trial by fixating a central fixation cross that was presented together with four placeholder characters ("8"). Shortly afterwards, a movement cue (an arrow pointing in the direction of one of the four placeholders) was presented to indicate the saccade target (ST) of the current trial. Participants were instructed to execute a saccade as quickly and accurately as possible to ST upon presentation of an acoustical go-signal, played either 0 ms or 1000 ms after movement cue presentation. Presaccadic attention allocation was measured by presenting an attention probe ("3" or "E") along with three distractors ("2" or "5") during saccade preparation (i.e., in the time between go-signal and saccade onset). This probe display was subsequently masked. After saccade execution, participants indicated the identity of the attention probe by manual key press.

Fig. 2 summarizes the main differences between experimental phases and experimental conditions. Each participant completed two experimental sessions, taking place on two consecutive days. The first session started with four blocks of 30 trials of the saccade task (Saccade Only). In these practice trials, no probe display (cf. Fig. 1) was presented. Participants received visual feedback about task performance after their response saccade (see Section 2.4.) had landed. To train participants to perform fast saccades, a central green circle was presented when the saccade had been initiated between 0 and 400 ms after go-signal onset. A central yellow circle was presented when a blink had been detected after the movement cue presentation. A central red circle with the label "too early" was presented when the saccade had been initiated before the gosignal, and with the label "too late" when saccade latency exceeded 400 ms.

Next, participants completed eight blocks of 30 trials of the discrimination task (Discrimination Only). In these trials, no movement cue and no go-signal was presented (cf. Fig. 1) and participants were asked to keep fixation throughout a trial. The attention probe was presented in 80 % of trials at a specific placeholder position. In the remaining 20 % of trials, the probe was presented with equal probability at one of the remaining placeholder positions. The likely position of the probe was randomly selected and held constant for each trial block. Participants were informed about the likely probe position by displaying the position (e.g., "Position: 1" for the upper right position) above the stimulus configuration. The Discrimination Only task of the first experimental session served as a screening phase to ensure that participants were capable of reliably discriminating the probe stimulus at a position toward which attention was deployed. For this purpose, discrimination performance (see Section 2.4.) was calculated for probes at the likely probe position in the last two trial blocks of this task. Participants continued the experiment only if this value exceeded 60 %. The last two trial blocks of the Discrimination Only task were also used to compute probe discrimination measures for attended positions (containing the probe with a high probability) and unattended positions (containing the probe with a low probability) in the absence of a

concurrent saccade task. By computing corresponding measures for an identical Discrimination Only task performed at the very end of the experiment (see further below), we were able to assess potential overall improvements in probe discrimination capacities across the experiment.

The initial Discrimination Only task was followed by a training of the dual-task (Attention Training) in which participants performed the saccade and discrimination task simultaneously. For the Attention Training, participants were randomly assigned to one of three training groups, differing from each other in the placeholder position at which the attention probe was presented. In Training Same, the probe was presented in 100 % of trials at the cued ST. In Training Relative, the probe was always presented at one specific placeholder position relative to ST, namely either at the placeholder  $90^\circ,\,180^\circ,\,\text{or}\,270^\circ$  clockwise to ST (but never at ST). The selection of this relative probe position was counterbalanced (e.g., participant 1: placeholder 90° clockwise to ST, participant 2: placeholder 180° clockwise to ST, participant 3: placeholder 270° clockwise to ST, etc.). In Training Fixed, the probe was always displayed at a fixed spatial position (i.e., either at the upper right, bottom right, bottom left, or upper left placeholder position), regardless of the current ST position. Again, this fixed probe position was counterbalanced across participants of the Training Fixed group (e.g., participant 1: upper right placeholder, participant 2: lower right placeholder, participant 3: lower left placeholder, participant 4: upper left placeholder, etc.). Prior to the start of the Attention Training, participants of all training groups were informed about the respective position at which the probe would appear in 100 % of trials. In the first experimental session, participants completed 24 blocks of 30 trials of the Attention Training.

At the beginning of the second session, participants completed another set of six blocks (30 trials each) of the Attention Training. For each participant, probe contingencies were identical to the Attention Training of the first session. The continuation of the Attention Training in the second session served to refresh potential group-specific learning effects from the previous day.

Next, to assess such training-induced learning effects on presaccadic



**Fig. 2.** Experimental phases and conditions. The first session began with a training of the saccade task (Saccade Only), in which saccades were performed to a centrally cued saccade target (ST) whose position varied randomly across trials. Next, participants completed a training of the discrimination task (Discrimination Only) in which they discriminated a probe stimulus ("3" vs. "E"; highlighted in white for illustration purposes only) presented with 80% probability at a specific placeholder position that was held constant over a trial block. Then, participants completed one of three Attention Training conditions in which they performed the saccade and discrimination task in parallel. In *Training Same* (upper panels), the attention probe was always presented at ST. In *Training Relative* (central panels), the probe always appeared at a specific position relative to ST (e.g., at the opposite position). In *Training Fixed* (lower panels), the probe was always displayed at a fixed spatial position (e.g., at the bottom right position), regardless of the ST position. The second session began with a refresh phase of the Attention Training, followed by a Test Phase in which the probe was presented at a random placeholder position. The second session was concluded with another series of trial blocks of the Discrimination Only task.

attention allocation, participants completed a Test Phase (24 blocks of 30 trials), in which the attention probe was displayed with equal probability at one of the four placeholder positions. Yet, to prevent potential training-induced effects on attention allocation from being quickly unlearned, participants were not informed about the randomized presentation of the attention probe prior to the Test Phase. They were only informed that they would no longer receive feedback about the correctness of their discrimination response. The randomization of the probe position in the Test Phase led to different trial types with regard to the spatial relationship between the position at which participants had been trained to expect the probe in the Attention Training (trained position), the actual (randomly drawn) probe position, and the ST position. Specifically, there were four distinct trial types in the Test Phase: ST/trained trials in which the probe appeared at the ST position matching the trained position, ST/non-trained trials in which the probe appeared at the ST position not matching the trained position, non-ST/ trained trials in which the probe appeared at the trained position not matching the ST position, and neutral trials in which the probe appeared at a position neither matching the trained position nor the ST position. However, by design, not all of these trial types were included in the Test Phase of each training group. Training Fixed included all four trial types in equal numbers: 180 ST/trained trials, 180 ST/non-trained trials, 180 non-ST/trained trials and 180 neutral trials. In Training Relative, there were 180 ST/non-trained trials, 180 non-ST/trained trials, and 360 neutral trials (i.e., no ST/trained trials). In Training Same, there were 180 ST/trained trials and 540 neutral trials (i.e., no ST/non-trained trials and no non-ST/trained trials).

At the end of the second session, participants performed another six

blocks of 30 trials of the Discrimination Only task. As mentioned above, this final phase served to assess possible overall learning effects regarding discrimination performance.

#### 2.4. Data analysis

Preprocessing of behavioral and eye-tracking raw data was performed in MATLAB (Mathworks, Natick, MA). Saccadic eye movements were detected offline using the velocity-based approach proposed by Engbert and Mergenthaler (2006) with a detection threshold parameter  $\lambda = 5$  and a minimum saccade duration of 15 ms. The first saccade that landed outside a radius of 2.5° from fixation was defined as the response saccade, which was subjected to further analyses. Saccade latency was calculated relative to go-signal onset.

For offline analyses of all experimental phases that included the saccade task, we discarded trials if no saccade was detected (No saccade), if an anticipatory response saccade (saccade latency < 80 ms; for an identical approach, see for example: Born, Ansorge, & Kerzel, 2013; Born, Mottet, & Kerzel, 2014) was detected (Saccade too early), if the latency of the response saccade deviated from participant's median by more than three times the median absolute deviation (Leys et al., 2013; Saccade latency outlier), if a blink occurred after movement cue onset (Blink violation), if the response saccade did not land within a radius of  $2.5^{\circ}$  relative to ST (Saccade inaccurate), or if the attention probe was still displayed after saccade onset (Saccade before probe offset). For data analysis of the Discrimination Only task, we excluded trials if gaze was not maintained within  $2.5^{\circ}$  from fixation (Fixation violation) or if a blink occurred (Blink violation).

Four participants were excluded from the experiment because they did not reach the threshold of discrimination performance in the screening phase of the initial Discrimination Only task (see Section 2.3.). Of the remaining sample (N = 37 out of 41), we discarded the data set of one participant of the *Training Same* group, three participants of the *Training Relative* group, and one participant of the *Training Fixed* group from the analyses because more than 45 % of the trials (for an identical approach, see Arkesteijn et al., 2019) of the Test Phase had to be rejected after applying the exclusion criteria described in the previous paragraph. The final sample (N = 32) comprised 11 participants in *Training Fixed*. A summary of the proportion of Test Phase trials rejected based on the applied exclusion criteria is presented for each training group in the Appendix (see Table S1 under "Supplementary Table").

Statistical data analyses were carried out with JASP version 0.17.3 (JASP Team). For all statistical tests performed, a p-value < 0.05 was used as the threshold for statistical significance. Reported mean values represent the grand mean across single-subject means for a given experimental condition, with corresponding measures of dispersion (standard error of the mean, standard deviation) being computed relative to the grand mean based on single-subject means. Performance in the discrimination task was expressed as the percentage of correct manual responses regarding the identity ("3" vs. "E") of the attention probe (discrimination performance). For analysis of performance in the Discrimination Only task, we conducted a repeated measures analysis of variance (ANOVA) with factors probe position (attended position vs. unattended position) and session (first session vs. second session). To ensure that only trials with stable task performance were included, we only analyzed the data of the last two trial blocks from the first experimental session. From the second session, all trials of the Discrimination Only task were included. For analysis of the Test Phase, we computed discrimination performance separately for each training group (Training Same vs. Training Relative vs. Training Fixed) and for each combination of SOA condition (SOA-0 vs. SOA-1000) and probe position. As described at the end of Section 2.3., the number of levels of factor probe position (i.e., the number of distinct trial types) in the Test Phase differed between training groups: Training Fixed (ST/trained vs. ST/non-trained vs. non-ST/trained vs. neutral), Training Relative (ST/non-trained vs. non-ST/ trained vs. neutral), Training Same (ST/trained vs. neutral). Due to these differences in the number of trial types, we analyzed discrimination performance separately for each training group by means of repeated measures ANOVAs with factors SOA and probe position. In case of sphericity violations, Greenhouse-Geisser corrections were applied. Post-hoc pairwise comparisons were Bonferroni-adjusted. Note that we further explored specific aspects of our data by performing several additional analyses, which are described in detail in Section 3.3.

#### 3. Results

To examine expectancy-driven top-down modulations on presaccadic attention allocation (as induced in the Attention Training), we analyzed eye movement data (as assessed via the saccade task) and discrimination performance data (as assessed via the attention probing task) obtained in the Test Phase.

#### 3.1. Saccade performance

We first investigated whether saccade performance within the Test Phase, defined as saccade latency (i.e., time between go-signal onset and saccade onset) and saccade accuracy (i.e., distance between the endpoint of the response saccade and the target position), was affected by SOA (*SOA-0* vs. *SOA-1000*) and training condition (*Training Same* vs. *Training Relative* vs. *Training Fixed*). Descriptive results of saccade performance are shown in Table 1.

Inspection of descriptive results suggests that *Training Relative* was associated with longer saccade latencies than *Training Same* and *Training* 

#### Vision Research 221 (2024) 108424

#### Table 1

Test Phase data of saccade latency in ms and saccade accuracy in visual degrees for each training condition (*Training Same* vs. *Training Relative* vs. *Training Fixed*) and stimulus onset asynchrony (SOA; 0 ms vs. 1000 ms). Data are presented as mean  $\pm$  SD.

	Training Same	Training Relative	Training Fixed
Latency: SOA-0	$388 \pm 51$	$420\pm 61$	$\textbf{379} \pm \textbf{39}$
Latency: SOA-1000	$337\pm49$	$367\pm59$	$327\pm42$
Accuracy: SOA-0	$1.1\pm0.2$	$1.2\pm0.2$	$1.1\pm0.1$
Accuracy: SOA-1000	$1.0\pm0.2$	$1.2\pm0.2$	$1.0\pm0.1$

Fixed in each SOA condition. However, results of an analysis of variance (ANOVA) showed no significant main effect of training condition, F(2,29) = 1.93, p = 0.163,  $\eta_p^2 = 0.12$ , and no significant interaction between training and SOA condition, F(2, 29) = 0.01, p = 0.986,  $\eta_p^2 < 0.01$ , for saccade latency. In contrast, saccade latencies were significantly affected by SOA condition, F(1, 29) = 122.71, p < 0.001,  $\eta_p^2 = 0.81$ , indicating shorter latencies across training groups in SOA-1000 trials (M = 343 ms, SD = 52 ms) than in SOA-0 trials (M = 395 ms, SD = 52 ms). This suggests that, as expected, the SOA-1000 trials permitted at least some pre-programming of saccades. Yet, latencies were still relatively high in SOA-1000 trials, which at first glance seems to contradict the assumption that these trials allowed for completion of motor preparation prior to the go-signal. However, this can probably be attributed to the fact that SOA-1000 trials required participants to suppress saccade execution for an extended period of time (i.e., 1000 ms). Thus, participants probably had to overcome initial motor inhibition before they could execute the saccade in response to the go-signal. Moreover, in our recent study on pointing movements (Topfstedt, Wollenberg, & Schenk, 2023) we observed longer movement latencies in a task including both short and long delays compared to a task comprising only one short movement delay. This suggests that the use of variable movement delays generally slows down movement initiation by inducing temporal uncertainty (i.e., uncertainty as to whether movement execution has to be withheld or not). Since we used two different movement delays in the current study, this type of uncertainty could also explain (or contribute to) the relatively long saccade latencies in SOA-1000 trials.

Regarding saccade accuracy, descriptive results indicate slightly less accurate saccades in *Training Relative* than in *Training Same* and *Training Fixed* in each SOA condition. However, ANOVA results showed no significant main effect of SOA, F(1, 29) = 2.57, p = 0.120,  $\eta_p^2 = 0.08$ , no significant main effect of training condition, F(2, 29) = 3.01, p = 0.065,  $\eta_p^2 = 0.17$ , and no significant interaction between SOA and training condition, F(2, 29) = 2.39, p = 0.110,  $\eta_p^2 = 0.14$ .

In sum, we observed no statistically reliable evidence that oculomotor performance differed between training conditions. Thus, overall, our results provide no indication for the assumption that participants used different strategies to perform the saccade task depending on the training condition (which is relevant regarding the interpretation of discrimination performance data, see Section 3.2.). However, at the descriptive level, there was a tendency toward slightly increased saccade latency and reduced saccade accuracy in Training Relative compared to the other two training groups. Since it is possible that this betweengroup difference might have reached statistical significance in a larger sample, we addressed this aspect in the context of the discrimination performance data in Section 3.3.2. In addition, we provide and discuss the results of further analyses comparing saccade latency and accuracy measures within each training group as a function of the probe position (i.e., trial type) in the Appendix (see "Supplementary Saccade Performance Results"). However, the results of these complementary analyses do not suggest that the probe position pronouncedly affected saccade parameters.

#### 3.2. Discrimination performance

In order to detect and quantify potential overall learning effects across the experiment, we used average discrimination performance at attended (i.e., likely) and unattended (i.e., unlikely) probe positions to compare performance between the first and second Discrimination Only task (i.e., last two trial blocks of first session vs. trial blocks of second session). A visual depiction of the results of this analysis can be found in the Appendix (see Fig. S1 under "Supplementary Figure"). In the first session, mean discrimination performance was 96.0 % (SD = 6.2 %) at attended positions and 59.2 % (SD = 15.7 %) at unattended positions. Relative to the first session, performance in the second session barely changed at attended positions (M = 96.4 %, SD = 2.3 %), whereas performance at unattended positions (M = 66.2 %, SD = 15.0 %) increased slightly. However, results of a mixed ANOVA only showed a significant main effect of probe position (attended vs. unattended positions), F(1, 31) = 259.41, p<0.001,  $\eta_p^2=0.89,$  but a non-significant main effect of session, F(1, 31) = 4.01, p = 0.054,  $\eta_p^2$  = 0.12, and no significant interaction between session and probe position, F(1, 31) = 3.59, p =0.068,  $\eta_p^2 = 0.10$ . Accordingly, it can be concluded that discrimination performance without concurrent saccadic eye movements was enhanced at attended compared to unattended positions, while we found no

statistical evidence for a reliable change across the experiment in the overall capacity to discriminate the attention probe.

Next, we analyzed discrimination performance for each training condition in the Test Phase to examine possible effects of learned spatial congruence or incongruence between the attention probe and the saccade target (ST) on presaccadic attention allocation (Fig. 3). This was done by subjecting discrimination performance data of each training condition to separate repeated measures ANOVAs with factors SOA (SOA-0 vs. SOA-1000) and probe position (*Training Same: ST/trained vs. neutral; Training Relative: ST/non*-trained vs. *non-ST/trained vs. neutral; Training Fixed: ST/trained vs. ST/non*-trained vs. *non-ST/trained vs. neutral*).

For Training Same, ANOVA results showed a significant main effect of probe position, F(1, 10) = 134.64, p < 0.001,  $\eta_p^2$  = 0.93, indicating enhanced discrimination performance across SOA conditions at the *ST/* trained position (M = 97.4 %, SD = 2.8 %) compared to performance at neutral probe positions (M = 58.0 %, SD = 10.9 %). The main effect of SOA, F(1, 10) = 0.07, p = 0.804,  $\eta_p^2$  = 0.01, and the interaction between SOA and probe position, F(1, 10) = 1.36, p = 0.271,  $\eta_p^2$  = 0.12, were not significant. These results suggest that participants directed attention to the saccade target position at which they also expected the attention probe to appear. We found no evidence to suggest that this effect



**Fig. 3.** Discrimination performance in Test Phase. Graphs depict mean discrimination performance for each training condition as a function of probe position. (A) Mean discrimination performance pooled across *SOA-0* and *SOA-1000* conditions. Asterisks indicate statistical significance of pairwise comparisons between probe positions within a given training condition (\*  $p \le .05$ ; \*\*  $p \le .01$ ; \*\*\*  $p \le .001$ ). (B) Mean discrimination performance plotted separately for *SOA-0* condition (upper panel) and *SOA-1000* condition (lower panel). Error bars represent standard error of the mean (SEM).

depends on the time available for motor preparation.

For Training Relative, we found that discrimination performance differed significantly between probe positions, F(2, 18) = 25.50, p <0.001,  $\eta_p^2 = 0.74$ . However, there was no significant main effect of SOA condition, F(1, 9) < 0.01, p = 0.986,  $\eta_p^2 <$  0.01, and no significant interaction between SOA and probe position, F(2, 18) = 1.99, p = 0.166,  $\eta_p^2 = 0.18$ . Post-hoc pairwise comparisons revealed that discrimination performance across SOAs was significantly enhanced at the non-ST/ trained position (M = 86.6 %, SD = 10.1 %) compared to both the ST/*non-trained* position (*M* = 64.4 %, *SD* = 13.0 %, *t*(9) = -3.95, *p* = 0.010,  $d_z = -1.95$ ) and neutral positions (M = 56.6 %, SD = 6.9 %, t(9) = 9.13, p < 0.001,  $d_z = 2.66$ ). Moreover, there was no significant difference in performance between the ST/non-trained position and neutral positions  $(t(9) = 2.07, p = 0.207, d_z = 0.71)$ . Taken together, these results demonstrate that participants learned to shift attention to the expected probe position, even though this position did not coincide with the saccade target. This pattern of results was not significantly affected by the time available for motor preparation.

Regarding Training Fixed, ANOVA results showed a significant main effect of probe position on discrimination performance, F(1.20, 11.96) = 15.06, p = 0.002,  $\eta_p^2 = 0.60$ . The main effect of SOA, F(1, 10) = 2.75, p = 0.128,  $\eta_p^2 = 0.22$ , and the interaction between SOA and probe position, F(3, 30) = 0.15, p = 0.932,  $\eta_p^2 = 0.01$ , were not significant. Posthoc pairwise comparisons showed that overall discrimination performance at the ST/trained position (M = 95.3 %, SD = 6.3 %) was significantly enhanced relative to performance at all remaining probe positions (*ST*/non-trained: *M* = 70.5 %, *SD* = 16.1 %, *t*(10) = 4.04, *p* =  $0.014, d_z = 1.81; non-ST/trained: M = 82.1 \%, SD = 15.0 \%, t(10) = 3.69,$  $p = 0.025, d_z = 0.95$ ; neutral positions: M = 57.9 %, SD = 12.2 %, t(10)= 8.19, p < 0.001,  $d_z = 2.71$ ). Moreover, performance at the non-ST/ trained position was significantly higher compared to performance at neutral probe positions, t(10) = 3.62, p = 0.028,  $d_z = 1.76$ . In contrast to Training Relative, discrimination performance at the ST/non-trained position was significantly higher than performance at neutral positions, t (10) = 4.36, p = 0.009,  $d_z = 0.90$ , and did not differ compared to performance at the non-ST/trained position, t(10) = -1.33, p > 0.999,  $d_z =$ -0.86. These results suggest that participants directed attention to both the expected probe position and the saccade target. Furthermore, the finding of enhanced discrimination performance at the ST/trained position compared to all other probe positions in this condition provides evidence for an additive attentional enhancement effect when saccade target and expected probe position spatially coincide.

#### 3.3. Results of further analyses

#### 3.3.1. No evidence for a spatial reference hypothesis

In addition to examining the possibility of a decoupling of attentional resources from targets of forthcoming saccades through training, we aimed at investigating whether the feasibility of such decoupling during ongoing oculomotor programming depends on the spatial relationship between visual and saccadic targets (spatial reference hypothesis; see Introduction). To this end, we computed, separately for the Training Relative and Training Fixed condition, an index of the training-induced decoupling effect in SOA-0 trials by subtracting discrimination performance at the ST/non-trained position from performance at the non-ST/ trained position. We then performed an unpaired t-test to statistically compare this decoupling index between Training Relative and Training Fixed. Surprisingly, other than predicted by a spatial reference hypothesis, we found no significant difference between training conditions, t (19) = -0.68, p = 0.504, d = -0.30. Thus, our data do not provide evidence to suggest that the capacity to decouple attention from motor targets depends on the specific spatial relationship between a motor target and a task-relevant visual target.

Vision Research 221 (2024) 108424

## 3.3.2. Attention decoupling does not rely on compromised oculomotor performance

As reported in Section 3.1., there was a tendency toward increased saccade latency and reduced saccade accuracy for both SOAs in Training Relative compared to the other two training conditions. Even though we observed no statistically reliable modulation of these two saccade parameters across groups, this indication of reduced saccadic speed and accuracy leaves open the possibility that the observed attention decoupling in Training Relative was achieved only by compromising oculomotor performance. Put differently, the discrimination performance results in this condition may have resulted from a prioritization of the discrimination task over the saccade task rather than being indicative of a genuine decoupling of attention from saccade programming. To resolve this ambiguity, we re-examined discrimination performance data of Training Relative in an exploratory analysis including only trials indicative of fairly uncompromised saccadic control. This entailed the following steps. For each participant of Training Relative, we first performed, separately for each SOA condition, a median-split on the saccade latency data and selected the subset of trials with comparably fast (i.e., below median latency) saccades. For each resulting dataset, we then calculated the median saccade accuracy and used it to select only those trials representing comparably accurate (i.e., above median accuracy) saccades. Thus, the final datasets comprised only the most accurate among the fastest saccades of each SOA condition, which were subjected to a repeated measures ANOVA with factors probe position and SOA, using discrimination performance as the dependent variable. Note that we performed two additional variants of this exploratory analysis with different subsets of uncompromised saccade trials to ensure that the statistical results reported here did not depend on the specific method used for trial selection. Details of these analyses and corresponding results are described in the Appendix (see "Supplementary Discrimination Performance Results"). If attentional decoupling depends on compromising saccadic speed or accuracy, there should be no discrimination benefit at non-saccade targets in uncompromised saccade trials. In contrast, if true attentional decoupling is possible, a discrimination benefit at non-saccade targets should be observed in this subset of trials.

For the Training Relative data included in this analysis, mean saccade latency was 378 ms (SD = 55 ms) in SOA-0 trials and 321 ms (SD = 53ms) in SOA-1000 trials. Mean saccade accuracy was  $0.7^{\circ}$  (SD =  $0.2^{\circ}$ ) in SOA-0 trials and 0.7° (SD = 0.2°) in SOA-1000 trials. Thus, for both SOAs, oculomotor performance in this subset of trials was even better than that of Training Same and Training Fixed in our main analysis (cf. Table 1). Accordingly, possible attentional effects observed in the current data cannot be attributed to a strategy that involves compromising saccadic speed or accuracy. In fact, we found that the pattern of discrimination performance (see Fig. 4) was highly similar to that observed in the main analysis including the full data set of the Training Relative condition (cf. Fig. 3). ANOVA results revealed a significant main effect of probe position on discrimination performance, F(2, 18) = 18.93, p < 0.001,  $\eta_p^2 = 0.68$ , whereas the main effect of SOA, F(1, 9) = 0.66,  $p=0.439, \eta_p^2=0.07,$  and the interaction SOA by probe position, F $(2,\,18)=0.55,\,p=0.588,\,\eta_p^2=0.06,$  were non-significant. Moreover, post-hoc pairwise comparisons showed that discrimination performance across SOAs was significantly enhanced at the non-ST/trained position compared to the ST/non-trained position, t(9) = -3.62, p = 0.017,  $d_z =$ -1.61, and neutral positions, t(9) = 8.92, p < 0.001,  $d_z = 2.17$ . The difference in performance between the ST/non-trained position and neutral positions was not significant, t(9) = 1.45, p = 0.542,  $d_z = 0.55$ . Hence, even in trials with uncompromised saccade performance, the largest discrimination benefit was still observed at a movementirrelevant position. This suggests that the attention decoupling observed in Training Relative (as reported in our main analysis) did not merely reflect the consequence of compromised oculomotor performance.

45

C.E. Topfstedt et al.

Vision Research 221 (2024) 108424



**Fig. 4.** Discrimination performance for subset of Test Phase trials representing the most accurate among the fastest saccades in *Training Relative* condition. Graphs depict mean discrimination performance as a function of probe position. (A) Mean discrimination performance pooled across trial subsets of both SOA conditions. Asterisks indicate statistical significance of pairwise comparisons between probe positions (\*  $p \le .05$ ; \*\*\*  $p \le .001$ ). (B) Mean discrimination performance plotted separately for *SOA-0* and *SOA-1000* condition trial subsets. Error bars represent standard error of the mean (SEM).

#### 3.3.3. Attention decoupling increases over the course of training

Finally, since results of *Training Relative* and *Training Fixed* demonstrated that an anticipation of spatial incongruence allowed participants to shift attentional resources to non-motor targets (i.e., the *non-ST/trained* position) in the Test Phase, we aimed at further exploring the temporal development of this capacity over the course of the Attention Training. To this end, we first divided data of the Attention Training (including the Refresh Phase) into five time-ordered trial bins, each consisting of 180 trials. Next, we computed, for each bin, separate measures of discrimination performance at the *non-ST/trained* position for the different training (*Training Relative* vs. *Training Fixed*) and SOA (*SOA-0* vs. *SOA-1000*) conditions. As highlighted in Fig. 5,

discrimination performance in both *Training Relative* and *Training Fixed* was above chance level in the first trial bin, but increased over the course of the Attention Training without being considerably modulated by SOA. To test whether these training improvements were statistically significant, we subjected discrimination performance data of *Training Relative* and *Training Fixed* to separate repeated measures ANOVAs with factors SOA and trial bin (first vs. last). For *Training Relative*, results showed a non-significant main effect of SOA, F(1, 9) = 0.73, p = 0.415,  $\eta_p^2 = 0.08$ , and a non-significant interaction between SOA and trial bin, F (1, 9) = 0.55, p = 0.477,  $\eta_p^2 = 0.06$ . However, we observed a significant main effect of trial bin, F(1, 9) = 7.54, p = 0.023,  $\eta_p^2 = 0.46$ , affirming that performance reliably increased from the first bin (M = 74.2 %, SD =



**Fig. 5.** Discrimination performance in Attention Training. Graphs depict mean discrimination performance at the *non-ST/trained* position for different trial bins (i.e., trials of Attention Training, including the Refresh Phase, divided into five equally sized bins of 180 trials each) in each SOA condition and pooled across SOA conditions. (A) Mean discrimination performance in *Training Relative* condition. (B) Mean discrimination performance in *Training Fixed* condition. Asterisks indicate statistical significance for the comparison between the first and last trial bin as observed for the data pooled across both SOA conditions (\*  $p \le .05$ ; \*\*\*  $p \le .001$ ). Error bars represent standard error of the mean (SEM).

14.9 %) to the last bin (M = 84.6 %, SD = 9.1 %). Similarly, for *Training Fixed*, there was a non-significant main effect of SOA, F(1, 10) = 3.42, p = 0.094,  $\eta_p^2 = 0.26$ , a non-significant interaction, F(1, 10) < 0.01, p = 0.995,  $\eta_p^2 < 0.01$ , but a significant main effect of trial bin, F(1, 10) = 37.73, p < 0.001,  $\eta_p^2 = 0.79$ , suggesting enhanced performance in the last bin (M = 87.0 %, SD = 9.6 %) relative to the first bin (M = 76.6 %, SD = 13.5 %). Consequently, the pronounced discrimination benefits found at the *non-ST/trained* position for *Training Relative* and *Training Fixed* in the Test Phase indeed reflect training-induced improvements in the capacity to shift attention to non-movement targets.

#### 4. Discussion

It has been widely demonstrated that programming a saccadic eye movement toward a given motor target is accompanied by a spatially congruent shift of visual attention, a finding often taken as evidence for an obligatory coupling between covert visual attention and processes of motor preparation. Here, we addressed the question whether this coupling is facilitated by top-down processes linked to an overlearned and therefore habitual expectation that behaviorally relevant visual and motor targets typically coincide in space. To this end, we asked participants to perform a dual-task (i.e., concurrent saccade and attention probing task) and tested whether expecting a mismatch of visual and motor targets can lead to a decoupling between attention and oculomotor programming. In an initial training phase, they learned to anticipate an attention probe either at the same position as a saccade target (ST; Training Same), at a specific position relative to ST (Training Relative), or at a fixed position not varying with ST (Training Fixed). In a subsequent Test Phase, the probe position was randomized, which allowed us to assess whether top-down expectation about the probe position modulated presaccadic attention allocation. In addition, we varied the duration of movement delays to probe attention either during or after the assumed phase of motor preparation. Thereby, it was possible to further examine whether potential training-induced attentional effects require saccade pre-programming or already emerge during ongoing saccade preparation.

Overall, our results demonstrate that presaccadic attention allocation was strongly biased by participants' expectations (see Section 3.2.). We found that a learned expectation of spatial congruence between the saccade target and the attention probe caused participants to selectively shift attention to the saccade target (i.e., ST/trained position in Training Same). In contrast, an expectation of spatial incongruence of positions allowed participants to deploy attentional resources to the anticipated probe position, regardless of whether it matched the saccade target (i.e., ST/trained position in Training Fixed) or diverged from it (i.e., non-ST/ trained position in Training Relative and Training Fixed). Importantly, the robustness of the latter effect of attentional facilitation at positions other than the saccade target (relative to neutral control positions) is underscored by the fact that it was observed in two independent groups of participants (Training Relative and Training Fixed). Moreover, we found no evidence suggesting that the capacity to allocate attentional resources to movement-irrelevant positions was associated with a discernible impairment in saccade performance in these conditions (see Section 3.1.). There was only an indication of some (non-significant) costs in saccade performance specific to Training Relative. Importantly, as observed in an exploratory analysis (see Section 3.3.2.), a pronounced attentional benefit at the expected probe position (i.e., non-ST/trained position) was still present in this condition in trials without apparent costs in saccade performance (i.e., trials associated with relatively fast and accurate saccades). Our data therefore provide no indication that participants accomplished shifting attention away from saccadic targets by strategically prioritizing the discrimination task at the cost of the saccade task (Kowler et al., 1995). Similarly, as reported in Section 3.2., the results of the Discrimination Only task (which participants performed both before the Attention Training and after the Test Phase) revealed no statistical evidence that modulations of presaccadic

attention allocation were caused by non-specific learning effects (e.g., an overall improvement in discrimination performance across the experiment). Rather, our data indicate that the observed attentional effects resulted from training-induced expectations about the probe position. Moreover, the observed top-down modulations of attention did not depend on the time available for movement preparation. Considering all of these aspects, the current results challenge the assumption that covert visual attention and processes of motor preparation are obligatorily coupled to each other and rely on the same mechanism (Rizzolatti et al., 1987; Rizzolatti, Riggio, & Sheliga, 1994), thus complementing our previous findings on manual pointing movements (Topfstedt, Wollenberg, & Schenk, 2023).

Importantly, as can be seen in Fig. 3, discrimination performance at the expected probe position (i.e., *non-ST/trained* position) exceeded performance at the saccade target position (i.e., *ST/non-trained* position) in *Training Relative* and *Training Fixed*. In the former condition, we observed a significant performance benefit at the expected probe position compared to the saccade target position, supporting the idea that attentional resources were predominantly allocated toward a movement-irrelevant position rather than toward the motor target. Interestingly, despite showing a similar pattern, results of the latter condition did not reveal a significant relative performance enhancement at the expected probe position. Taken together, these findings therefore imply that, depending on the specific task, participants were capable of learning to allocate attentional resources to a movement-irrelevant position as efficiently as, or even more efficiently than, to the motor target itself.

So far, the discussed results highlight the feasibility of a decoupling between attention and motor programming in terms of participants being able to direct attention to a considerable extent to a position other than the motor target. However, while this implies that attention is not restricted to the spatial parameters of upcoming motor actions, it does not allow to conclude that motor programming can occur in the absence of attentional selection. To assess whether this kind of complete decoupling (i.e., complete withdrawal of attentional resources from motor target) is possible, we compared discrimination performance between the saccade target (i.e., ST/non-trained position) and neutral control positions in Training Relative and Training Fixed. In the case of complete decoupling, no benefit in performance should be observed at the saccade target compared to neutral positions. Indeed, in Training Relative, we found no significant saccade target benefit. At first glance, this points toward the notion that endogenous (i.e., top-down) attentional control can operate independently of processes of motor preparation (Gabay, Henik, & Gradstein, 2010; Gregoriou, Gotts, & Desimone, 2012; Juan et al., 2008; Smith, Rorden, & Jackson, 2004; Smith, Schenk, & Rorden, 2012). However, inspection of data (see Fig. 3) suggests a small advantage in discrimination performance at the saccade target over the neutral positions, which might have potentially reached statistical significance with a larger sample size. Moreover, in Training Fixed, there was a small but significant enhancement in performance at the saccade target, suggesting that some attentional resources remained at this position. The present results therefore do not establish a sufficient basis for a definitive conclusion regarding the possibility of a complete decoupling between attention and action. Nonetheless, we found that performance at the saccade target was rather low in both conditions, which implies that saccade preparation requires at least fewer attentional resources than previously assumed (e.g., Deubel, 2008; Deubel & Schneider, 1996).

Similar to the present results, our earlier study on pointing movements (Topfstedt, Wollenberg, & Schenk, 2023) revealed that attention was substantially biased toward a non-movement target at which participants had learned to anticipate the attention probe. Notably, discrimination performance at the motor target did not differ significantly from performance at neutral control positions (see Topfstedt, Wollenberg & Schenk, 2023, Exp. 2). In our previous study, however, participants were exclusively trained to expect an attention probe at a

position defined *relative* to the motor target. Thus, even if we had observed a significant performance benefit at the motor target, it would not have been possible to determine whether attention was shifted toward this position due to motor programming or because this position was required as a spatial reference to identify the expected probe position (spatial reference hypothesis, see also Introduction). To address this question in the present study, we therefore included not only a condition in which the expected probe position was defined relative to the saccade target (Training Relative), but also one in which the expected probe position did not depend on the saccade target position (Training Fixed). Interestingly, we observed exactly the opposite pattern of what would be expected under a spatial reference hypothesis (see Section 3.3.1.). As discussed above, a small but reliable performance benefit at the saccade target emerged in the condition in which the expected probe position was not defined relative to the saccade target (Training Fixed). In contrast, no reliable saccade target benefit was found when the expected probe position was defined relative to the saccade target (Training Relative). These findings contradict the assumption that attention had to be deployed at the motor target for probe position identification. Moreover, assuming that the spatial reference hypothesis holds, a larger attentional decoupling effect should be found in Training Fixed compared to Training Relative. However, we found no significant difference regarding the extent of attentional decoupling (measured as the difference in discrimination performance between the non-ST/trained position and the ST/non-trained position) during the preparation of undelayed saccades between these two conditions. In conclusion, our data therefore do not suggest that a spatial reference hypothesis provides a valid explanation for a possible retention of attentional resources at motor targets in the current study and similar previous training studies (Dignath et al., 2019; Topfstedt, Wollenberg, & Schenk, 2023) investigating a decoupling of attention and action.

In line with previous studies (Deubel, 2008; Deubel & Schneider, 1996, 2003; Hoffman & Subramaniam, 1995; Jonikaitis & Deubel, 2011), we observed a marked enhancement of visual discrimination performance at the saccade target position in Training Same. However, in Training Same, participants were trained to anticipate the attention probe at the saccade target. It is thus likely that the learned anticipation of spatial congruence between positions at least additionally facilitated attention shifts toward the motor target in this training condition. This assumption is supported by the results of Training Fixed, which showed that the attentional benefit caused either purely by top-down expectation (i.e., performance at non-ST/trained position) or saccade preparation (i.e., performance at ST/non-trained position) was smaller than the benefit found for a combination of these two components (i.e., performance at ST/trained position). Put differently, an additive attentional enhancement effect in Training Fixed was observed for trials in which the expected probe position and the saccade target coincided (i.e., those trials that effectively mirrored trials of Training Same). This indicates that top-down expectations led to similar additional attentional facilitation at the saccade target in Training Same. Consistent with this view, discrimination performance at the saccade target in Training Same (i.e., 97.4 %) was substantially higher than in similar previous studies (Deubel, 2008; Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011).

Interestingly, contrary to the current results, similar previous dualtask studies have suggested that attention cannot be decoupled substantially from saccade targets during motor preparation (Deubel, 2008; Deubel & Schneider, 1996) or that saccade programming deteriorates the capacity to attend to movement-irrelevant objects (Hanning et al., 2022). While we can only speculate about the cause for this discrepancy, we believe that our study, in contrast to these previous studies, established optimal circumstances for a decoupling of attention from motor programming. First, our study involved a distinct phase in which participants were specifically trained to decouple attention from the motor target. Second, within a given training condition, the spatial characteristics of this decoupling were kept constant across trials. Third, as realized by means of an explicit instruction, the task-relevant probe position was made fully predictable. To our knowledge, none of the previous studies included all of these features, which might have rendered a decoupling of attention from motor preparation more difficult than in the current study. In particular, our results imply that the distinct training phase played an important role in the decoupling observed here. We found a significant improvement in discrimination performance at the anticipated (trained) probe position over the course of the training phase in *Training Relative* and *Training Fixed* (see Section 3.3.3.). Despite this temporal modulation, performance at these positions was already relatively high at the beginning of the Attention Training, presumably reflecting a general effect of probe predictability. An interesting endeavor for future research would therefore be to examine the preconditions for a successful decoupling of attentional and oculomotor control in more detail (e.g., via systematic and gradual variation of training duration and probe predictability).

In our study, we decided not to inform participants about probe randomization prior to the Test Phase. This was done to prevent training-induced top-down biases from rapidly decaying in this phase. In fact, advance knowledge of the randomized probing procedure would have likely abolished expectancy-driven attentional modulations in the Test Phase. Nonetheless, one might argue that concealment of the probe position randomization in the Test Phase constitutes a limitation of our study, as this may have led participants to perceptually ignore the saccade target. We believe, however, that this assumption is not warranted for three reasons. First, we observed a significant attentional benefit at the (non-trained) saccade target in Training Fixed, suggesting that participants did not ignore the saccade target in the discrimination task. Second, we found no evidence for impaired saccade performance in Training Relative and Training Fixed compared to Training Same. Therefore, we found no evidence to suggest that the attentional enhancement effect at the trained non-movement target (in Training Relative and Training Fixed) was achieved by ignoring the saccade target. Third, upon examination after the experiment, the majority of participants reported that they had noticed that the probe no longer always appeared at the expected (trained) position during the Test Phase, but sometimes at different positions. This indicates that participants were generally aware of the potential importance of positions other than the anticipated probe position. Taking all these aspects into account, we believe that the effects observed here are best accounted for in terms of specific traininginduced and expectancy-driven top-down modulations of presaccadic attention allocation. Importantly, the very fact that participants can learn to perform accurate saccades while shifting attention away from the saccade target shows that motor preparation and covert attention shifts can be decoupled.

In summary, our results demonstrate that participants can be trained to decouple attentional resources from an upcoming movement target to a considerable extent. However, the data of one of our training conditions (*Training Fixed*) suggests that some attentional resources may remain locked to the saccade target even when observers have learned that the discrimination probe is most likely to appear at a different location. Accordingly, we do not claim that our findings refute the existence of a tight link between attentional control and motor programming. Rather, we advocate the idea that the attention-action link is at least partially consolidated through a habitual expectation that motor targets typically contain highly relevant visual information. To account for this expectation, attention is shifted to targets of forthcoming actions by default. Crucially, as demonstrated here, it is possible to modify this expectation through training and voluntarily shift attentional resources to movement-irrelevant, yet behaviorally relevant, positions or objects.

#### 5. Conclusions

The data presented here demonstrate that the linkage of covert visual attention and saccadic eye movements is less strict than previously assumed. Whereas our results suggest that a learned anticipation of spatial congruence between a visual and a motor target boosts the

commonly observed presaccadic shift of attention, a learned anticipation of spatial incongruence leads to a pronounced withdrawal of attentional resources from the target of imminent saccades. More specifically, top-down expectancy allows to flexibly allocate the greater part of attentional resources to task-relevant visual targets, even if they diverge from current motor targets. Importantly, these top-down modulations of presaccadic attention allocation are not limited to preprogrammed movements, but can occur during ongoing oculomotor preparation. This implies that habitual top-down processes may play an important and so far largely neglected role for the emergence of the wellestablished attention-action coupling in saccadic eye movements.

#### Funding

This research was financially supported by German Research Foundation (Deutsche Forschungsgemeinschaft, DFG) grants SCHE-735/4-1 (T.S.), SCHE 735/2-2 (T.S.), SCHE 735/3-2 (T.S.), and WO 2552/2-1 (L.W.).

#### CRediT authorship contribution statement

**Christof Elias Topfstedt:** Writing – review & editing, Writing – original draft, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luca Wollenberg:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Thomas Schenk:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization.

#### **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data availability

All raw data are publicly available at https://osf.io/x45dr

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.visres.2024.108424.

#### References

- Arkesteijn, K., Belopolsky, A. V., Smeets, J. B. J., & Donk, M. (2019). The limits of predictive remapping of attention across eye movements. *Frontiers in Psychology*, 10, 1146. https://doi.org/10.3389/fpsyg.2019.01146
- Born, S., Ansorge, U., & Kerzel, D. (2013). Predictability of spatial and non-spatial target properties improves perception in the pre-saccadic interval. *Vision Research*, 91, 93–101. https://doi.org/10.1016/j.visres.2013.08.003
- Born, S., Mottet, I., & Kerzel, D. (2014). Presaccadic perceptual facilitation effects depend on saccade execution: Evidence from the stop-signal paradigm. *Journal of Vision*, 14 (3), 1–10. https://doi.org/10.1167/14.3.7
- (3), 1–10. https://doi.org/10.1167/14.3.7
  Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., & Shulman, G. L. (1998). A common network of functional areas for attention and eye movements. *Neuron*, 21(4), 761–773. https://doi.org/10.1016/S0896-6273(00)80593-0
- de Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, 1204, 102–111. https://doi.org/10.1016/j.brainres.2008.01.105
- Deubel, H. (2008). The time course of presaccadic attention shifts. Psychological Research Psychologische Forschung, 72(6), 630–640. https://doi.org/10.1007/s00426-008-0165-3
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, 36(12), 1827–1837. https://doi.org/10.1016/0042-6989(95)00294-4
- Deubel, H., & Schneider, W. X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals of the New York Academy of Sciences*, 1004(1), 289–296. https://doi.org/10.1196/annals.1303.026

#### Vision Research 221 (2024) 108424

- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition*, 5(1–2), 81–107. https://doi.org/10.1080/713756776
- Dignath, D., Herbort, O., Pieczykolan, A., Huestegge, L., & Kiesel, A. (2019). Flexible coupling of covert spatial attention and motor planning based on learned spatial contingencies. *Psychological Research Psychologische Forschung*, 83(3), 476–484. https://doi.org/10.1007/s00426-018-1134-0
- Engbert, R., & Mergenthaler, K. (2006). Microsaccades are triggered by low retinal image slip. Proceedings of the National Academy of Sciences, 103(18), 7192–7197. https:// doi.org/10.1073/pnas.0509557103
- Findlay, J. M., & Gilchrist, I. D. (2003). Active vision: The psychology of looking and seeing. Oxford University Press. https://doi.org/10.1093/acprof:oso/ 9780198524793.001.0001
- Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention in patients with Duane Retraction Syndrome. *Neuropsychologia*, 48(10), 3102–3109. https://doi.org/10.1016/j.neuropsychologia.2010.06.022
- Gregoriou, G. G., Gotts, S. J., & Desimone, R. (2012). Cell-type-specific synchronization of neural activity in FEF with V4 during attention. *Neuron*, 73(3), 581–594. https:// doi.org/10.1016/j.neuron.2011.12.019
- Hanning, N. M., Wollenberg, L., Jonikaitis, D., & Deubel, H. (2022). Eye and hand movements disrupt attentional control. *PLoS One*, 17(1), Article e0262567. https:// doi.org/10.1371/journal.pone.0262567
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787–795. https://doi.org/10.3758/ BF03206794
- Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*, 22(3), 339–347. https://doi.org/10.1177/0956797610397666
- Juan, C.-H., Muggleton, N. G., Tzeng, O. J. L., Hung, D. L., Cowey, A., & Walsh, V. (2008). Segregation of visual selection and saccades in human frontal eye fields. *Cerebral Cortex*, 18(10), 2410–2415. https://doi.org/10.1093/cercor/bhn001
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. Vision Research, 35(13), 1897–1916. https://doi.org/ 10.1016/0042-6989(94)00279-U
- Leys, C., Ley, C., Klein, O., Bernard, P., & Licata, L. (2013). Detecting outliers: Do not use standard deviation around the mean, use absolute deviation around the median. *Journal of Experimental Social Psychology*, 49(4), 764–766. https://doi.org/10.1016/ j.jesp.2013.03.013
- Moehler, T., & Fiehler, K. (2014). Effects of spatial congruency on saccade and visual discrimination performance in a dual-task paradigm. *Vision Research*, 105, 100–111. https://doi.org/10.1016/j.visres.2014.10.001
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, 7(14), 1–16. https://doi.org/10.1167/7.14.8
- Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology*, 91(1), 152–162. https://doi.org/ 10.1152/jn.00741.2002
- Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences*, 102(3), 524–529. https://doi.org/10.1073/ pnas.0408311101
- Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. Journal of Experimental Psychology: General, 109(2), 160–174. https://doi. org/10.1037/0096-3445.109.2.160
- Reeves, A., & McLellan, J. S. (2020). The 'anti-shift': Shifting attention opposite to a saccade. Vision Research, 167, 31–38. https://doi.org/10.1016/j.visres.2019.06.009
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1), 31–40. https://doi.org/10.1016/0028-3932(87) 90041-8
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà, & M. Moscovitch (Eds.), Attention and performance XV: Conscious and nonconscious information processing (pp. 232–265). The MIT Press.
- Schiegg, A., Deubel, H., & Schneider, W. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*, 10(4), 409–431. https://doi.org/ 10.1080/13506280244000140
- Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Visual Cognition, 2* (2–3), 331–376. https://doi.org/10.1080/13506289508401737
- Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatialmotor-action are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In W. Prinz, & B. Hommel (Eds.), Attention and performance XIX: Common mechanisms in perception and action (pp. 609–627). Oxford University Press.
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, 14(9), 792–795. https://doi.org/10.1016/j.cub.2004.04.035
- Smith, D. T., & Schenk, T. (2012). The Premotor theory of attention: Time to move on? *Neuropsychologia*, 50(6), 1104–1114. https://doi.org/10.1016/j. neuropsychologia.2012.01.025
- Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology: Human Perception and Performance*, 38(6), 1438–1447. https://doi.org/ 10.1037/a0027794

Vision Research 221 (2024) 108424

Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *The Journal of Neuroscience*, 25(41), 9479–9487. https://doi.org/10.1523/jneurosci.0741-05.2005

C.E. Topfstedt et al.

- Topfstedt, C. E., Wollenberg, L., & Schenk, T. (2023). The role of habitual learning in premotor attention allocation. *Journal of Vision*, 23(5), 1–18. https://doi.org/ 10.1167/jov.23.5.19
- Van der Stigchel, S., & de Vries, J. P. (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. *Journal of Vision*, 15(15), 1–12. https://doi.org/10.1167/15.15.17
- Wollenberg, L., Deubel, H., & Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. *PLOS Biology*, 16(6), Article e2006548. https://doi. org/10.1371/journal.pbio.2006548
- Wollenberg, L., Hanning, N. M., & Deubel, H. (2020). Visual attention and eye movement control during oculomotor competition. *Journal of Vision*, 20(9), 1–17. https://doi. org/10.1167/jov.20.9.16
- Wollenberg, L., Deubel, H., & Szinte, M. (2019). Investigating the deployment of visual attention before accurate and averaging saccades via eye tracking and assessment of visual sensitivity. *JoVE*, *145*, Article e59162. https://doi.org/10.3791/59162

## Appendix - Supplementary Material

## Supplementary Table

Exclusion criteria	Training Same	Training Relative	Training Fixed
No Saccade	1.3	1.0	0.9
Saccade too early	5.1	3.4	5.3
Saccade latency outlier	8.3	7.6	8.2
Blink violation	6.1	8.6	5.9
Saccade inaccurate	6.2	13.8	7.7
Saccade before probe offset	9.8	6.2	11.0
Total excluded trials	24.4	30.6	25.7

**Table S1.** Percentages of excluded trials of the Test Phase for each training condition. Note that the different exclusion criteria percentages do not add up to the total percentage of excluded trials, since multiple criteria could apply for a single trial.

## **Supplementary Figure**



**Fig. S1.** Discrimination performance in Discrimination Only task. Graph depicts mean discrimination performance pooled across training conditions at "attended" and "unattended" positions in the First Session and Second Session of the Discrimination Only task. Asterisks indicate significant main effect of probe position (\*\*\*  $p \le .001$ ). Error bars represent standard error of the mean (SEM).

#### Supplementary Saccade Performance Results

To complement our main analysis of eye movement data in the Test Phase (see Section 3.1.), we further explored whether oculomotor behavior within a given training condition was systematically modulated by the probe position. In analogy to our main analysis of discrimination performance data (see Section 3.2.), saccade latency data and saccade accuracy data of the Test Phase of each training condition were subjected to separate repeated measures ANOVAs with factors SOA (SOA-0 vs. SOA-1000) and probe position (Training Same: ST/trained vs. neutral; Training Relative: ST/non-trained vs. non-ST/trained vs. neutral; Training Fixed: ST/trained vs. ST/non-trained vs. non-ST/trained vs. neutral). By doing so, we were able, for each training condition, whether the appearance of the probe stimulus itself (rather than the mere expectation that the probe will appear at a particular position) interacted with saccade performance. In particular, this approach provided a means to scrutinize potential oculomotor interference effects related to the actual processing of the probe depending on its position (e.g., whether processing the probe at an attended position other than the saccade target has a detrimental effect on saccade performance). Ultimately, such interference effects may hint toward specific dual-task trade-offs potentially relevant regarding the interpretation of a decoupling between attention and saccade programming. Results of these analyses are summarized below and depicted in Fig. S2 and Fig. S3.

#### Saccade Latency

Regarding saccade latency data of *Training Same*, we observed a significant main effect of SOA, F(1, 10) = 54.92, p < .001,  $\eta_p^2 = 0.85$ , indicating slightly longer latencies in *SOA-0* than in *SOA-1000*. However, there was neither a significant main effect of probe position, F(1, 10) = 1.28, p = .284,  $\eta_p^2 = 0.11$ , nor a significant interaction between SOA and probe position, F(1, 10) = 0.78, p = .399,  $\eta_p^2 = 0.07$ .

The same pattern of results emerged for *Training Relative*. Saccade latency was significantly affected by SOA, F(1, 9) = 33.95, p < .001,  $\eta_p^2 = 0.79$ , with longer latencies in *SOA-0* than in *SOA-1000*. Again, there was neither a significant main effect of probe position, F(2, 18) = 0.88, p = .433,  $\eta_p^2 = 0.09$ , nor a significant interaction between SOA and probe position, F(2, 18) = 0.81, p = .460,  $\eta_p^2 = 0.08$ .

Results of *Training Fixed* slightly differed from the other two training conditions. Saccade latency was not only significantly modulated by SOA (longer latencies in *SOA-0* than in *SOA-1000* trials), F(1, 10) = 42.98, p < .001,  $\eta_p^2 = 0.81$ , but also by probe position, F(1.31, 13.06) = 8.36, p = .009,  $\eta_p^2 = 0.46$ . The interaction between SOA and probe position was not significant, F(3, 30) = 0.78, p = .515,  $\eta_p^2 = 0.07$ . Pairwise post-hoc comparisons conducted to examine the significant main effect of probe position only revealed a consistent trend toward significance for all comparisons involving the

*ST/trained* position (*ST/trained* vs. *ST/non-trained*: t(10) = -2.99, p = .082,  $d_z = -0.61$ ; *ST/trained* vs. *non-ST/trained*: t(10) = -3.11, p = .066,  $d_z = -0.64$ ; *ST/trained* vs. *neutral*: t(10) = -3.11, p = .066,  $d_z = -0.42$ ). As visible in Fig. S2, saccade latencies were slightly, albeit not significantly, shorter when the probe appeared at the *ST/trained* position compared to when it appeared at any other position. This may suggest that temporal aspects of saccade programming were most efficient when the probe was processed at a position that fell within the current expectancy-guided locus of attention and also represented the saccade target. Importantly, all other comparisons yielded non-significant results (*ST/non-trained* vs. *non-ST/trained*: t(10) = -0.39, p > .999,  $d_z = -0.03$ ; *ST/non-trained* vs. *neutral*: t(10) = 2.27, p = .278,  $d_z = 0.19$ ; *non-ST/trained* vs. *neutral*: t(10) = 2.21, p = .311,  $d_z = 0.22$ ). Accordingly, there is no evidence to suggest that the mere processing of the probe at an attended position diverging from the saccade target considerably delayed saccade execution.

Taken together, the saccade latency results observed in the different training conditions provide no consistent evidence for the idea that temporal aspects of oculomotor programming were differentially influenced to any considerable extent depending on the position at which the probe appeared.



**Fig. S2.** Saccade latency in Test Phase. Graphs depict mean saccade latency for each training condition as a function of probe position. (A) Mean saccade latency pooled across *SOA-0* and *SOA-1000* conditions. Note that none of the performed pairwise comparisons between probe positions yielded statistically significant effects. (B) Mean saccade latency plotted separately for *SOA-0* condition (upper panel) and *SOA-1000* condition (lower panel). Error bars represent standard error of the mean (SEM).

## Saccade Accuracy

Saccade accuracy data of *Training Same* yielded no significant main effect of SOA, F(1, 10) = 1.46, p = .255,  $\eta_p^2 = 0.13$ , no significant main effect of probe position, F(1, 10) = 2.32, p = .159,  $\eta_p^2 = 0.19$ , and no significant interaction between SOA and probe position, F(1, 10) = 3.66, p = .085,  $\eta_p^2 = 0.27$ .

Likewise, in *Training Relative*, there was no significant main effect of SOA, F(1, 9) = 0.70, p = .424,  $\eta_p^2 = 0.07$ , no significant main effect of probe position, F(2, 18) = 2.61, p = .101,  $\eta_p^2 = 0.23$ , and no significant interaction between SOA and probe position, F(2, 18) = 0.89, p = .430,  $\eta_p^2 = 0.09$ .

With respect to saccade accuracy in *Training Fixed*, we observed a significant main effect of SOA, F(1, 10) = 5.72, p = .038,  $\eta_p^2 = 0.36$ , implying slightly higher accuracy in *SOA-0* than in *SOA-1000* trials. The main effect of probe position only approached statistical significance, F(1.70, 16.98) = 3.50, p = .060,  $\eta_p^2 = 0.26$ . Exploratory post-hoc pairwise comparisons between probe positions, however, yielded no significant results (*p*-values for all comparisons  $\ge .257$ ). As for the other two training groups, there was no significant interaction between SOA and probe position, F(1.40, 14.04) = 0.41, p = .601,  $\eta_p^2 = 0.04$ .

Thus, in keeping with the saccade latency results, we found no reliable evidence for a general modulation of saccade accuracy by the probe position.



**Fig. S3.** Saccade accuracy in Test Phase. Graphs depict mean saccade landing error for each training condition as a function of probe position. (A) Mean saccade landing error pooled across *SOA-0* and *SOA-1000* conditions. Note that none of the performed pairwise comparisons between probe positions yielded statistically significant effects. (B) Mean saccade landing error plotted separately for *SOA-0* condition (upper panel) and *SOA-1000* condition (lower panel). Error bars represent standard error of the mean (SEM).

## Summary of Results

Altogether, the results of this supplementary eye movement data analysis do not indicate a critical influence of the probe position on oculomotor parameters in the Test Phase. Neither saccade latency nor saccade accuracy were found to reliably differ depending on the position at which the probe occurred on a given trial. Thus, it is very unlikely that differences in discrimination

performance between probe positions (reported in the main text) are linked to concomitant proberelated modulations at the level of oculomotor programming.

#### **Supplementary Discrimination Performance Results**

As mentioned in Section 3.3.2. in the main text, we aimed at validating the statistical results of our exploratory analysis of the *Training Relative* data, in which we examined only the most accurate among the fastest saccadic eye movements. Put differently, we wanted to ensure that the reported results of the exploratory analysis did not depend on the specific selection of trials. Therefore, we reran the analysis using two different approaches for trial selection.

The first approach was similar to the one described in the main text with the only difference being the order in which accuracy and latency selection criteria were applied. More specifically, for the current approach, we applied the accuracy criterion first and then the latency criterion. We first performed, separately for each SOA condition, a median-split on the saccade accuracy data of each participant and selected the trials with comparably accurate (i.e., above median accuracy) saccades. For each resulting dataset, we then calculated the median saccade latency and used it to select only those trials representing comparably fast (i.e., below median latency) saccades. Thus, the final datasets comprised only the fastest among the most accurate saccades (rather than the most accurate among the fastest saccades as examined in the analysis in the main text) of each SOA condition. These datasets were subjected to a repeated measures ANOVA with factors probe position and SOA, using discrimination performance as the dependent variable. Results of this analysis can be found below under *First additional exploratory analysis results*.

The second approach differed from the previous ones (i.e., the exploratory analysis in the main text and the first additional exploratory analysis described above) in that selection criteria were not applied sequentially. Rather, we jointly applied the accuracy criterion *and* the latency criterion to the full dataset in a single step. We performed, separately for each SOA condition, median-splits on both the saccade latency data and the saccade accuracy data of each participant and selected the trials with *both* comparably fast and comparably accurate saccades (i.e., trials falling below median latency and above median accuracy). Thus, the final datasets comprised only the fastest as well as most accurate saccades of all trials within each SOA condition. These datasets were subjected to a repeated measures ANOVA with factors probe position and SOA, using discrimination performance as the dependent variable. Results of this analysis can be found below under *Second additional exploratory analysis results*. Note, however, that this approach, while being the most conservative one regarding trial selection, yielded only a small number of trials in some experimental conditions for a few participants.

#### First additional exploratory analysis results

In the data subset included in this analysis, mean saccade latency was 377 ms (SD = 56 ms) in SOA-0 trials and 320 ms (SD = 53 ms) in SOA-1000 trials. Mean saccade accuracy was 0.7° ( $SD = 0.2^{\circ}$ )

in *SOA-0* trials and 0.7° (*SD* = 0.2°) in *SOA-1000* trials. Discrimination performance data are shown in Fig. S4. Results of the repeated measures ANOVA showed a significant main effect of probe position on discrimination performance, F(1.24, 11.15) = 21.14, p < .001,  $\eta_p^2 = 0.70$ . The main effect of SOA, F(1, 9) = 1.94, p = .197,  $\eta_p^2 = 0.18$ , and the interaction SOA by probe position, F(2, 18) = 0.35, p = .708,  $\eta_p^2 = 0.04$ , were not significant. Post-hoc pairwise comparisons revealed that discrimination performance across SOAs was significantly enhanced at the *non-ST/trained* position compared to the *ST/non-trained* position, t(9) = -3.74, p = .014,  $d_z = -1.93$ , and neutral positions, t(9) = 9.33, p < .001,  $d_z$ = 2.39. The difference in performance between the *ST/non-trained* position and neutral positions was not significant, t(9) = 1.31, p = .665,  $d_z = 0.46$ . Thus, in essence we found the same pattern of results as in our original main analysis of this training condition reported in the main text (cf. Fig. 3).



**Fig. S4.** Discrimination performance for subset of Test Phase trials representing the fastest among the most accurate saccades in *Training Relative* condition. Graphs depict mean discrimination performance as a function of probe position. (A) Mean discrimination performance pooled across trial subsets of both SOA conditions. Asterisks indicate statistical significance of pairwise comparisons between probe positions (\*  $p \le .05$ ; \*\*\*  $p \le .001$ ). (B) Mean discrimination performance plotted separately for *SOA-0* and *SOA-1000* condition trial subsets. Error bars represent standard error of the mean (SEM).

#### Second additional exploratory analysis results

In the data subset included in this analysis, mean saccade latency was 378 ms (*SD* = 54 ms) in *SOA-0* trials and 321 ms (*SD* = 54 ms) in *SOA-1000* trials. Mean saccade accuracy was 0.7° (*SD* = 0.2°) in *SOA-0* trials and 0.7° (*SD* = 0.2°) in *SOA-1000* trials. Discrimination performance data are shown in Fig. S5. Results of the repeated measures ANOVA showed a significant main effect of probe position on discrimination performance, *F*(2, 18) = 19.08, *p* < .001,  $\eta_p^2$  = 0.68. The main effect of SOA, *F*(1, 9) = 1.48, *p* = .255,  $\eta_p^2$  = 0.14, and the interaction SOA by probe position, *F*(2, 18) = 0.32, *p* = .732,  $\eta_p^2$  = 0.03, were not significant. Post-hoc pairwise comparisons revealed that discrimination performance across SOAs was significantly enhanced at the *non-ST/trained* position compared to the *ST/non-trained* position, *t*(9) = -3.68, *p* = .015, *d<sub>z</sub>* = -1.72, and neutral positions, *t*(9) = 9.01, *p* < .001, *d<sub>z</sub>* = 2.14.

The difference in performance between the *ST/non-trained* position and neutral positions was not significant, t(9) = 1.16, p = .826,  $d_z = 0.42$ . Again, the findings from this analysis confirm those from our original main analysis of the *Training Relative* condition reported in the main text (cf. Fig. 3).



**Fig. S5.** Discrimination performance for subset of Test Phase trials representing the fastest and most accurate saccades in *Training Relative* condition. Graphs depict mean discrimination performance as a function of probe position. (A) Mean discrimination performance pooled across trial subsets of both SOA conditions. Asterisks indicate statistical significance of pairwise comparisons between probe positions (\*  $p \le .05$ ; \*\*\*  $p \le .001$ ). (B) Mean discrimination performance plotted separately for *SOA-0* and *SOA-1000* condition trial subsets. Error bars represent standard error of the mean (SEM).

### Summary of findings

Overall, the three different approaches (i.e., the exploratory analysis in the main text and the two variants of this analysis reported here) to selecting trials with relatively uncompromised oculomotor performance yielded a very similar pattern of results for *Training Relative*. Namely, discrimination performance was best at the expected probe position. This provides a further indication that the attentional decoupling effect observed in *Training Relative* cannot be attributed to an impairment of saccade programming.

## 3 General discussion

Goal-directed movements are typically preceded by a spatially congruent shift of attention toward the target location of the motor action (premotor shift of attention). Motor-based theories of spatial attention have attributed this assumed mandatory attentional selection of future motor target locations to a strict link between spatial attention and motor programming. Whereas the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994) proposes that covert attentional selection represents an epiphenomenon of motor programming, the visual attention model (Schneider, 1995) assumes that the selection of future motor targets consitutes a precondition of motor programming. However, some previous studies have challenged the assumption of an obligatory attention-action coupling (see Chapter 1.2.1), raising the question of whether the selection of future motor targets could be mediated by a process unrelated to motor programming. In this dissertation, two studies were presented that both investigated whether the selection of the target of an upcoming goal-directed motor action can also be attributed to habitual top-down processes induced by an overlearned expectation that motor target locations contain visual information of high behavioral relevance (habitual attention-action coupling hypothesis). Specifically, we investigated whether a training-induced alteration of the presumed habitual expectation (i.e., a learned expectation of spatial incongruence between relevant visual information and motor target positions) enables a decoupling of attention from future motor targets. Indeed, such a decoupling effect would provide support for the habitual attention-action coupling hypothesis, but would be difficult to reconcile with the notion that attentional orienting is an integral feature of motor programming per se. In the following, the two experimental studies and their key findings are briefly summarized. Then, the central findings of the two studies are discussed in more detail as well as their implications for motor-based theories of spatial attention and our general understanding of covert attentional orienting.

## 3.1 Summary of studies

The first study of this dissertation (Chapter 2.1) was motivated by a previously reported decoupling effect (Dignath et al., 2019), highlighting that a learned anticipation of spatial incongruence between visual and motor targets enables a disengagement of attentional resources from the target of an upcoming manual pointing movement. However, this effect had only been demonstrated in a task that likely allowed to complete motor programming before attention was probed, thus rendering it difficult to draw conclusions about the relationship between attentional orienting and processes related to the programming of motor actions. In the first study, we therefore

aimed to replicate the decoupling effect reported by Dignath et al. (2019) and, more importantly, to examine, whether such an effect could also be observed during the more critical motor programming phase. For this purpose, we conducted two experiments in which we asked participants to perform a psychophysical dual-task consisting of a movement task and a concurrent attention task. In the movement task of Experiment 1, participants had to point toward cued target stimuli after a short (100 ms) or long (800 ms) movement delay (i.e., stimulus onset asynchrony between a movement cue and a movement go-signal). In the attention task, an attention probe was presented shortly (i.e., 50 ms) after the movement go-signal, so that - depending on the duration of the movement delay attention allocation was assessed at different time points (i.e., during or after assumed motor programming) prior to movement execution. In Experiment 2, the movement task involved only a short movement delay (100 ms) to focus on measurements of attention allocation during ongoing motor programming. In both experiments, participants performed a training phase and a subsequent test phase. The training phase aimed at eliciting different expectations regarding the spatial relationship of the attention probe and the pointing target. In Experiment 1, this was implemented by always presenting the probe either at the pointing target (Training Same), opposite the pointing target (Training Opposite), or at an unpredictable position (Control Same, Control Opposite). In Experiment 2, there was only a Training Opposite group and a Control group with unpredictable probe position. In the test phase of both experiments, the probe position was randomized to allow measurements of possible effects of training-induced expectations on attention allocation. The test phase was identical in both experiments, except that attention probes were presented for an individually adjusted presentation time (determined by an adaptive procedure in the training phase) in Experiment 1 and for a fixed presentation time (83 ms) in Experiment 2. Although results of Experiment 1 were of limited explanatory power (as the length of adjusted presentation times differed between training groups and likely confounded the results of the attention task), Experiment 2 provided strong evidence for a decoupling effect. While we observed a typical premotor shift of attention in the Control group, spatial attention allocation was markedly biased toward the expected, movement-irrelevant probe position in *Training Opposite*. This effect was observed at short movement delays, suggesting that a decoupling of attention from motor targets occurred during ongoing motor programming. The results of Experiment 2 thus complement the earlier findings of Dignath et al. (2019) by demonstrating that a learned expectation of spatial incongruence between visual and motor targets allows for a decoupling of the attention-action link even when motor programming is still in progress.

Although the first study demonstrated a decoupling effect in pointing movements, it is the oculomotor system that plays the central role in spatial attention research due to its complex intertwining with attentional orienting (see Chapter 1.1). The second study (Chapter 2.2) therefore

aimed to investigate whether our observations from the first study can be generalized to the more critical saccadic eye movements. To this end, we applied a similar experimental paradigm to that of the first study. Participants performed a dual-task consisting of a movement task and a concurrent attention task. In the movement task, participants had to saccade toward cued targets after a short (0 ms) or long (1000 ms) movement delay. In the attention task, attention allocation was assessed by presenting an attention probe shortly (i.e., 100-150 ms) after a movement go-signal. The attention probe was displayed with a fixed presentation time (83 ms). As in the first study, participants performed a training phase and a subsequent test phase. In the training phase, participants learned to expect the probe to always appear either at the saccade target (*Training Same*), at a specific position relative to the varying saccade target (i.e., either one, two, or three placeholder positions clockwise from the saccade target) (Training Relative), or at a spatially fixed, non-changing position (i.e., either at the upper right, bottom right, bottom left, or upper left placeholder position) (Training Fixed). In the test phase, we presented the probe at a randomized position to assess possible training effects on attention allocation. Overall, the second study yielded results similar to our study on pointing movements (first study). We found that spatial attentional allocation was substantially biased toward the anticipated position of the attention probe (Training Same, Training Relative, Training Fixed). Importantly, this effect was observed even in the trial conditions in which the anticipated probe position was different from the saccade target position (Training Relative, Training Fixed), indicating a decoupling of attentional resources from motor targets. Moreover, results were not influenced by the length of movement delays, suggesting that the observed decoupling effects were not dependent on the presumed completion of motor programming but also occurred during ongoing motor programming. The second study therefore complemented our results from the first study by showing that a decoupling effect can also be observed in saccadic eye movements.

## 3.2 Evidence for a habitual attention-action coupling hypothesis

The central objective of both the first and the second study was to test whether the attentional selection of future motor targets can be accounted for by a habitual attention-action coupling hypothesis, stating that the movement target location is selected due to a habitual top-down expectation of spatial congruence between that location and behaviorally relevant visual information (rather than being the consequence of a requisite linkage between covert attentional orienting and motor programming). If this hypothesis is correct, a learned anticipation of spatial incongruence between a task-relevant visual target and a motor target should allow attentional resources to be diverted from motor programming so that processing of the visual target can be prioritized.

Both studies provided evidence in favor of this prediction. For pointing movements (first study), we found a strict attention-action coupling in participants who had not been trained to expect the attention probe at a specific position (*Control* group, Experiment 2), as reflected in increased attentional performance at the pointing target compared to the remaining placeholder positions. This finding is consistent with previous observations of premotor attention shifts in manual movements (Deubel et al., 1998; Hanning et al., 2022; Jonikaitis & Deubel, 2011; Khan et al., 2011; Schiegg et al., 2003). In contrast, our results suggest that participants trained to anticipate spatial incongruence between positions (Training Opposite, Experiment 2) were able to allocate more attentional resources toward the anticipated probe position than toward the pointing target or neutral control positions, suggesting a pronounced decoupling of the attention-action link. Importantly, as opposed to previous studies of the attention-action link in pointing movements (Deubel & Schneider, 2003; Dignath et al., 2019), this decoupling effect was observed at short movement delays (i.e., delays of 100 ms), which indicates that expectancy-driven top-down modulations of attention allocation occurred during ongoing motor programming. Furthermore, we found no evidence to assume that the ability to direct attentional resources to a position deviating from the pointing target was associated with an impairment in motor performance (i.e., latency or duration of pointing movements). Thus, our data do not suggest that participants adopted a strategy to prioritize the attention task at the expense of the movement task (Kowler et al., 1995). Overall, we obtained similar findings in saccadic eye movements (second study). Specifically, we found that a learned anticipation of spatial congruence between positions (Training Same) led to a corresponding shift of attention toward the target of an upcoming saccadic eye movement, as indicated by enhanced attentional performance at this position compared to neutral control positions. In contrast, a learned anticipation of spatial incongruence between positions (Training Relative, Training Fixed) resulted in increased attentional performance at the expected probe position compared to neutral control positions. This attentional benefit was observed regardless of whether there was a spatial match (i.e., in the trial condition specific to *Training Fixed*, in which the varying saccade target occasionally coincided with the trained, spatially fixed probe position) or mismatch between the probe and the saccade target (i.e., in the trials of the two spatial incongruence conditions in which the probe appeared at the trained, movement-irrelevant probe position). Interestingly, in the case of a spatial mismatch between positions, results of both Training Relative and Training Fixed showed increased attentional performance at the expected probe position compared to the saccade target position. However, this performance difference was only statistically significant in the former training condition. The results of *Training Fixed* and *Training Relative* thus indicate that, depending on the type of learned expectation of spatial incongruence, attentional resources can be shifted toward a movement-irrelevant position to the same or even greater extent than toward the target of an
upcoming saccadic eye movement. Importantly, the observed decoupling effects were not influenced by the length of movement delays, implying that the presumed top-down modulations of attention allocation also occurred during ongoing motor programming (rather than being dependent on a completion of motor programming). In contrast to our findings in pointing movements (first study), we observed a small, but non-significant, reduction in motor performance (i.e., latency and accuracy of saccades) in one of the spatial incongruence conditions (*Training Relative*). However, an additional exploratory analysis revealed that the attentional benefit observed at the anticipated probe position was still present in subsets of trials with fairly uncompromised saccade performance (e.g., trials associated with the most accurate among the fastest saccades). This indicates that the observed decoupling effect in Training Relative was not due to a strategic prioritization of probe identification to the detriment of saccade performance. Taken together, the results of the two studies demonstrate that a learned expectation of spatial incongruence between visual and motor targets enables a decoupling of attentional resources from the target of both imminent manual pointing movements and imminent saccadic eye movements, in line with the prediction of the habitual attention-action coupling hypothesis. Furthermore, the capability of shifting attentional resources toward a movement-irrelevant location during ongoing motor programming contradict in particular the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994), according to which covert shifts of attention are solely attributable to neural processes related to the programming of goal-directed motor actions.

The findings discussed so far do not support the claim that covert spatial attention is a byproduct of motor programming activity (Rizzolatti et al., 1987; Rizzolatti et al., 1994), since we demonstrated that attentional resources can be substantially decoupled from future motor targets. However, this observation alone is not sufficient to draw conclusions about the validity of the assumption that attentional motor target selection constitutes a precondition for motor programming (Allport, 1987; Neumann, 1987; Schneider, 1995). In particular, it is conceivable that despite our observation of a pronounced training-induced attention decoupling effect, some attentional resources were still retained at the motor target as a prerequisite for programming the upcoming movement. In contrast, a finding of a complete withdrawal of attentional resources from the motor target would indicate that motor programming can indeed occur without attentional selection of motor targets. We therefore tested this assumption by examining performance differences between motor target positions and neutral control positions in the spatial incongruence conditions of both studies, as this allowed us to determine whether expectancy-driven top-down modulations of attention enabled such a complete decoupling of the attention-action link. In fact, we found no significant difference in attentional performance between motor target positions and neutral control positions in the two spatial incongruence conditions, in which the trained probe

position was defined relative to the motor target (*Training Opposite*, Experiment 2, first study; Training Relative, second study). In contrast, results of the spatial incongruence condition, in which the trained probe position was not defined relative to the motor target (*Training Fixed*, second study), revealed a small and significant performance benefit at motor targets (i.e., in the trial condition with a spatial mismatch between motor targets and expected probe position). This indicates that some attentional resources remained locked at this position in this training group. Training Fixed, however, was the only spatial incongruence condition in the two studies in which the varying motor target position occasionally matched the expected (spatially fixed) probe position. It is thus conceivable that the observed attentional benefit at motor targets resulted from the fact that this position was relevant not only for the movement task but also for the attention task in this particular training condition. Put differently, it is likely that the increased attentional performance at motor targets in Training Fixed was largely driven by the specific task condition rather than being the sole result of processes related to the programming of the upcoming saccadic eye movement. Nonetheless, a closer look at the data of the remaining spatial incongruence conditions, Training Opposite (Experiment 2, first study) and Training Relative (second study), indicates that attentional performance at motor target positions was also slightly, albeit not significantly, higher than at neutral control positions. It is therefore possible that these relative performance differences would have reached significance in larger samples. Further research is therefore needed to investigate whether and, if so, to what extent attentional resources are truly required for the programming of goaldirected movements. However, it should be noted that even if motor programming requires a minimum level of attention, this would not refute the habitual attention-action coupling hypothesis, as habitual top-down processes could still be the primary driver of future motor target selection. Notwithstanding this, the very fact that we observed relatively low attentional performance at motor targets in both pointing movements and saccadic eye movements suggests that, regardless of the type of goal-directed movement, motor programming is less reliant on spatial attention than commonly assumed.

To summarize, our results from two independent groups of participants (*Training Opposite*, Experiment 2, first study; *Training Relative*, second study) suggest that expectancy-driven top-down processes enable a decoupling of the greater part of attentional resources from the target location of an upcoming movement, irrespective of the effector system involved. Only in one spatial incongruence condition (*Training Fixed*, second study) we observed no difference in attentional enhancement between the task-relevant visual target and the motor target. It is however likely that the observed retention of attentional resources at motor targets in this training condition (*Training Fixed*) was largely caused by the specific task condition (i.e., by the relevance of the motor target position to the attention task). Furthermore, we found no evidence to assume that decoupling

attention from motor targets led to a deterioration of motor programming. Considering all of these aspects, our results therefore suggest that habitual top-down processes are a critical factor, if not the main cause, of the typically observed attentional selection of future motor targets.

#### 3.3 No evidence for a spatial reference hypothesis

As mentioned in the last chapter, we observed a small, albeit not significant, attentional benefit at motor targets in the spatial incongruence condition of the first study (Training Opposite, Experiment 2). In the first study, however, we elicited an expectation of spatial incongruence between positions solely by presenting the attention probe at a position defined relative to the motor target (i.e., similar to the previous study of Dignath et al., 2019). Thus, even if we had observed a significant attentional enhancement at pointing targets, there would have been at least two explanations for a possible retention of attentional resources at the motor target (i.e., attentional selection of the motor target). First, it could be interpreted as a precondition for motor programming (Allport, 1987; Neumann, 1987; Schneider, 1995). Second, it could be attributed to the fact that the motor target was needed as a landmark to localize the expected probe position (spatial reference hypothesis), which may have required attentional selection of the motor target before attention could be redirected toward the expected probe position. In other words, only the first interpretation implies that attentional facilitation at motor targets represents an effect driven by processes related to the programming of motor actions, whereas the second interpretation does not. In the second study, we aimed at disentangling these two interpretations. To this end, we introduced Training Fixed (in addition to Training Relative) as a second spatial incongruence condition, which allowed us to examine the spatial reference hypothesis by comparing test phase results of two different types of spatial incongruence conditions. In particular, if the spatial reference hypothesis is correct, one would expect that attentional resources remain partially locked at motor target positions in Training Relative (to enable probe position identification) but not in Training Fixed (in which the trained probe position did not vary with the motor target). However, as mentioned in the last chapter, we observed no reliable evidence that attentional resources remained partially locked at motor target positions in Training Relative. In contrast, we found a significant partial retention of attentional resources at motor targets in Training Fixed. This pattern of results is exactly the opposite of what the spatial reference hypothesis would predict. Furthermore, if the spatial reference hypothesis were true, one might also expect that less attentional resources could be decoupled from motor targets in spatial incongruence conditions in which the trained probe position is defined relative to the motor target than in spatial incongruence conditions in which it is not. We tested this assumption in the second study by comparing the extent of attentional decoupling from motor

targets (i.e., difference in attentional performance between the motor target and the expected probe position) between *Training Relative* and *Training Fixed* in the critical condition with short movement delays. However, no such difference was observed between the two groups. Thus, our data provide no indication that a possible retention of attentional resources at motor targets is related to a specific type of spatial relationship between a motor and a visual target when spatial incongruence between positions is expected.

### 3.4 Training is important to divert attention from motor targets

In contrast to our observations, the results of several previous psychophysical dual-task studies indicated that a substantial decoupling of attention from future motor targets is impossible (Deubel, 2008; Deubel & Schneider, 1996; Deubel et al., 1998; Hoffman & Subramaniam, 1995; Kowler et al., 1995; Schiegg et al., 2003). This suggests that sufficient training may be required to overcome the attention-action link (Dignath et al., 2019; Reeves & McLellan, 2020). Our findings in both studies support this assumption. In Experiment 1 of the first study, we found that individual adaptation of attention probe presentation times in the training phase resulted in differences between training groups in final threshold values (i.e., final probe presentation times determined by the used adaptive procedure). Although these between-group differences limited the explanatory power of our attention task results in the test phase (since final thresholds were applied in this phase and likely confounded results) of this experiment, they provided evidence for a differential difficulty in establishing a learned spatial congruence or incongruence between positions. In particular, the observed prolonged presentation times in Training Opposite compared to Training Same show that it was more difficult for participants to direct attention toward a movement-irrelevant position than toward the pointing target. This suggests that sufficient training may indeed be critical to enable a decoupling of the attention-action link. Consistent with this view, we found that participants in both spatial incongruence conditions of the second study (Training Relative and Training Fixed) improved over the training phase in attentional performance at the movement-irrelevant position at which they expected the attention probe. In addition to these training-related effects, however, attentional performance at this position was already relatively high at the beginning of the training phase of these two training conditions. This can presumably be attributed to the high predictability of the probe position, resulting from explicitly informing participants about the probe position and presenting the probe at this position with 100% validity (i.e., the probe appeared at the expected probe position in 100% of training phase trials). This suggests that the high predictability of the probe position may have contributed to the decoupling effects we observed in the subsequent test phase. Future studies could therefore seek to determine more precisely which specific factors or

combinations of factors facilitate a successful decoupling of spatial attention from motor targets. However, other dual-task studies with a similarly high predictability of the attention probe position (Deubel, 2008; Deubel & Schneider, 1996; Schiegg et al., 2003) did not report a substantial decoupling of attentional resources from motor targets. This indicates that training is indeed one of the key factors in overcoming the linkage between spatial attention and motor actions.

### 3.5 Top-down processes at least facilitate motor target selection

In both the first (Experiment 1) and the second study, we observed a strict attention-action coupling in *Training Same*, as indicated by enhanced attentional performance at motor target positions compared to the remaining, movement-irrelevant placeholder positions. Since participants of the Training Same condition had been trained to expect the attention probe at the motor target position, it is conceivable that an expectation of spatial congruence between positions at least facilitated attention shifts toward this position. Overall, our data support this assumption. In the first study (Experiment 1), we observed that adapted probe presentation times were shorter in *Training* Same than in Control Same, a control condition in which presentation times were adjusted analogously to Training Same (i.e., based on trials with a spatial match between probe and pointing target) and which only differed from *Training Same* in that participants were not trained to expect the probe at a specific position (i.e., the probe was presented at a random placeholder position). Given that incorrect responses led to an increase in presentation times in the training phase, this finding shows that attention was directed more frequently toward the pointing target in *Training* Same than in Control Same. However, assuming that spatial attention is solely related to motor programming (Rizzolatti et al., 1987; Rizzolatti et al., 1994), prior attention training (as in Training Same) should not lead to an advantage in presentation times as observed in our study. The shorter presentation times in Training Same therefore indicate that an expectation of spatial congruence indeed facilitate an attention-action coupling. It is however possible that participants in Control Same became aware of the randomized probe position and therefore attempted to direct attention to positions other than the pointing target, which would also explain the longer presentation times in this control group. Nevertheless, our second study provided more robust evidence for the assumption that an expectation of spatial congruence at least contributes to an attention-action coupling. Specifically, the test phase results of Training Fixed showed that attentional performance at the saccade target location was higher in trials with a spatial match between the expected probe position and the saccade target position than in trials with a spatial mismatch between those positions. This indicates the presence of an additive effect in attentional performance when the directionality of motor programming and expectancy-driven top-down modulation of attention

coincided. Since the saccade target in *Training Same* always corresponded to the expected probe position, it is likely that top-down processes similarly contributed to the observed high attentional performance at saccade targets in this condition. Put differently, the attentional benefit observed in this trial condition (i.e., in trials in which the expected probe position matched the saccade target) of Training Fixed and Training Same was likely caused by two different factors, a training-induced and expectancy-driven top-down factor and a factor presumably related to motor programming. However, assuming that the habitual attention-action coupling hypothesis is correct, it is also conceivable that the latter factor represents the effect of a long-term habitual expectation of spatial congruence between motor targets and relevant visual information (rather than being motorrelated). In this case, it would be the short-term training-induced top-down factor and the long-term habitual top-down factor that converged spatially and led to the observed additive attention effect. If true, this could also explain a possible retention of attentional resources at motor targets in spatial incongruence conditions (see Section 3.2), namely that short-term training-induced modulations of attention allocation were not sufficient to fully overcome a stubborn habitual expectation that motor targets contain important visual information (rather than a motor-related attention-action coupling). Overall, the data obtained in the second study therefore suggest that top-down modulations of spatial attention at least contribute to an attention-action coupling. Since the results of both studies provide no indication that the attention-action coupling differs depending on the type of goaldirected movement, this may also apply to manual movements.

# 3.6 Implications for attention models and our understanding of covert attentional orienting

The results of both the first and the second study of this dissertation demonstrate that attention can be largely decoupled from ongoing processes related to the programming of a motor action when participants are trained to anticipate spatial incongruence between a task-relevant visual target and a motor target. Since we observed this effect in both manual pointing movements and saccadic eye movements, our results further suggest that the capacity to decouple attention from future motor targets is not restricted to a specific effector system. Moreover, our results did not provide any evidence to assume that a disengagement of attentional resources from ongoing motor programming leads to a deterioration of subsequent movement performance, as could be expected if the decoupled attentional resources were required for programming the motor action. Our results are therefore difficult to reconcile with the idea that attentional selection of future motor targets is merely a product of a link between spatial attention and motor programming. In particular, our results contradict the claim of the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti

et al., 1994) that covert attentional orienting is nothing more than an epiphenomenon of motor programming, since this would predict that attention should always shift in congruence with the directionality of a motor program, rather than toward positions deviating from future motor targets. However, our data are also hard to explain by other motor-based theories of spatial attention, such as the visual attention model (Schneider, 1995). Specifically, the visual attention model posits that attentional selection of an object as a motor target leads to a strict coupling of the perceptual processing system to that object, so that perceptual performance should be best at this location compared to other locations in the visual scene (Schneider, 1995; Schneider & Deubel, 2002). In contrast to that prediction, our results however suggest that expectancy-driven top-down modulations of attention enable superior processing of locations other than the target location of an upcoming motor action. Nevertheless, this observation does not refute the assumption that planning a goal-directed movement requires at least some attentional processing capacity to extract movement-relevant information about the motor target (Allport, 1987; Neumann, 1987). In fact, we found some indications that despite our observation of a pronounced training-induced decoupling of attention from motor targets, few attentional resources were retained at this position, indicating that a minimum level of attention at motor targets may be required for motor programming (but see Chapter 3.5, for an alternative explanation). Much more important, however, is our finding that the possible dependence of motor programming on spatial attention is much smaller than generally assumed, challenging the assumption that the typical attention-action coupling is primarily caused by a strict link between attention and motor-related processes. Rather, our data provide strong evidence for the notion that the primary cause of attentional selection of motor targets are habitual top-down processes elicited by an overlearned expectation that the target location of a motor action contain highly relevant visual information. To accommodate this expectation, attention might be selectively coupled to this location (i.e., the motor target) by default, resulting in the typically observed phenomenon of a premotor shift of attention. However, we have shown that this default mode can be significantly modulated in an experimental setting, demonstrating that the attention system is not hard-wired to motor programming, but allows a high degree of flexibility in covert attentional orienting.

### 4 Conclusions

Taken together, the data of both studies presented in this dissertation provide evidence for the notion that expectancy-driven top-down processes play an integral role in the generation of the commonly observed premotor shift of attention toward motor targets. Our results suggest that a

learned anticipation of spatial incongruence between visual and motor targets enables a substantial decoupling of attentional resources from ongoing motor programming. They further indicate that this top-down modulation of attention allocation occurs regardless of the effector system involved, as decoupling effects were observed in both manual pointing movements and saccadic eye movements. This suggests that the typical coupling of covert spatial attention and goal-directed motor actions is not solely attributable to motor programming, but involves a hitherto widely neglected habitual component related to an expectation that motor target locations contain behaviorally relevant visual information.

## 5 References

- Allport, A. (1987). Selection for Action: Some Behavioral and Neurophysiological Considerations of Attention and Action In H. Heuer & A. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 395–419). Routledge. <u>https://doi.org/10.4324/978131562799</u>
- Attwell, D., & Laughlin, S. B. (2001). An Energy Budget for Signaling in the Grey Matter of the Brain. Journal of Cerebral Blood Flow & Metabolism, 21(10), 1133-1145. https://doi.org/10.1097/00004647-200110000-00001
- Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research*, 184(3), 411-425. <u>https://doi.org/10.1007/s00221-007-1114-x</u>
- Baldauf, D., & Deubel, H. (2009). Attentional Selection of Multiple Goal Positions Before Rapid Hand Movement Sequences: An Event-related Potential Study. *Journal of Cognitive Neuroscience*, 21(1), 18-29. <u>https://doi.org/10.1162/jocn.2008.21021</u>
- Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goaldirected hand movements. *Vision Research*, 46(26), 4355-4374. <u>https://doi.org/10.1016/j.visres.2006.08.021</u>
- Beauchamp, M. S., Petit, L., Ellmore, T. M., Ingeholm, J., & Haxby, J. V. (2001). A Parametric fMRI
  Study of Overt and Covert Shifts of Visuospatial Attention. *NeuroImage*, *14*(2), 310-321.
  <a href="https://doi.org/10.1006/nimg.2001.0788">https://doi.org/10.1006/nimg.2001.0788</a>
- Born, S., Ansorge, U., & Kerzel, D. (2013). Predictability of spatial and non-spatial target properties improves perception in the pre-saccadic interval. *Vision Research*, *91*, 93-101. <u>https://doi.org/10.1016/j.visres.2013.08.003</u>
- Born, S., Mottet, I., & Kerzel, D. (2014). Presaccadic perceptual facilitation effects depend on saccade execution: Evidence from the stop-signal paradigm. *Journal of Vision*, *14*(3), 1-10. <u>https://doi.org/10.1167/14.3.7</u>
- Cameron, E. L., Tai, J. C., & Carrasco, M. (2002). Covert attention affects the psychometric function of contrast sensitivity. *Vision Research*, 42(8), 949-967. <u>https://doi.org/10.1016/S0042-6989(02)00039-1</u>
- Carrasco, M. (2011). Visual attention: The past 25 years. *Vision Research*, *51*(13), 1484-1525. <u>https://doi.org/10.1016/j.visres.2011.04.012</u>
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., Petersen, S. E., Raichle, M. E., Van Essen, D. C., & Shulman, G. L. (1998). A Common Network of Functional Areas for Attention and Eye Movements. *Neuron*, *21*(4), 761-773. https://doi.org/10.1016/S0896-6273(00)80593-0

- Craighero, L., & Rizzolatti, G. (2005). The premotor theory of attention. In *Neurobiology of Attention* (pp. 181-186). Elsevier.
- de Haan, B., Morgan, P. S., & Rorden, C. (2008). Covert orienting of attention and overt eye movements activate identical brain regions. *Brain Research*, *1204*, 102-111. https://doi.org/10.1016/j.brainres.2008.01.105
- Deubel, H. (2008). The time course of presaccadic attention shifts. *Psychological Research*, 72(6), 630–640. <u>https://doi.org/10.1007/s00426-008-0165-3</u>
- Deubel, H., & Schneider, W. X. (1996). Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Research*, *36*(12), 1827-1837. <u>https://doi.org/10.1016/0042-6989(95)00294-4</u>
- Deubel, H., & Schneider, W. X. (2003). Delayed Saccades, but Not Delayed Manual Aiming Movements, Require Visual Attention Shifts. *Annals of the New York Academy of Sciences*, 1004(1), 289-296. <u>https://doi.org/10.1196/annals.1303.026</u>
- Deubel, H., Schneider, W. X., & Paprotta, I. (1998). Selective Dorsal and Ventral Processing: Evidence for a Common Attentional Mechanism in Reaching and Perception. *Visual Cognition*, 5(1-2), 81-107. <u>https://doi.org/10.1080/713756776</u>
- Dewey, J. (1896). The reflex arc concept in psychology. *Psychological Review*, *3*(4), 357-370. https://doi.org/10.1037/h0070405
- Dignath, D., Herbort, O., Pieczykolan, A., Huestegge, L., & Kiesel, A. (2019). Flexible coupling of covert spatial attention and motor planning based on learned spatial contingencies. *Psychological Research*, *83*(3), 476-484. <u>https://doi.org/10.1007/s00426-018-1134-0</u>
- Eimer, M., Van Velzen, J., Gherri, E., & Press, C. (2006). Manual response preparation and saccade programming are linked to attention shifts: ERP evidence for covert attentional orienting and spatially specific modulations of visual processing. *Brain Research*, *1105*(1), 7-19. <u>https://doi.org/10.1016/j.brainres.2005.10.060</u>
- Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision: The psychology of looking and seeing*. Oxford University Press. <u>https://doi.org/10.1093/acprof:oso/9780198524793.001.0001</u>
- Gabay, S., Henik, A., & Gradstein, L. (2010). Ocular motor ability and covert attention in patients with Duane Retraction Syndrome. *Neuropsychologia*, 48(10), 3102-3109.
   <a href="https://doi.org/10.1016/j.neuropsychologia.2010.06.022">https://doi.org/10.1016/j.neuropsychologia.2010.06.022</a>
- Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: An electrophysiological investigation of links between action and attention. *Neuropsychologia*, 48(4), 961-969. <u>https://doi.org/10.1016/j.neuropsychologia.2009.11.017</u>

- Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance*, 29(5), 882-896. <u>https://doi.org/10.1037/0096-1523.29.5.882</u>
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20-25. <u>https://doi.org/10.1016/0166-2236(92)90344-8</u>
- Gregoriou, Georgia G., Gotts, Stephen J., & Desimone, R. (2012). Cell-Type-Specific Synchronization of Neural Activity in FEF with V4 during Attention. *Neuron*, *73*(3), 581-594.
   <a href="https://doi.org/10.1016/j.neuron.2011.12.019">https://doi.org/10.1016/j.neuron.2011.12.019</a>
- Hanning, N. M., Szinte, M., & Deubel, H. (2019). Visual attention is not limited to the oculomotor range. *Proceedings of the National Academy of Sciences*, *116*(19), 9665-9670.
  <a href="https://doi.org/10.1073/pnas.1813465116">https://doi.org/10.1073/pnas.1813465116</a>
- Hanning, N. M., Wollenberg, L., Jonikaitis, D., & Deubel, H. (2022). Eye and hand movements disrupt attentional control. *PLOS ONE*, *17*(1), 1-17, Article e0262567.
  https://doi.org/10.1371/journal.pone.0262567
- Hoffman, J. E., & Subramaniam, B. (1995). The role of visual attention in saccadic eye movements. *Perception & Psychophysics*, 57(6), 787-795. <u>https://doi.org/10.3758/BF03206794</u>
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, 7(1), 56-64. https://doi.org/10.1038/nn1169

James, W. (1890). The Principles of Psychology. H. Holt.

- Jonikaitis, D., & Deubel, H. (2011). Independent Allocation of Attention to Eye and Hand Targets in Coordinated Eye-Hand Movements. *Psychological Science*, *22*(3), 339-347. https://doi.org/10.1177/0956797610397666
- Juan, C.-H., Muggleton, N. G., Tzeng, O. J. L., Hung, D. L., Cowey, A., & Walsh, V. (2008). Segregation of Visual Selection and Saccades in Human Frontal Eye Fields. *Cerebral Cortex*, 18(10), 2410-2415. <u>https://doi.org/10.1093/cercor/bhn001</u>
- Khan, A. Z., Song, J.-H., & McPeek, R. M. (2011). The eye dominates in guiding attention during simultaneous eye and hand movements. *Journal of Vision*, 11(1), 9-9. <u>https://doi.org/10.1167/11.1.9</u>
- Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. Vision Research, 35(13), 1897-1916. <u>https://doi.org/10.1016/0042-6989(94)00279-</u> <u>U</u>
- Lennie, P. (2003). The Cost of Cortical Computation. *Current Biology*, *13*(6), 493-497. <u>https://doi.org/10.1016/S0960-9822(03)00135-0</u>

Mack, A., & Rock, I. (2000). Inattentional Blindness. The MIT Press.

- Mishkin, M., Ungerleider, L. G., & Macko, K. A. (1983). Object vision and spatial vision: two cortical pathways. *Trends in Neurosciences*, *6*, 414-417. <u>https://doi.org/10.1016/0166-</u> 2236(83)90190-X
- Moehler, T., & Fiehler, K. (2014). Effects of spatial congruency on saccade and visual discrimination performance in a dual-task paradigm. *Vision Research*, *105*, 100-111. <u>https://doi.org/10.1016/j.visres.2014.10.001</u>
- Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision*, 7(14), 1-16. <u>https://doi.org/10.1167/7.14.8</u>
- Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences*, *98*(3), 1273-1276. <u>https://doi.org/10.1073/pnas.98.3.1273</u>
- Moore, T., & Fallah, M. (2004). Microstimulation of the Frontal Eye Field and Its Effects on Covert Spatial Attention. *Journal of Neurophysiology*, *91*(1), 152-162. <u>https://doi.org/10.1152/jn.00741.2002</u>
- Moore, T., & Zirnsak, M. (2017). Neural Mechanisms of Selective Visual Attention. *Annual Review of Psychology*, 68, 47-72. <u>https://doi.org/10.1146/annurev-psych-122414-033400</u>
- Müller, J. R., Philiastides, M. G., & Newsome, W. T. (2005). Microstimulation of the superior colliculus focuses attention without moving the eyes. *Proceedings of the National Academy of Sciences*, 102(3), 524-529. <u>https://doi.org/10.1073/pnas.0408311101</u>
- Neumann, O. (1987). Beyond Capacity: A Functional View of Attention. In H. Heuer & A. Sanders (Eds.), *Perspectives on Perception and Action* (pp. 361-394). Routledge. <u>https://doi.org/10.4324/978131562799</u>
- Nobre, A. C., Gitelman, D. R., Dias, E. C., & Mesulam, M. M. (2000). Covert Visual Spatial Orienting and Saccades: Overlapping Neural Systems. *NeuroImage*, *11*(3), 210-216. <u>https://doi.org/10.1006/nimg.2000.0539</u>
- Perry, R. J., & Zeki, S. (2000). The neurology of saccades and covert shifts in spatial attention: An event-related fMRI study. *Brain*, 123(11), 2273-2288. https://doi.org/10.1093/brain/123.11.2273
- Posner, M. I. (1980). Orienting of Attention. *Quarterly Journal of Experimental Psychology*, 32(1), 3-25. <u>https://doi.org/10.1080/00335558008248231</u>
- Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology: General*, *109*(2), 160-174. <u>https://doi.org/10.1037/0096-</u> <u>3445.109.2.160</u>

- Pratt, J., & Gozli, D. (2015). Action and Attention. In J. Fawcett, E. Risko, & A. Kingstone (Eds.), *The Handbook of Attention* (pp. 325-348). The MIT Press. https://doi.org/10.7551/mitpress/10033.003.0016
- Reeves, A., & McLellan, J. S. (2020). The 'anti-shift': Shifting attention opposite to a saccade. *Vision Research*, *167*, 31-38. <u>https://doi.org/10.1016/j.visres.2019.06.009</u>
- Rensink, R. A., O'Regan, J. K., & Clark, J. J. (1997). To See or not to See: The Need for Attention to Perceive Changes in Scenes. *Psychological Science*, *8*(5), 368-373. <u>https://doi.org/10.1111/j.1467-9280.1997.tb00427.x</u>
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: Evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1), 31-40. https://doi.org/10.1016/0028-3932(87)90041-8
- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. In C. Umiltà & M. Moscovitch (Eds.), *Attention and Performance XV: Conscious and Nonconscious Information Processing* (pp. 232-265). The MIT Press.
- Schiegg, A., Deubel, H., & Schneider, W. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition*, *10*(4), 409-431. <u>https://doi.org/10.1080/13506280244000140</u>
- Schneider, W. X. (1995). VAM: A neuro-cognitive model for visual attention control of segmentation, object recognition, and space-based motor action. *Visual Cognition*, 2(2-3), 331-376. <u>https://doi.org/10.1080/13506289508401737</u>
- Schneider, W. X., & Deubel, H. (2002). Selection-for-perception and selection-for-spatial-motoraction are coupled by visual attention: A review of recent findings and new evidence from stimulus-driven saccade control. In W. Prinz & B. Hommel (Eds.), *Attention and Performance XIX: Common Mechanisms in Perception and Action* (pp. 609-627). Oxford University Press.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye movements. *Experimental Brain Research*, *98*(3), 507-522. <u>https://doi.org/10.1007/BF00233988</u>
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous Orienting of Attention Depends upon the Ability to Execute Eye Movements. *Current Biology*, 14(9), 792-795. https://doi.org/10.1016/j.cub.2004.04.035
- Smith, D. T., Schenk, T., & Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. *Journal of Experimental Psychology: Human Perception* and Performance, 38(6), 1438–1447. <u>https://doi.org/10.1037/a0027794</u>
- Thompson, K. G., Biscoe, K. L., & Sato, T. R. (2005). Neuronal Basis of Covert Spatial Attention in the Frontal Eye Field. *The Journal of Neuroscience*, 25(41), 9479-9487. https://doi.org/10.1523/jneurosci.0741-05.2005

- Treue, S. (2001). Neural correlates of attention in primate visual cortex. *Trends in Neurosciences*, 24(5), 295-300. <u>https://doi.org/10.1016/S0166-2236(00)01814-2</u>
- Van der Stigchel, S., & de Vries, J. P. (2015). There is no attentional global effect: Attentional shifts are independent of the saccade endpoint. *Journal of Vision*, 15(15), 1-12. https://doi.org/10.1167/15.15.17
- Van der Stigchel, S., & Theeuwes, J. (2007). The relationship between covert and overt attention in endogenous cuing. *Perception & Psychophysics*, 69(5), 719-731. <u>https://doi.org/10.3758/BF03193774</u>

von Helmholtz, H. (1867). Handbuch der physiologischen Optik. Voss.

- Wollenberg, L., Deubel, H., & Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. *PLOS Biology*, *16*(6), 1-23, Article e2006548.
  <a href="https://doi.org/10.1371/journal.pbio.2006548">https://doi.org/10.1371/journal.pbio.2006548</a>
- Wollenberg, L., Deubel, H., & Szinte, M. (2019). Investigating the Deployment of Visual Attention
  Before Accurate and Averaging Saccades via Eye Tracking and Assessment of Visual
  Sensitivity. *JoVE*(145), 1-9, Article e59162. <u>https://doi.org/10.3791/59162</u>
- Wollenberg, L., Hanning, N. M., & Deubel, H. (2020). Visual attention and eye movement control during oculomotor competition. *Journal of Vision*, *20*(9), 1-17.
  <a href="https://doi.org/10.1167/jov.20.9.16">https://doi.org/10.1167/jov.20.9.16</a>
- Yeshurun, Y., & Carrasco, M. (1998). Attention improves or impairs visual performance by enhancing spatial resolution. *Nature*, *396*(6706), 72-75. <u>https://doi.org/10.1038/23936</u>