# Visual attention and working memory in action:

## How eye and hand movements shape what we perceive and remember

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# Summary

This doctoral thesis employed a psychophysical approach to investigate the relationship between goal-directed eye and hand movements, visual attention, and visual working memory.

To establish a solid methodological basis for investigating visual attention, the first study compared the strengths and weaknesses of a set of discrimination stimuli frequently used in attention research (**Chapter 2.1**). Based on the results, we used a novel pink noise stimulus for approaching the following research questions concerning visual attention.

In the second study, we investigated the dependence of attentional orienting on oculomotor programming (**Chapter 2.2**). Motivated by the claim that attention can only be allocated to locations reachable by saccadic eye movements, we measured visual sensitivity – a proxy for visual attention – within and beyond the oculomotor range using an eye abduction paradigm. Contrary to previous findings, we found that attention can be shifted without restriction to locations to which saccades cannot be executed, ruling out the necessity to program a saccadic eye movement as a prerequisite for spatial attention.

The third study attempted to resolve the longstanding debate as to whether eye and hand movement targets are selected by a single attentional mechanism or by independent, effector-specific systems (**Chapter 2.3**). Results revealed that during simultaneous eye and hand movements, attention – an index of motor target selection – was allocated in parallel to the saccade and the reach targets. Motor target selection mechanisms moreover did not compete for attentional resources at any time during movement preparation, demonstrating that separate, effector-specific mechanisms attentionally select eye and hand movement targets.

The fourth study tested the assumption of effector-specific selection mechanisms in the framework of visual working memory (**Chapter 2.4**). Participants memorized several locations and performed eye, hand, or simultaneous eye-hand movements during the maintenance interval. When participants performed an eye and a hand movement simultaneously to distinct locations, memory at both motor targets was enhanced with no tradeoff between the two. This suggests that the two effector systems improve working memory at their selected motor targets independently.

In the final study, we dissociated the relative contributions of the two highly interdependent parameters, task relevance and oculomotor selection, to the memory benefits consistently observed at eye movement targets (**Chapter 2.5**). Participants memorized shapes while simultaneously either avoiding or selecting a specific location as a delayed saccade target. While oculomotor selection was consistently associated with an increased working memory performance, mere task relevance was not, indicating that the frequently reported memory benefits for task-relevant items might, in fact, be caused by oculomotor selection.

In summary, goal-directed eye and hand movements selectively boost the visual processing of the currently most relevant information, and likewise bias our memory capacities according to behavioral priority. The observed motor-induced enhancements in both the attention and working memory domains appear to be independent and effector-specific, allowing for the most flexible assignment of our limited cognitive resources as we traverse through our crowded environment.

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# General Introduction

The following introduction provides an overview of the most significant findings and theories relating visual attention as well as visual working memory to goal-directed actions and to each other. Based on the respective theoretical background, this section explains the motivation for each of the five studies that constitute the present thesis and gives a summary of the overall objectives.

## 1.1 Visual attention

### 1.1.1 Attention: A key component of goal-directed behavior

Every time we open our eyes, we face an overwhelming amount of visual input, far more than we can simultaneously process. To ensure goal-directed and intelligent behavior, we must selectively filter the flood of information we are confronted with in order to extract the currently most relevant aspects.

The key to this process is termed *visual attention*. Much of what we know about this mechanism today, William James already brought to the point in his classic description: “Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others…” (James, 1890; pp. 381-382). Many years later, this definition still applies and the interest in the mechanisms of visual attention has been steadily growing, as reflected in the continuously increasing rate of publications (Carrasco, 2011).

Visual attention enables us to selectively focus on specific locations or features of a scene while ignoring irrelevant aspects of the available information (Treue, 2001; Carrasco, 2011). The outcome of this attentional selection is improved processing of the attended content, usually at the expense of the unattended. Compiled evidence relying on diverse methodologies – which range from single-unit recordings (Reynolds & Desimone, 1999; Reynolds, Pasternak, & Desimone, 2000; Treue, 2001; Martinez-Trujillo & Treue, 2002; Reynolds & Desimone, 2003) to event-related potentials (Hillyard & Anllo-Vento, 1998; Mangun, Buonocore, Girelli, & Jha, 1998) and neuroimaging (Brefczynski & De Yoe, 1999; Gandhi, Heeger, & Boynton, 1999; Saenz, Buracas, & Boynton, 2002) – shed light on the underlying neural substrate of this process. Attention biases the neuronal representation of the visual scene towards behavioral relevance: By regulating the neuronal activity throughout the visual cortex at various stages of processing, the same retinal input can elicit different neuronal responses depending on the attentional state of the observer. The influence of visual attention even extends to early visual areas, where attention modulates low-level feature perception. This impact on visual processing also transfers to behavior. Several perceptual studies report attentional effects on visual search (Nakayama & Mackeben, 1989; Carrasco & Yeshurun, 1998; Carrasco & McElree, 2001; Carrasco, Giordano, & McElree, 2004), spatial resolution (Mackeben & Nakayama, 1993; Yeshurun & Carrasco, 1998; Yeshurun & Carrasco, 2000; Carrasco, Williams, & Yeshurun, 2002), as well as contrast sensitivity (Lu & Dosher, 1998; Lee, Itti, Koch, & Braun, 1999; Carrasco, Penpeci-Talgar, & Eckstein, 2000; Cameron, Tai, & Carrasco, 2002) and appearance (Carrasco, Ling, & Read, 2004).

A popular approach to investigate the aforementioned effects at the behavioral level is to assess reaction times as an indicator of the spatial deployment of attention. It is well established that the covert deployment of attention (i.e., without overtly shifting gaze) towards a particular location increases detection times for stimuli appearing within the focus of attention, as compared to stimuli appearing at unattended locations (Posner, 1980; Posner, Snyder, & Davidson, 1980). The obtained reaction times, however, reflect the sum of the time for detecting the stimulus and the time taken to indicate the response (usually via button press), which makes this measure dependent on motor variance. A more direct indicator of attentional deployment can be assessed by measuring the sensitivity to discriminate visual features using a psychophysical approach. In a typical paradigm, a test stimulus is briefly presented among several distractors. Participants are either instructed to detect a specific target or feature (*detection task;* e.g., target present or absent) or discriminate its identity (*discrimination task;* e.g., tilt to the right vs. tilt to the left). Similar to the reaction time approach, numerous studies have shown that attending to a particular location results in a higher discrimination performance for items presented in the focus of attention compared to unattended items. In this context, a variety of discrimination stimuli, such as characters (e.g., Deubel & Schneider, 1996; Jonikaitis & Deubel, 2011), oriented Gabors (e.g., Gersch, Kowler, & Dosher, 2004; Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011; Rolfs & Carrasco, 2012; Klapetek, Jonikaitis, & Deubel, 2016; Wollenberg, Deubel, & Szinte, 2018) noise patches (Hanning, Aagten-Murphy, & Deubel, 2018), line offset (e.g., Born, Ansorge, & Kerzel, 2012), or patches of moving dots (e.g., Szinte, Carrasco, Cavanagh, & Rolfs, 2015) have been established.

The first aim of this thesis was to evaluate six of the most frequently used stimuli regarding temporal and spatial specificity, their dependence on the tested set-size, as well as their influence on saccade metrics in order to find the stimulus best suited to examine visual attention in the context of motor actions (see **Chapter 2.1**).

Although, as described above, attention can be deployed to peripheral locations in the absence of eye movements, there is compelling evidence that under normal circumstances, visual attention is frequently coupled with our own actions. The following chapters contain a review of the recent studies on how eye and hand movements affect the deployment of attention.

### 1.1.2 Models of attention-action coupling

When we inspect our environment, visual attention functions as a selection mechanism that allows us to specifically prioritize certain locations, objects, or other aspects of the scene. This selection process is usually achieved by the rapid succession of goal-directed eye movements, so-called saccades, performed to sample the most relevant information by bringing it into our fovea where we can process its characteristics with high precision. Interestingly, a broad body of literature has demonstrated that our visual sensitivity for the upcoming target is enhanced even before our eyes have landed on it since, already during saccade preparation, the focus of attention shifts towards the future fixation location (Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996; Deubel & Schneider, 2003; Montagnini & Castet, 2007; Deubel, 2008). This pre-saccadic attention shift is linked to the saccade target and locked to movement onset. Moreover, it has been argued that this coupling is mandatory, i.e., attention even shifts with the eye movement when participants try to voluntarily attend elsewhere (e.g., Deubel & Schneider, 1996; Deubel & Schneider, 2003). However, it is well established that besides such *overt* shifts (i.e., accompanied by an eye movement), attention can also be allocated *covertly* towards peripheral locations without moving the eyes (Posner, 1980; Posner et al., 1980). This raised the question of whether, and to what extent, *overt* and *covert attention* rely on the same cognitive processes.

A common mechanism for overt and covert attention has been proposed by the influential yet controversial ***premotor theory of attention*** (Rizzolatti, Riggio, Dascola, & Umiltá, 1987; Rizzolatti, Riggio, & Sheliga, 1994; Craighero, Fadiga, Rizzolatti, & Umiltà, 1999; see Smith & Schenk, 2012 for a review). The theory postulates that (1) both spatial attention and motor preparation are based on the same neuronal substrate, namely the oculomotor system, and that (2) any shift of spatial attention is contingent on preceding motor activation. In other words, the deployment of covert attention arises through the activation of an – ultimately canceled – saccade plan.

Indeed, neurophysiological evidence supports the first assumption that visual attention is generated by the oculomotor system: Activity in the same neural networks has been observed during tasks involving attentional orienting with and without eye movements (Corbetta et al., 1998; Nobre, Gitelman, Dias, & Mesulamet, 2000). These overlapping neuronal circuits include the parietal cortex, the frontal eye fields (FEF), and the superior colliculus (SC) – oculomotor structures that form the so-called *priority maps* (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Zelinsky & Bisley, 2015) that are supposed to guide the allocation of attention to salient or action-relevant locations. Feedback signals originating in these maps projecting back to early visual areas (e.g., V1 - V4) are assumed to enhance visual processing (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Zelinsky & Bisley, 2015; Rolfs & Szinte, 2016).

In line with this and the second claim of the premotor theory, stating that attention shifts arise through motor activation, neurophysiological evidence has demonstrated that sub-threshold micro-stimulation of the oculomotor areas FEF and SC (which, if stimulated above threshold, would lead to the execution of a saccade) improves visual performance at the movement field location of the stimulated neurons (Moore & Armstrong, 2003; Moore & Fallah, 2004; Müller, Philiastides, & Newsome, 2005), presumably due to the above described feedback activation.

Another line of evidence in support of the premotor theory is based on studies in which observers' ability to execute eye movements is restricted; patients who cannot perform eye movements also show attentional deficits, whether as a result of cortical (Heide & Kömpf, 1998) or subcortical lesions (Rafal, Posner, Friedman, Inhoff, & Bernstein, 1988), peripheral oculomotor palsy (Craighero, Carta, & Fadiga, 2001), or limited elasticity of the eye muscles (Smith, Rorden, & Jackson, 2004). This suggests that limitations at various oculomotor processing stages, even at the muscle level, may affect the feedback signals responsible for attentional enhancements.

Interestingly, similar oculomotor deficits can also be induced experimentally in healthy individuals. Studies using the eye abduction paradigm to limit the range of saccadic eye movements to one side of the visual field (by rotating participants' heads in the opposite direction) report impaired visual attention at locations unreachable by eye movements, i.e., outside the so-called *oculomotor range* (Smith, Ball, Ellison, & Schenk, 2010; Smith, Schenk, & Rorden, 2012; Boon, Theeuwes, &

Belopolsky, 2017). This is remarkable because it suggests that even a temporary inability to execute eye movements due to limitations by the eye muscle system may affect hard-wired feedback connections. These observations were interpreted as evidence for the central claim of the premotor theory of attention, namely that visual attention results from oculomotor programming.

Since none of the previous studies had used a saccade paradigm, nor measured visual sensitivity, the second aim of the present thesis was to disentangle attentional orienting and oculomotor programming by measuring visual sensitivity while participants attempt to saccade to locations that their eyes could not reach (see **Chapter 2.2**), in order to shed light on the dependence of attentional orienting on oculomotor programming.

Another model concerned with the interplay of action and attention is the neuro-cognitive ***visual attention model*** (VAM; Schneider, 1995). This model postulates two main functions of visual attention: *selection-for-object-recognition* (e.g., LaBerge & Brown, 1989) and *selection-for-action* (e.g., Allport, 1987). More specifically, the core functions of the attention mechanism are the selection of object information for goal-directed motor actions – computed within the dorsal, posterior parietal “where”-pathway – and the selection of information from the same object for visual object recognition – computed within the ventral, inferior temporal “what”-pathway. Once an object is attended, this object can be recognized and its spatial parameters computed for potential motor actions like eye or hand movements. In this sense, next to “where”-based information of the dorsal pathway, “what”-based information of the ventral pathway can also be used to guide attention. Crucially, and in direct contrast to the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Craighero et al., 1999), motor programming following VAM is a consequence of attentional allocation, and not its origin. The question though, according to VAM, is not how motor actions and attention are related, but rather whether there is a common attentional selection mechanism that serves both motor target selection and object recognition.

### 1.1.3 How hand movements mold visual attention

Eye movements have become a popular model for the study of goal-directed movements and the evidence for the link between saccades and visual attention is compelling. However, as every eye movement is necessarily accompanied by a change to the retinal input, saccades are inseparably linked to visual processing. The investigation of goal-oriented actions by means of hand movements, during which the input to the retina stays constant, is therefore of high ecological value.

Perceptual studies revealed similar effects of reach preparation on visual attention as those observed for saccade preparation, with highest sensitivity prior to reach onset at the reach target (Deubel, Schneider, & Paprotta, 1998; Deubel & Schneider, 2003; Baldauf, Wolf, & Deubel, 2006; Baldauf & Deubel, 2008; Baldauf & Deubel, 2009; Rolfs, Lawrence, & Carrasco, 2013). Despite these parallels when inferring attentional selection with behavioral measurements, the neurophysiological basis underlying pre-motor attention shifts to eye and hand movement targets seems to be, at least partly, effector-specific (see **Figure 1**). While the FEF and the lateral intraparietal area (LIP) of the intraparietal sulcus are involved in saccade preparation (Snyder, Batista, & Andersen, 1997; Bisley & Goldberg, 2003; Dickinson, Calton, & Snyder, 2003; Lawrence & Snyder, 2009), the parietal reach region (PRR) selectively encodes hand movement targets (Andersen, Essick, & Siegel, 1985; Johnson,

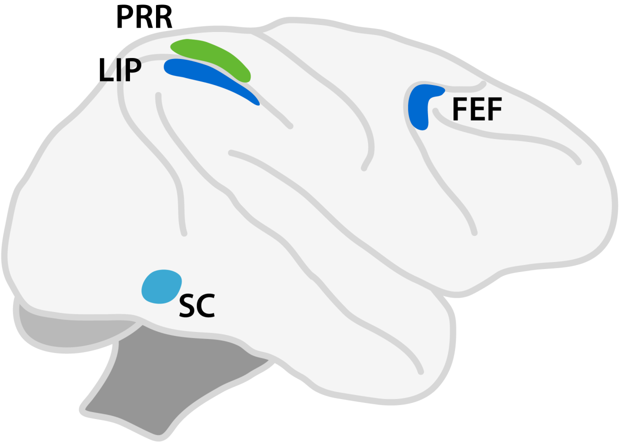

**Figure 1.** Eye and hand motor control networks. Lateral surface of a macaque brain showing some of the brain areas involved in eye and hand movement control. Areas include the frontal eye fields (FEF), as well as the lateral intraparietal area (LIP) and the parietal reach region (PRR), both located inside the intraparietal sulcus, and the superior colliculus (SC) in the midbrain.

Ferraina, Bianchi, & Caminiti, 1996; Snyder et al., 1997; Calton, Dickinson, & Snyder, 2002). At the subcortical level, however, the SC receives projections from oculomotor as well as from reach-related areas, and reportedly serves the selection of targets for both eye and hand movements regardless of the effector (Song, Rafal, & McPeek, 2011; Borra, Gerbella, Rozzi, Tonelli, & Luppino, 2012; Song & McPeek, 2015).

### 1.1.4 Effects of combined eye-hand movements on visual attention

While the perceptual consequences of eye and hand movements and their neurophysiological bases have been studied for each effector separately, little is known about their interaction. In everyday life, eye and hand movement control does not appear to be independent; when we interact with objects in our environment, the performed eye and hand movements are normally highly coupled, both spatially and temporally. In free-viewing tasks, our gaze tends to systematically shift to reach targets before the hand starts moving (Neggers & Bekkering, 2000; Land & Hayhoe, 2001; Horstmann & Hoffmann, 2005). This raised the question of whether eye and hand movements are attentionally selected in unison by one common mechanism, or rather individually by independent attention systems.

The idea that one shared attentional mechanism selects motor targets across different effector-systems has already been proposed by VAM (Schneider, 1995). Given the observed interplay between both motor systems, many behavioral studies measuring various motor parameters (such as movement precision, amplitudes, velocity profiles, movement trajectories, and latencies) have likewise favored the view that one shared system underlies the selection of eye and hand movement targets (Bekkering, Adam, van den Aarssen, Kingma, & Whiting, 1995; Song & McPeek, 2009; Huestegge & Adam, 2011; Khan, Song, & McPeek, 2011; Huestegge, Pieczykolan, & Koch, 2014; Nissens & Fiehler, 2017). However, such eye-hand synchronization typically observed in behavioral parameters could also emerge from mutual influences between the two effector systems at later, post-attentional processing stages. In support of this latter view, recent psychophysiological evidence indicates that eye and hand movements are selected by largely independent, effector-specific attentional mechanisms (Jonikaitis & Deubel, 2011).

Neurophysiology cannot resolve this ambiguity since there is evidence both for effector-specific areas, separately serving the control saccades (e.g., FEF and LIP;

Snyder et al., 1997; Bisley & Goldberg, 2003; Dickinson et al., 2003; Lawrence & Snyder, 2009) and reaches (e.g., PRR; Andersen et al., 1985; Johnson et al., 1996; Snyder et al., 1997; Calton et al., 2002), but also evidence for overlapping parietal and prefrontal cortical areas (Levy, Schluppeck, Heeger, & Glimcher, 2007; Beurze, De Lange, Toni, & Medendorp, 2009), as well as subcortical structures like SC (Song et al., 2011; Borra et al., 2012; Song & McPeek, 2015), which are argued to be responsible for effector-independent movement control.

The third aim of this thesis was to use a psychophysical approach to unravel this controversial issue of whether eye and hand targets are selected by a unitary or by independent attentional systems (see **Chapter 2.3**).

## 1.2 Visual working memory

To interact successfully with our environment, we not only need to be able to selectively attend to the most pertinent elements within the overwhelming flow of visual information, but also to monitor our own mental representations as they might have substantial behavioral relevance. While orienting towards external, perceptual events has been extensively investigated in the context of attention research, attentional orienting to internal memory representations has not been subjected to the same academic rigor. Overall, the two mechanisms – visual attention and visual working memory – seem to be tightly linked, as indicated by converging evidence based on a variety of research methods.

### 1.2.1 The link between visual working memory and attention

The assumption of a close coupling between visual attention and working memory intuitively seems plausible when considering how we perform everyday tasks. When preparing a cocktail, for example, we must shift our gaze and/or attention in quick succession to the appropriate ingredients to sample task-relevant information while simultaneously keeping track of what is where in the continually changing scene (Land & Hayhoe, 2001). During this flow of processing, we use our working memory to maintain access to information that is no longer available to the retina because of eye, head, and body movements (Franconeri, Alvarez, & Cavanagh, 2013).

In line with the behavioral evidence for such a linkage, visual attention and working memory have also been shown to rely on partially overlapping neuronal circuits extending through frontal and parietal brain regions (e.g., Awh et al., 1999; LaBar, Gitelman, Parrish, & Mesulam, 1999; Awh & Jonides, 2001), and there is evidence that both deploying attention to a particular location and holding this location in working memory similarly modulate the neuronal activity in early visual areas (Awh et al., 1999; Awh, Anllo-Vento, & Hillyard, 2000).

Psychophysical evidence in support of a tight coupling between visual attention and working memory was reported by Awh and colleagues (1998) who measured discrimination times for letter-like stimuli. They observed faster responses when the discrimination target appeared at a location already held in working memory compared to when it appeared elsewhere on the screen.

Closer examination concerning the interplay of attentional selection and memory revealed that the deployment of visual attention and working memory are not only spatially correlated but mutually influential as well. In one direction, working memory has been shown to bias visual attention towards items matching the information stored (Downing, 2000), and it has been argued that working memory content elicits a neuronal signal that biases attentional selection (Desimone & Duncan, 1995). In the opposite direction, attentional selection determines what is memorized and remembered. This influence of visual attention extends through several working memory phases (Awh & Jonides, 2001; Awh, Vogel, & Oh, 2006; Gazzaley & Nobre, 2012). Already at encoding, visual attention gates access to working memory, biasing which information gets stored (Averbach & Coriell, 1961; Treisman, 1998; Vogel, Woodman, & Luck, 2005). After the encoding phase, when the perceptual information has vanished, attention can still affect working memory performance: When a secondary task requires shifting attention away from the working memory content, overall memory performance is impaired (Smyth & Scholey, 1994).

This observation supports the hypothesis that information stored in visual working memory is rehearsed by selective shifts of attention to the memorized content (Smyth & Scholey, 1994; Awh et al., 1999). If this so-called *attention-based rehearsal* gets disrupted, for example when attention is attracted or voluntarily allocated elsewhere, memory performance suffers. Indeed, behavioral evidence demonstrated that deploying attention to certain mental representations (i.e., during the maintenance phase) selectively biases performance by improving memory for the retrospectively attended contents at the expense of the unattended material (Sperling, 1960; Sergent et al., 2013; Souza, Rerko, & Oberauer, 2014).

Given the aforementioned dependencies between visual attention and visual working memory, and considering the well established fact that goal-directed movements are associated with pre-motor shifts of attention to their movement targets (Kowler et al., 1995; Deubel & Schneider, 1996; Deubel et al., 1998; Deubel & Schneider, 2003; Baldauf et al., 2006; Montagnini & Castet, 2007; Deubel, 2008; Baldauf & Deubel, 2008; Baldauf & Deubel, 2009; Rolfs et al., 2013), it is not surprising that both eye movements, as well as hand movements, have been reported to interact with visual working memory.

### 1.2.2 Effects of motor actions on visual working memory

The modulatory effects of eye and hand movements on visual working memory largely reflect the previously reviewed effects caused by shifts of attention. In accordance with the observation that directing attention away from the stored content impairs memory performance (Smyth & Scholey, 1994; Lawrence, Myerson, & Abrams, 2004), several studies reported a disruptive effect of eye (Lawrence, Myerson, Oonk, & Abrams, 2001; Pearson & Sahraie, 2003; Lawrence et al., 2004; Postle, Idzikowski, Sala, Logie, & Baddeley, 2006; Schut, Van der Stoep, Postma, & Van der Stigchel, 2017) and hand movements (Lawrence et al., 2001) performed during the maintenance phase on spatial working memory performance. This was attributed to movement-associated attention shifts that interrupt the rehearsal process (Lawrence et al., 2001; Lawrence et al., 2004).

Besides these detrimental effects, other studies reported selectively enhanced visual working memory at both eye (Bays & Husain, 2008; Shao et al., 2010; Melcher & Piazza, 2011; Hanning, Jonikaitis, Deubel, & Szinte, 2016; Ohl & Rolfs, 2017; Hanning & Deubel, 2018) and hand (Heuer, Crawford, & Schubö, 2017; Hanning & Deubel, 2018) movement targets, resembling the working memory enhancements observed for covertly attended items (Sperling, 1960; Averbach & Coriell, 1961; Treisman, 1998; Vogel et al., 2005; Sergent et al., 2013; Souza et al., 2014). Consistent with the view of working memory as a limited resource distributed among the various elements of a scene (Bays & Husain, 2008; Bays, Catalao, & Husain, 2009; van den Berg, Shin, Chou, George, & Ma, 2012; Franconeri et al., 2013), this indicates that, rather than harming memory performance in general, goal-directed actions tend to bias memory priority according to behavioral relevance, preferentially enhancing memory performance at their motor targets at the expanse of action-irrelevant items.

Such prioritization of a subpart of the stored content over other elements is reminiscent of the perceptual enhancements induced by attentional selection, and it has indeed been argued that the working memory benefits observed at action goals arise from the shifts of attention associated with movement preparation (Hanning et al., 2016).

As motor-target specific memory enhancements have been reported for both eye and hand movements, the question arises of how simultaneous eye-hand movements (when directed to different locations) affect visual working memory. Given the assumption of effector-specific attentional mechanisms that drive attention to eye and hand targets independently (Jonikaitis & Deubel, 2011; Hanning et al., 2018), it is conceivable that the two effector systems also separately interact with working memory.

Thus, the fourth aim of the present thesis was to test this conjecture by investigating spatial working memory performance in the context of simultaneous eye-hand movements. If the two effector systems enhance memory performance independently of each other, the simultaneous use of two effectors could lead to higher overall working memory performance (see **Chapter 2.4**).

### 1.2.3 The interplay between memory, motor selection, and task relevance

Although it is well established that different kinds of goal-directed actions like eye movements (Lawrence et al., 2001; Pearson & Sahraie, 2003; Lawrence et al., 2004; Postle et al., 2006; Bays & Husain, 2008; Shao et al., 2010; Melcher & Piazza, 2011; Ohl & Rolfs, 2017; Schut et al., 2017; Hanning & Deubel, 2018), hand movements (Lawrence et al., 2001; Heuer et al., 2017; Hanning & Deubel, 2018), and grasping movements (Heuer & Schubö, 2017) affect visual working memory for various types of content like locations (Lawrence et al., 2001; Pearson & Sahraie, 2003; Lawrence et al., 2004; Postle et al., 2006; Bays & Husain, 2008; Hanning & Deubel, 2018), orientations (Bays & Husain, 2008; Shao et al., 2010; Melcher & Piazza, 2011; Heuer, et al., 2017; Ohl & Rolfs, 2017), color (Heuer & Schubö, 2017), and shape (Schut et al., 2017), the underlying mechanisms remain unclear.

Considering the tight pairing between goal-directed actions and visual attention, it seems plausible that the memory benefits at action goals are elicited by motor-associated shifts of attention. However, it has been demonstrated that increasing the *task relevance* of specific items – for example by informing participants which elements will be tested after the maintenance phase (Averbach & Coriell, 1961; Vogel et al., 2005) or by retrospectively directing attention towards a subset of the stored content (Sergent et al., 2013; Souza et al., 2014) – also leads to increased working memory of the relevant items.

The specific effects of task relevance and motor selection are challenging to dissociate. First, a location that, by experimental instruction, has to be selected as a motor target is also task-relevant by definition. Thus, the observed memory benefits at motor targets could result instead from the instructed requirement to prioritize a particular location over the others rather than being driven by motor selection. Moreover, it has been shown that the oculomotor system represents task-relevant locations during fixation (Clark, Noudoost, & Moore, 2012). This indicates that motor selection may play a role in working memory even in the absence of executed actions.

Since none of the previously reviewed studies could dissociate the different variables interacting with working memory, the final aim of this thesis was to investigate the relative contribution of task relevance and motor selection to the memory benefits observed at eye movement targets (see **Chapter 2.5**).

## 1.3 Aims of the present thesis

The present thesis comprises five experimental studies that aim at shedding light on how our goal-directed movements influence our perception and affect what we keep in working memory.

The first study (**Chapter 2.1**) was conducted to establish a solid methodological basis for the investigation of visual attention during motor actions. We performed a set of experiments in which we compared different sensitivity measures that are frequently used to investigate visuospatial attention. The study determined the most suitable stimulus for approaching the following research questions concerning visual attention.

We used this stimulus in the second study (**Chapter 2.2**) to investigate the dependence of attentional orienting on oculomotor programming. We disentangled the two parameters by measuring visual sensitivity within and beyond the oculomotor range to answer the question of whether visual attention can only be deployed to locations reachable by saccadic eye movements.

The third study (**Chapter 2.3**) attempted to resolve a longstanding debate as to whether eye and hand movement targets are selected by a single attentional mechanism or individually by independent, effector-specific systems. Since previous psychophysical studies addressing this question have come to opposite conclusions, this study furthermore sought to identify the reasons why these studies have produced divergent results.

The fourth study (**Chapter 2.4**) tested the assumption of separate, effector-specific selection mechanisms in the framework of visual working memory. Since the effects of eye and hand movements on working memory had exclusively been studied in isolation (i.e., separately for each effector), we investigated visual working memory with combined eye-hand movements to determine whether eye and hand movements enhance memory performance at their motor targets independently.

The aim of the last study (**Chapter 2.5**) was to dissociate different variables interacting with working memory in the context of motor actions. The particular objective was to specify the relative contributions of *task relevance* and *oculomotor selection* to the memory benefits consistently observed at eye movement targets. To this end, we developed a novel paradigm that allowed us to unravel these two interdependent parameters for the first time.

# Cumulative Thesis

The following section contains five original studies: One manuscript in preparation (**Chapter 2.1**), one manuscript submitted for publication (**Chapter 2.2**), and three peer-reviewed, published studies (**Chapter 2.3**, **2.4**, and **2.5**).

## 2.1 Sensitivity measures of visuospatial attention

The corresponding manuscript is in preparation.

**Author Contributions:**

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

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

Martin Szinte contributed to the study design, and participated in interpreting the results and writing the manuscript.

# Sensitivity measures of visuospatial attention

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## Abstract

Measuring visual sensitivity has become popular to determine the deployment of visuospatial attention. In this context, a variety of different stimuli and paradigms have been used. We evaluated the strengths and weaknesses of six commonly used stimuli. While preparing an eye movement towards an endogenously cued target, observers discriminated a stimulus-specific visual feature, either at the cued or other equidistant locations. Stimuli differed in their visual features (*Digital letters*, *Gabors*, *Crosses*, *Pink noise*, *Random Dot Kinematograms*, and *Gabor streams*) and their presentation mode (static or dynamic stimuli). Our paradigm allowed us to evaluate these stimuli regarding temporal and spatial specificity, as well as their dependence on the tested set-size, and their influence on saccade metrics. Irrespective of the stimulus type, we observed a clear increase of visual sensitivity at the cued location. Time course, spatial specificity, and magnitude of this improvement, however, were specific to each stimulus. Based on our findings, we present guidelines to help researchers select the stimulus best suited to their specific research question.

**Keywords:** Visuospatial attention, visual sensitivity, saccade

## Introduction

Our complex environment provides us with far more information than we can simultaneously process. To yet achieve goal-directed behavior, we must selectively filter the vast amount of information with which we are confronted, and extract the most relevant aspects at any given moment. Visual attention functions as a selection mechanism that allows us to specifically prioritize particular locations, objects or features of the scene while ignoring other aspects of the available information (Carrasco, 2011, Treue, 2001). By modulating the neuronal activity at various stages of visual processing, attention biases the neuronal representation of the visual scene, such that, depending on the attentional state of the observer, the same retinal input can elicit different neuronal responses (Hillyard & Anllo-Vento, 1998; Gandhi, Heeger, & Boynton, 1999; Reynolds, Pasternak, & Desimone, 2000; Martinez-Trujillo & Treue, 2002). The influence of attention on visual processing can also be assessed at the behavioral level. Perceptual studies report attentional effects on visual search (Nakayama, & Mackeben, 1989; Carrasco & McElree, 2001), spatial resolution (Yeshurun & Carrasco, 1998; Carrasco, Williams, & Yeshurun, 2002), as well as contrast sensitivity (Lee, Itti, Koch, & Braun, 1999) and appearance (Carrasco, Ling, & Read, 2004). Since it is well established that the covert deployment of attention (i.e., without shifting gaze) leads to faster detection times for items or features appearing within the focus of attention (Posner, 1980; Posner, Snyder, & Davidson, 1980), one can investigate the above-described effects behaviorally by measuring reaction times. A serious shortcoming of this approach, however, is that reaction times reflect both the time for detecting the stimulus plus the time taken to indicate the response (usually via button press), which makes this measure dependent on motor variance.

A more direct indicator of the deployment of attention, however, can be obtained by measuring the sensitivity to detect or discriminate visual features, using a psychophysical approach (Macmillan & Creelman, 1991). In a typical paradigm, a test stimulus is briefly presented amongst several distractors. Participants are either instructed to detect a specific target feature (*detection task:* e.g., target present or absent) or discriminate its identity (*discrimination task:* e.g., tilt to the right vs. tilt to the left). As attention enhances visual processing, a higher discrimination performance for a particular item reflects the allocation of attention towards it.

In this context, a variety of discrimination stimuli have been used, both under conditions in which participants had to keep their eyes steady (e.g. Pestilli & Carrasco, 2005; Ling & Carrasco, 2006; Liu, Abrams, & Carrasco, 2009; Störmer, McDonald, & Hillyard, 2009) but also in paradigms that combine the discrimination task with a movement task and present the discrimination signal for example during eye movement preparation. It is well established that motor actions, like saccadic eye movements, are preceded by a shift of attention towards the target (Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007). For this reason, it is of particular importance that the discrimination stimulus used does not interfere with saccade preparation, as this might influence what is to be measured – the shift of attention.

Using a dual-task paradigm that combines a discrimination task with a saccade task, we compared the strengths and weaknesses of six different discrimination stimuli commonly used to assess the deployment of visual spatial attention (Figure 1b). We evaluated these stimuli regarding their spatial and temporal specificity, set-size dependence, as well as their potential impact on eye movement parameters in order to provide guidelines for selecting the most suitable one for a specific research question.

## Methods

**Observers.** Ten observers (5 females, age 23-28, one author) completed the tasks. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München, in accordance with German regulations and the Declaration of Helsinki.

**Apparatus.** The dominant eye's gaze position was recorded using a SR Research EyeLink 1000 Desktop Mount eye tracker (Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The experiment was controlled by an Apple iMac Intel Core i5 computer (Cupertino, CA, USA) and the experimental software was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (Brainard 1997; Pelli 1997) and

EyeLink toolboxes (Cornelissen, Peters, & Palmer, 2002). Stimuli were presented at a viewing distance of 60 cm on a 21-in SONY GDM-F500R CRT screen (Tokyo, Japan) with a spatial resolution of 1,024 x 768 pixels and a vertical refresh rate of 120 Hz.

**Main task**. The study comprised six experimental conditions: *Digital letters*, *Gabors*, *Crosses*, *Pink noise*, *Random Dot Kinematograms*, or *Gabor streams.* The conditions differed only in stimulus characteristics (see *Stimuli*), experimental design and task were identical. Observers initially fixated a central fixation target, a black and white bull's eye (radius: 0.4 degrees of visual angle or dva) on a gray background (Figure 1a). Each trial started once we detected stable fixation within a virtual circle (radius: 2.0 dva) centered on the fixation target. Randomly within each experimental block, four (set-size 4: 1/3 of trials) or eight (set-size 8: 2/3 of trials) evenly spaced stimuli appeared at a distance of 8 dva from the fixation target (Figure 1b). Item size and visual features were specific to each stimulus condition (see *Stimuli*). Simultaneously, four or eight white direction lines (width: 0.1 dva, length: 0.4 dva) were displayed around the fixation target, pointing towards each of the stimuli. Between 400 and 800 ms after the trial onset and until the end of the trial, a black direction line appeared (cue), indicating the saccade target. Observers were instructed to move their eyes as fast and precisely as possible to the center of the item indicated by the cue. While all items initially were displayed as identical distractors, at a randomly selected time between 200 ms before and 200 ms after cue onset, for a stimulus-specific duration one of the items was replaced by a discrimination target while the others were replaced by distractor targets. Distractors, discrimination target and distractor targets were specific to each stimulus (see *Stimuli*). Importantly, the discrimination target was equally likely to appear at any position, irrespective of the cue. At the end of each trial, observers reported their discrimination judgment (specific to each stimulus) in a non-speeded manner via keyboard button press (right and left buttons or left, up, right an down buttons for 2 and 4 alternative forced-choice tasks, respectively). A negative feedback sound followed each incorrect response. To evaluate the influence of the discrimination target on different saccade metrics, in 6% of trials no discrimination signal was presented (unbeknownst to the observers). Furthermore, to investigate the effect of preparing a saccade, in another 6%

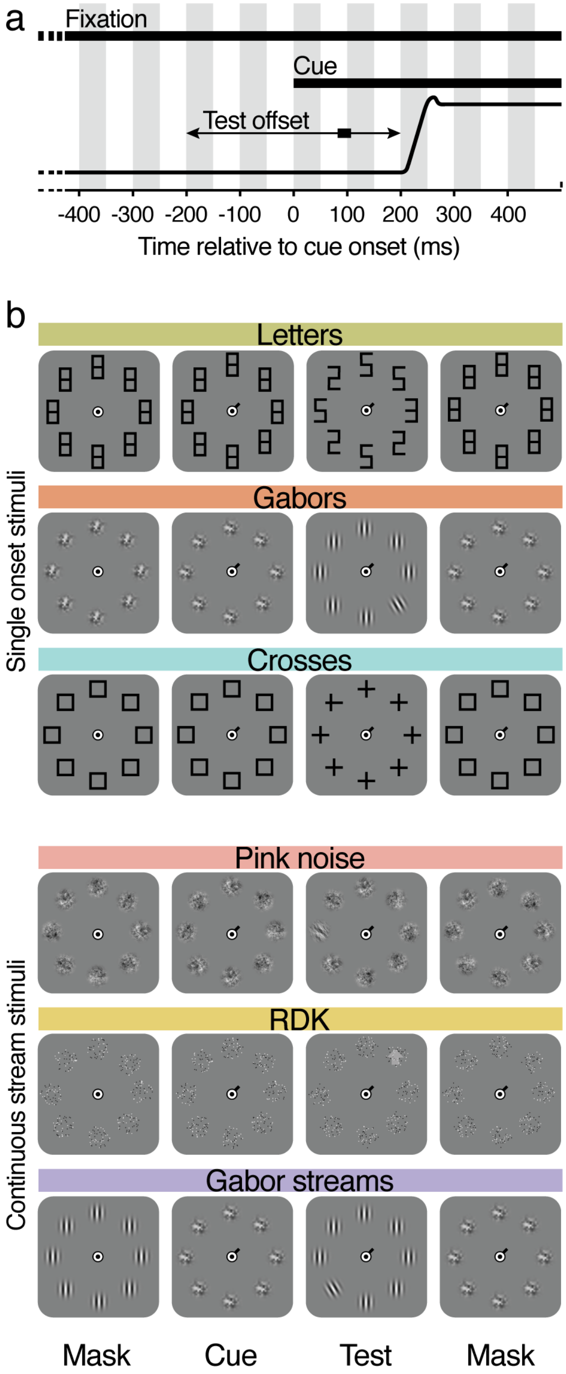

**Figure 1.** Experimental procedure. (a) Stimulus timing. The fixation target remained on the screen throughout the whole trial. 400 - 800 ms after trial start the saccade cue occurred. At different intervals relative to cue onset a discrimination target was shown. (b) Schematic depiction of the stimuli sequence of set-size 8. The first three rows depict static stimuli composed of *Digital letters*, *Gabors* or *Crosses*. The last three rows depict dynamic stimuli composed of *Pink noise*, *Random Dot Kinematograms* or *Gabor streams*.

of trials no direction cue was shown (no cue trials) and observers were instructed to maintain fixation over the whole duration of these trials.

Observers performed the stimulus conditions in randomly selected order in three to six experimental sessions on different days. They completed at least 1620 trials per stimulus. We monitored correct fixation and saccade execution online, and replaced incorrect trials at the end of each block. To maintain a consistent level of discrimination performance across observers and stimuli, the main task of each experimental condition was preceded by a threshold task.

**Threshold task**. The threshold task matched its respective main task with the exception that observers continuously maintained eye fixation and the discrimination target always occurred at the cued location. We used a procedure of constant stimuli and for each trial randomly selected the discrimination target strength out of 7 linear values specific to each stimulus (see *Stimuli* for details). Note that for the *Digital letter* stimulus we did not vary the discrimination target strength, as for this stimulus, probably due to a high level of letter discrimination automaticity, neither size nor the presentation duration (within some limits) affects discrimination performance (authors' discretion).

Observers completed at least 420 trials of the threshold task per stimulus. By fitting cumulative Gaussian functions, we determined the discrimination signal strength corresponding to 80% correct discrimination performance. Figure 2 shows the normalized stimulus strength (see *Stimuli*) obtained for each observer, separately for each stimulus and set-size.

Results within observers were significantly correlated for the two set-sizes of each stimulus (set-size 4 vs. 8, $0.007 > p > 0.001$). However, we found a considerable variability between observers, demonstrating the necessity of a threshold procedure. Note that we could not reliably estimate one participant's threshold for the *RDK* stimulus, as the range of stimulus strength did not match his visual capacity. This participant, therefore, did not take part in the *RDK* main task.

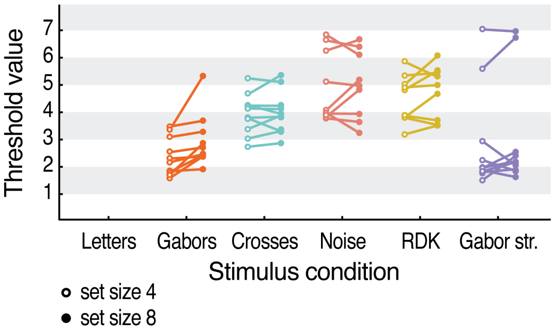

**Figure 2.** Threshold task. Colored dots represent individual observers normalized stimulus strength at threshold (80% correct discrimination) separately for each stimulus and split for set-size 4 (empty dots) and 8 (filled dots). *Digital letters* main task was not preceded by a threshold task.

**Stimuli**. The stimulus conditions differed both in the visual characteristics and in the presentation mode, which could be either static or dynamic (Figure 1b). Distractors of static stimuli (*Digital letters*, *Gabors*, and *Crosses)* only changed for a stimulus-specific duration into one static discrimination and several static distractor targets. In contrast, dynamic stimuli (*Pink noise*, *RDK*, and *Gabor streams*) continuously alternated or changed at a stimulus-specific refresh rate.

*Digital letters*. Stimuli adopted and modified from Deubel & Schneider (1996). Distractors consisted of static digital "8"s, which were replaced for a duration of 83 ms by randomly selected digital "2"s and "5"s (distractor targets) and one "E" or "Ǝ" (discrimination target). All characters had the same color (black), dimension (0.7 x 0.35 dva) and text width (0.15 dva). Observers reported whether the discrimination target was an "E" or a "Ǝ".

*Gabors*. Stimuli adopted and modified from Rolfs & Carrasco (2012). Distractors consisted of static noise patches, which were replaced for a duration of 25 ms by vertically oriented Gabor patches (distractor targets) and one tilted Gabor patch (discrimination target), rotated either clockwise or counter-clockwise relative to the vertical. Noise patches were composed of pixel noise (width ~0.22 dva), ranging randomly from black to white, windowed by a Gaussian envelope (standard deviation: 1.1 dva). All Gabor patches (frequency: 2.5 cpd; 100% contrast) had the same randomly selected phase and the same Gaussian window as the noise patches. Observers reported the orientation of the discrimination target (clockwise or counter-clockwise). The tilt angle was determined in the threshold task using seven linear steps between 1° and 25° (mean 80% discrimination threshold: 6.52 ± SEM 0.79 dva and 8.76 ± 1.11 dva, for set-size 4 and 8, respectively).

*Crosses*. Stimuli adopted and modified from Born, Ansorge, & Kerzel (2012). Distractors consisted of static squared frames, which were replaced for a duration of 100 ms by symmetric crosses (distractor targets) and one asymmetric cross (discrimination target), with the vertical bar crossing the horizontal bar to the left or right of its center. All frames and crosses had the same color (black), dimension (1.4 x 1.4 dva), and line width (0.2 dva). Observers reported the offset direction of the vertical bar of the discrimination target (left or right). The offset distance was determined in the threshold task using seven linear steps between 0.01 dva and 0.4 dva (mean 80% discrimination threshold: 0.20 ± 0.05 dva and 0.20 ± 0.05 dva, for set-size 4 and 8, respectively).

*Pink noise*. Stimuli adopted from Hanning, Aagten-Murphy, and Deubel (2018). Distractors consisted of dynamic pink noise streams, each composed of randomly generated 1/f noise patches flipping at 60 Hz. For a duration of 83 ms, the noise patches of one stream were orientation filtered, displaying a 40° clockwise or counterclockwise tilt relative to the vertical (discrimination target). The other noise streams remained unfiltered (distractor targets). Noise patches were created by Fourier transforming uniform white noise, convolving the filtered noise with its inverse radial frequency and transforming it back (inverse Fourier transformation). The patches were windowed by a symmetrical raised cosine (radius: 1.9 dva, sigma 0.5). Observers reported the orientation of the discrimination target (clockwise or counter-clockwise). The width of the orientation filter $\alpha$, i.e., the visibility of the orientation, was determined in the threshold task using seven linear $\alpha$-steps between 30 and 90 (mean 80% discrimination threshold: 69.40 ± 3.57 and 70.00 ± 3.40, for set-size 4 and 8, respectively).

*Random dot kinematograms (RDK)*. Stimuli adopted from Szinte, Carrasco, Cavanagh, & Rolfs (2015). Distractors consisted of dynamic patches of dots moving in random directions. For a duration of 100 ms, the dots of one patch showed a coherent motion direction (discrimination target), moving in one of four cardinal directions (right, 0°; up, 90°; left, 180°; or down, 270°). Dots of the other patches continued moving randomly (distractor targets). Each RDK patch was composed of half black and half white dots (radius: 10′), restricted within apertures of 2.5 dva radius. Dots moved at a constant speed of 5 dva per second (limited lifetime of 83 ms plus an exponentially distributed jitter with a mean of 67 ms). The motion direction of each dot was drawn from a circular normal distribution (von Mises) with a certain degree of concentration $K$ (inverse of the variance of a normal distribution) around one of the four cardinal directions. For distractors and distractor targets $K$ was 0 (uniform distribution across all directions), such that all dots moved randomly and incoherently in any direction. The discrimination target was created by increasing the degree of concentration $K$ of the dots in one randomly selected cardinal direction. Observers reported the coherent motion direction of the discrimination target (right, up, left or down). The coherence of the motion $K$, i.e., the strength of the motion signal, was determined in the threshold task using seven linear $K$-steps between 0.1 and 10 (mean 80% discrimination threshold: 5.89 ± 0.44 and 6.29 ± 0.47, for set-size 4 and 8, respectively).

*Gabor streams*. Stimuli adopted and modified from Rolfs, Jonikaitis, Deubel, & Cavanagh (2011). Distractors consisted of dynamic streams of vertically oriented Gabor patches and noise patches alternating at 40 Hz. For a duration of 25 ms, the Gabor patch of one stream was rotated either clockwise or counter-clockwise relative to the vertical (discrimination target), while the Gabor patches of the other streams remained vertical (distractor targets). To avoid apparent motion effects, the streams afterward continued with alternating noise patches and blanks. Noise and Gabors patches were identical to those of the static *Gabors*. Observers reported the orientation of the discrimination target (clockwise or counter-clockwise). The tilt angle was determined in the threshold task using seven linear steps between 1° and 25° (mean 80% discrimination threshold: 8.48 ± 2.07 dva and 9.16 ± 2.29 dva, for set-size 4 and 8, respectively).

**Data pre-processing**. We scanned the recorded eye-position data offline and detected saccades based on their velocity distribution (Engbert & Mergenthaler, 2006) using a moving average over twenty subsequent eye position samples. Saccade onset and offset were determined when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials if correct fixation was maintained within 2.0 dva from the fixation target until cue onset, if the saccade landed within 2.0 dva from the cued item center no later than 500 ms following cue onset (except no cue trials), and if no blink occurred during the trial. Finally, we excluded trials in which the saccade started before the presentation of the discrimination target had ended. In total, we included 78,805 trials in the analysis (89.6 % of the online selected trials, 76.43 % of all trials played; see Table 1 for details).

**Behavioral data analysis**. To determine the sensitivity to discriminate each stimulus' discrimination targets (d'): d' = z(hit rate) - z(false alarm rate), we took the percentage of correct discrimination performance as hit rate, and computed the false alarm rate by dividing the percentage of incorrect discrimination by the number of potential incorrect choices (1 in the 2 alternative forced-choice tasks, 3 in the 4 alternative forced-choice task). Observed correct performance of 100% and 0% was substituted by 99% and 1%, respectively. Performance below chance level (d' = 0 corresponding to 50% or 25% in the 2 or 4 alternative forced-choice tasks) were transformed to negative d' values.

For all statistical comparisons, we resampled our data and derived P-values by locating any observed difference on the permutation distribution (difference in means based on 1000 permutation resamples). To investigate the temporal dynamics of visual sensitivity, we binned trials as a function of discrimination target offset relative to cue onset in a 100 ms moving average (stepping every 20 ms) for target offsets of -200 to +200 ms around cue onset, separately for each set-size (Figure 3). To investigate the influence on saccade metrics, we likewise binned trials as a function of discrimination target offset relative to saccade onset (100 ms moving average stepping every 20 ms from discrimination target offset -400 to 0 ms before saccade onset, Figures 5).

## Results

On average, observers initiated their saccades 214.6 ± 4.1 ms after the onset of the cue. Saccade latencies did not differ between stimulus conditions, neither did saccade amplitudes (all $p > 0.05$, see Table 1 for details). In the following, we will compare the different stimulus conditions concerning the following criteria: Temporal specificity, attentional pop-out, set-size dependence, spatial specificity, and impact on saccade parameters.

**Temporal specificity**. We first analyzed the time course of visual sensitivity measured with the different stimuli. As saccades are preceded by shifts of attention to their target location (Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007), discrimination performance should increase at the cued target (CT) compared to uncued locations once saccade preparation is initiated, i.e., after cue onset. Figure 3a shows, separately for each stimulus and set-size, the averaged sensitivity (d') observed at cued and uncued locations as a function of discrimination target (DT) offset, covering a period of 400 ms around cue onset.

Irrespective of stimulus condition and set-size, we observed an improvement of visual sensitivity at the CT, with performance increasing after cue onset while remaining close to chance level at the uncued locations. To quantify the rising benefit at the CT, we compared the sensitivity at the CT with the sensitivity of trials in which no cue occurred, and attention should be equally distributed across all items. For each stimulus and set-size, we computed an *attentional latency*, which corresponds to the first time at which sensitivity at the CT was significantly ($p < 0.05$) superior to the average sensitivity at the uncued locations. While for most stimuli and set-sizes the first significant benefit at the CT occurred 50 - 150

| | *Digital letters* | *Gabors* | *Crosses* | *Pink noise* | *RDK* | *Gabor str.* |
|---|---|---|---|---|---|---|
| Trials included * | 13,547 | 13,643 | 13,421 | 12,250 | 12,838 | 13,106 |
| Saccade latencies | 214.3 ± 3.9 ms** | 214.4 ± 4.1 ms | 213.7 ± 4.4 ms | 215.5 ± 4.0 ms | 213.7 ± 4.2 ms | 216.2 ± 4.4 ms |
| Saccade amplitude | 8.10 ± 0.10° | 8.10 ± 0.10° | 8.09 ± 0.09° | 8.11 ± 0.10° | 8.09 ± 0.09° | 8.11 ± 0.10° |

**Table 1.** Saccade errors, latencies, and amplitude for the different stimulus conditions. * Sum over participants. ** SEM.

ms after cue onset (*Gabors*: 50 / 110 ms (set-size 4 / set-size 8), *Crosses*: 110 / 150 ms, *RDK*: 150 / 50 ms, *Gabor streams*: 110 / 110 ms), for the *Digital letters* and for the *Noise* (set-size 4 only) the CT benefit was present already before the onset of the cue (*Digital letters*: -30 / -50 ms, *Noise*: -10 / 90 ms).

Such a pre-cue benefit could indicate that the DT was not sufficiently masked so that the processing resources allocated towards the CT could retroactively reactivate the already vanished discrimination signal (Sergent et al., 2013).

**Attentional pop-out**. To adequately capture the distribution of visual attention, the DT should only be discriminable above chance level if attention is allocated towards it, i.e., it should not 'pop-out'. To estimate each stimulus' vulnerability to pop-out effects, we compared the average visual sensitivity in the trials without cue presentation (Figure 3b). As in these trials no particular item was cued and thus no attention modulation should have taken place, an increase in sensitivity can be considered an indicator of attentional pop-out.

Amongst most stimuli, the sensitivity to discriminate the target without cue was comparable and very low (*Letters*: 0.24 / 0.02 (set-size 4 / set-size 8), *Gabors*: 0.31 / 0.32, *Crosses*: 0.04 / 0.11, *Pink noise*: 0.22 / 0.24, *Gabor streams*: 0.02 / 0.12). For the *RDK* stimulus, however, we observed a notably high sensitivity especially for the small set-size (*RDK*: 0.63 / 0.27), which indicates that motion signals can be discriminated without selectively focussed attention if too few patches are used.

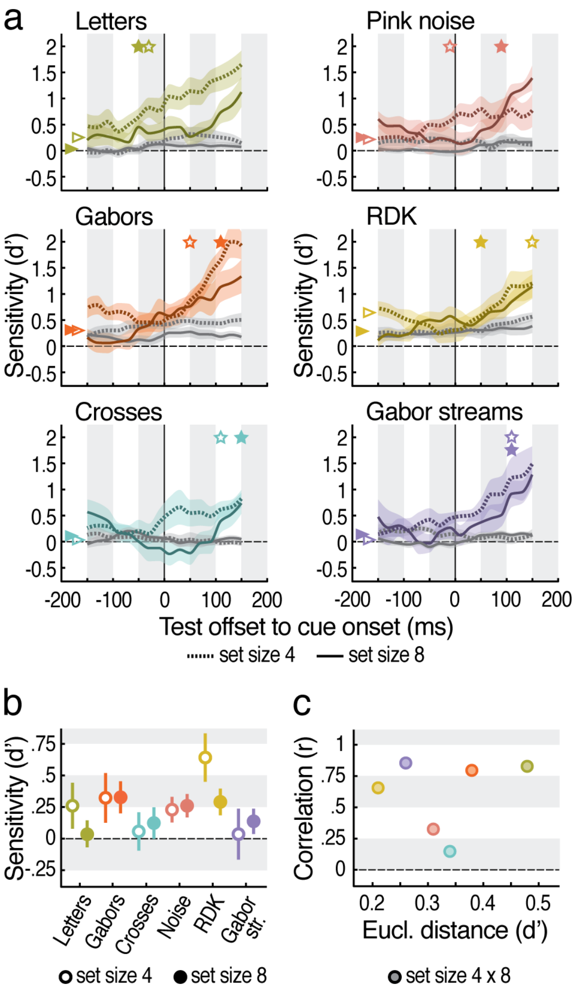

**Figure 3.** Temporal specificity, attentional pop-out, and set-size dependence. **(a)** Visual sensitivity as a function of test-offset to cue-onset delay at the CT (colored) and uncued locations (gray) for set-size 4 (dashed lines) and 8 (solid lines). Black horizontal dashed lines mark chance performance. Stars indicate the first time at which CT sensitivity is superior to the average sensitivity in the no-cue trials for set-size 4 (framed) and 8 (filled). $p < 0.05$. Colored/gray areas indicate the SEM. **(b)** Average sensitivity in the no-cue trials for each condition and set-size. Error bars indicate the SEM. **(c)** Set-size dependence. Correlation coefficients (y-axis) between each condition's set-size 4 and set-size 8 time courses of visual sensitivity at the CT (shown in (a)) plotted as a function of the respective average Euclidean distance of the two time curves (x-axis). Higher correlation coefficients and smaller distances indicate smaller set-size dependence.

**Set-size dependence**. To further investigate the stimuli's dependence on the number of distractors, we analyzed the deployment of attention towards the CT depending on the set-size used. For each stimulus, we computed the correlation between the attentional time courses (sensitivity at the CT relative to cue onset, Figure 3a) of the two set-sizes, as well as the average distance of these two curves. The less a stimulus depends on the set-size used, the greater the correlation and the smaller the distance between the time curves of the set-sizes should be. Figure 3c shows each condition's correlation coefficients as a function of the average distance. While the time course data of the different set-sizes for the *Gabor streams*, *Gabors* and *Digital letters* ($p < 0.01$), as well as for the *RDK* ($p < 0.05$) showed a significantly correlated trend, only the *Gabor streams* and the *RDK* furthermore showed an overall similar magnitude in sensitivity, reflected by the Euclidean distance (*Letters*: 0.48 / 0.83 (Euclidean distance *d'* / correlation coefficient *r* ), *Gabors*: 0.38 / 0.80, *Crosses*: 0.34 / 0.15, *Pink noise*: 0.31 / 0.33, *RDK*: 0.21 / 0.66, *Gabor streams*: 0.26 / 0.86). Thus, considering both criteria, the *Gabor streams* and the *RDK* depend least on the number of items on the screen, while the *Crosses* and *Digital letters* showed the most pronounced set-size effects.

**Spatial specificity.** Next, we analyzed the spatial distribution of visual attention. We included only trials in which the DT presentation ended within the last 150 ms before saccade onset, as we expected the most pronounced benefit at the saccade target within this time window. Radial plots in Figure 4a show the visual sensitivity at each of the 4 or 8 locations, relative to the CT (data rotated to always represent the cue directed to the right). A higher eccentricity from the plot center indicates a higher visual sensitivity (d'). For all stimuli and set-sizes we observed the highest sensitivity at the CT (0°). To statistically evaluate the benefit at the CT, we compared the visual sensitivity as a function of distance from CT (Figure 4b). Irrespective of the stimulus condition, the sensitivity at the CT was significantly superior already to the most adjacent locations only 45° away ($p < 0.05$). To quantify the spatial specificity of each stimulus, we calculated the attentional benefit at the CT over the nearby locations, i.e., the sensitivity at 0° minus the sensitivity at the locations ± 45° for set-size 8 of each stimulus (Figure 4c). The highest spatial specificity we observed for the *Digital letters* (0.89 ± 0.23) and the *Pink noise* (0.91 ± 0.16), followed by the *Gabors* (0.75 ± 0.25), the *RDK* (0.65 ± 0.17) and the *Gabor streams* (0.57 ± 0.20), while the *Crosses* (0.45 ± 0.23) showed the least attentional benefit.

**Impact on saccade parameters**. Lastly, we investigated the impact of each stimulus' DT presentation on saccade parameter, in particular, saccade latency and amplitude. This analysis aims to determine the potential influence of the DT on saccade preparation. Such influence would indicate that the stimulus used to measure attention affect its deployment. As neither saccade latencies nor amplitudes differed as a function of the DT location (at the CT or elsewhere), we conducted the following analyses independently of this factor. We defined pre- and post-cue periods by sorting trials as a function of DT offset relative to the cue onset.

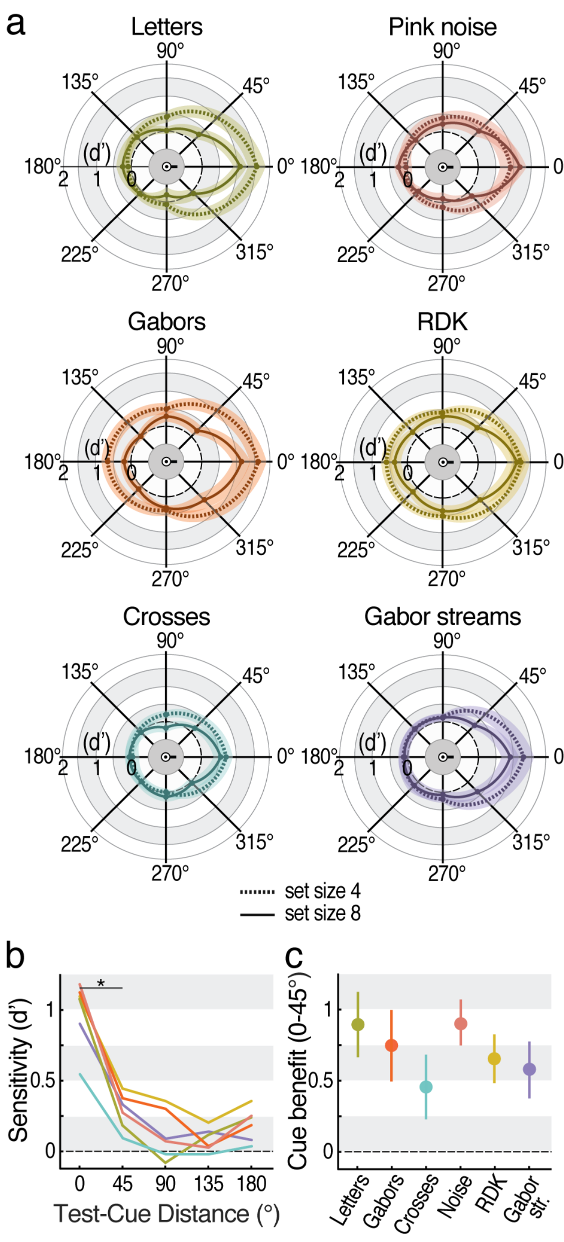

**Figure 4.** Spatial specificity in the last 150 ms before saccade onset. (**a**) Averaged visual sensitivity (d') for each stimulus (set-size 4 dashed, set-size 8 solid lines) as a function of test position relative to the CT. (**b**) Averaged sensitivity (d') for set-size 8 as a function of DT to CT distance (irrespective of direction). Colored/gray areas indicate the SEM. The horizontal dashed line marks chance performance. Color conventions as in (a). The asterisk shows a significant difference between the CT and the adjacent location (+/-45°) for all stimuli. *$p < 0.05$. (**c**) Attentional benefit of the CT over the adjacent location (0° - 45°) for set-size 8 of each stimulus. Error bars indicate the SEM. The horizontal dashed line marks no CT benefit.

Saccade latencies did not differ between pre- and post-cue trials for the *Pink noise* (pre-cue: 210.6 ± 5.8 ms vs. post-cue: 211.0 ± 5.5 ms, $p > 0.05$), and the *RDK* (pre-cue: 219.1 ± 4.5 ms vs. post-cue: 218.8 ± 4.9 ms, $p > 0.05$), indicating that the DT onset did not influence saccade latencies. *Gabor streams* showed marginally smaller latencies when the DT occurred in the post-cue period, i.e., just preceding saccade onset (Figure 5a, pre-cue: 208.9 ± 3.3 ms vs. post-cue: 205.5 ±

3.4 ms, $p < 0.001$). In contrast to the dynamic stimuli, the sudden onset of the static stimuli's DT consistently affected saccade preparation by slowing down saccade execution: We observed significantly prolonged latencies when the DT occurred after cue onset, i.e., during saccade preparation for *Gabors* (pre-cue: 211.0 ± 4.6 ms vs. post-cue: 220.9 ± 4.9 ms, $p < 0.001$) and *Crosses* (pre-cue: 212.1 ± 4.9 ms vs. post-cue: 223.0 ± 3.2 ms, $p < 0.007$). For the *Digital letters*, we observed the same trend, which, however, did not reach significance (pre-cue: 213.3 ± 5.7 ms vs. post-cue: 219.1 ± 4.9 ms, $p = 0.086$).

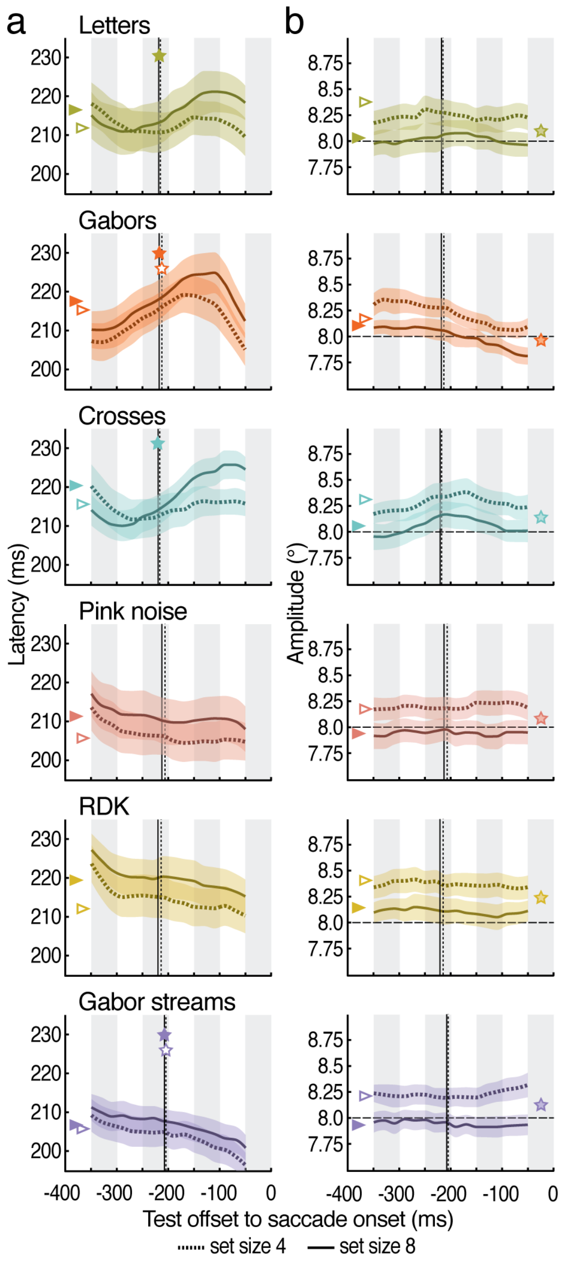

**Figure 5.** Impact on saccade parameters. Average saccade latencies (**a**) and amplitudes (**b**) for each stimulus as a function of DT offset to saccade onset, binned in 20 time windows for set-size 4 (dashed lines) and 8 (solid lines). Colored areas indicate the SEM. Vertical lines denote the mean cue onset. Horizontal dashed lines in (b) mark the actual saccade target amplitude. Triangles indicate average latencies and amplitudes in trials in which no test occurred. Stars show significant differences between the average latency in trials with DT offset pre-cue and DT offset post-cue onset (in a) or significant set-size differences (in b). $^{***}p < 0.05$. Framed symbols refer to set-size 4, filled symbols refer to set-size 8.

Moreover, for all stimuli we observed smaller saccade amplitudes (Figure 5b) when four compared to eight items were presented: *Digital letters* (set-size 4: 8.25 ± 0.12 dva vs. set-size 8: 8.01 ± 0.12 dva, $p < 0.001$), *Gabors* (set-size 4: 8.22 ± 0.09 dva vs. set-size 8: 8.01 ± 0.08 dva, $p < 0.001$), *Crosses* (set-size 4: 8.29 ± 0.11 dva vs. set-size 8: 8.05 ± 0.11 dva, $p < 0.001$), *Pink noise* (set-size 4: 8.20 ± 0.11 dva vs. set-size 8: 7.95 ± 0.11 dva, $p < 0.001$), *RDK* (set-size 4: 8.37 ± 0.11 dva vs. set-size 8: 8.12 ± 0.11 dva, $p < 0.001$), and *Gabor streams* (set-size 4: 8.22 ± 0.09 dva vs. set-size 8: 7.96 ± 0.09 dva, $p < 0.001$). However, none of the stimuli showed a difference in amplitude when comparing pre- and post-cue trials (all $p > 0.05$), which indicates that the set-size dependent amplitude differences rather reflect the impact of the display arrangement than a temporal disturbance of attentional deployment.

## Discussion

We compared the strengths and weaknesses of six discrimination stimuli that are commonly used in the literature of visual attention. All tested stimuli follow a common principle, by taking the sensitivity to discriminate a stimulus-specific discrimination target as a proxy for the allocation of visual attention.

**Threshold procedure**. Except for the *Digital letters*, participants performed a threshold task before the main experiment of each stimulus, in which we adjusted the discrimination signal strength of the stimulus-specific discrimination target to the visual capacity of each observer. Even though this procedure requires additional testing time, it offers decisive advantages. Threshold tasks increase the inter-subject comparability, as after a threshold procedure the performance of each observer in the upcoming main task can be expected to be equal. Furthermore, a threshold procedure ensures an appropriate level of difficulty for each observer, preventing both floor effects (the discrimination task is generally too difficult for an observer) and ceiling effects (the task is too easy) – which impede the successful measurement of the allocation of attention.

**Visual pop-out**. In order to successfully measure the distribution of attention, the discrimination target should only be discriminable above chance when attention is allocated towards it. In other words, the crucial discrimination signal of an effective stimulus should not be discriminable without the deployment of attention. To evaluate whether a discrimination target also is visible without selectively attending towards it, our paradigm featured randomly intermixed trials in which no cue appeared. In these trials, observers kept fixation and attention was not biased towards a particular item. In such trials, visual sensitivity should be close to chance level for discrimination targets that do not pop-out. However, it turned out that the motion direction of the RDK stimulus could be discriminated well above chance. This was just the case for the smaller set-size, indicating the importance of a decent number of distractors, in particular for motion signals.

**Set-size effect and retro-cue effect**. The set-size manipulation did not only allow to evaluate pop-out effects, but it also enabled the investigation of visual crowding in a saccade task (Greenwood, Szinte, Sayim, & Cavanagh, 2017). Results showed the most pronounced set-size effects for the *Digital letters*, the *Crosses*, and the *Pink noise*. A visual inspection of the temporal dynamics reveals that particularly the *Digital letters* are more effective when they are surrounded by close distractors, as we observed a later increase in attentional performance at set-size 8 as compared to set-size 4. At the smaller set-size, visual sensitivity started rising already far before cue onset. This suggests that the crowding by the adjacent items helped to prevent retro-cueing effects, i.e., attentional benefits at the cued item that arise already before cue presentation (Sergent et al., 2013). Likewise, the *Pink noise* stimulus was prone to this effect, with attentional performance rising at the future target already before cue onset – however, only at set-size 4 – indicating once more the benefit of a sufficiently large set-size.

**Effects on saccade metrics**. When investigating the effect of each stimulus on saccade parameters, it turned out that all tested static stimuli (*Digital letters*, *Gabors*, and *Crosses)* consistently influenced saccade latencies: When the discrimination target occurred after cue onset, i.e., within the period of saccade preparation, this sudden change of the otherwise static display prolonged the saccade execution. We observed no such effect for the continuously changing stimuli (*Pink noise*, *RDK*, *Gabor streams*), for which the discrimination target is embedded in a frequently changing display. Given the well established tight coupling of eye movement preparation and visual attention (Kowler, Anderson, Dosher, & Blaser, 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007), it is plausible that interrupting saccade preparation also affects the temporal dynamics of visual attention. Thus, stimuli that rely on a sudden onset of the discrimination target might bias what they intend to measure, the temporal dynamics of visual attention. Therefore, when it comes to temporal precision, dynamic stimuli should be favored.

**Stimulus specifications**. The temporal precision furthermore is influenced by the stimulus-specific test duration: While *Gabors* and *Gabor streams* allow for a shorter presentation of the discrimination target and therefore are more suitable when smaller time windows are of interest, the *RDK*, the *Pink noise*, the *Crosses* and the *Digital letters* require longer presentation times and are less suited for precise timing measurements.

Another criterion when selecting the stimulus for a given research design can be the stimulus size. Even though the required size is indirectly related to the presentation time (the longer the presentation time, the smaller the required size, for a constant discriminability), discrimination signals based on orientation judgments (e.g. *Gabors*) can be perceived at comparably smaller sizes, while identification stimuli like *Digital letters* and especially motion signals like *RDK* require larger sizes. Therefore, when the research design requires a high spatial resolution, orientation stimuli are an advantage and motion signals that require time for integration should be avoided.

However, motion signals as well as noise signals have a crucial advantage over the other tested stimulus conditions: Instead of presenting various discrete items or patches, the *RDK* and the *Pink noise* stimulus can be extended to a full field presentation mode by displaying randomly moving dots or pink noise across the entire screen. In such a setup, the discrimination signal can be embedded within any subpart of the field, not limited to particular pre-defined locations. While common discrimination paradigms rely on discrete objects that structure the visual field and might bias participants' attention towards specified locations, a full field paradigm does not reveal potential test areas. Observers consequently cannot deploy their attention to a subset of task-relevant locations, enabling an unbiased assessment of visuospatial attention across the visual field (see Hanning & Deubel, 2018).

**Conclusion**. All tested stimuli were able to measure the spatiotemporal distribution of attention. However, the efficiency of the tested stimuli varies with respect to the various criteria examined. What ultimately constitutes the perfect stimulus depends on the respective research question and design. For eye movement paradigms, however, single onset stimuli should be avoided.

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## 2.2 Visual attention is not limited to the oculomotor range

The corresponding manuscript has been submitted for publication.

**Author Contributions:**

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

Martin Szinte contributed to the study design, participated in interpreting the results and writing the manuscript.

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

# Visual attention is not limited to the oculomotor range

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**Abstract**

The premotor theory of attention postulates that any deployment of visual attention, with or without eye movements, arises from the activation of the oculomotor system. Providing strong evidence for this theory, both patients with eye movement disorders as well as healthy participants whose oculomotor range had been experimentally reduced were reported to show attentional deficits at locations unreachable by eye movements. While previous studies were mainly based on the evaluation of reaction times in fixation tasks, we measured, for the first time, visual sensitivity before saccadic eye movements that were aimed towards locations either within or beyond the oculomotor range. For this purpose, participants rotated their heads to prevent them from performing large rightward saccades. In this posture, they discriminated the orientation of a visual noise patch that was presented while they prepared a saccade towards a cue flashed either within or beyond their oculomotor range. Contrary to previous reports, when participants aimed towards a cue which they could not reach with their gaze, we observed an unaltered deployment of attention towards it, yet no benefit at their actual saccade endpoint. This demonstrates that spatial attention is not coupled to the executed motor program. Instead, attention can be deployed unrestrictedly towards locations to which no successful action can be executed and therefore is not limited to the oculomotor range.

**Keywords**: visual attention; saccadic eye movements; premotor theory of attention;

# Introduction

We are surrounded by far more visual information than we can process simultaneously. To ensure goal directed behavior, we need to attend to the most relevant input, ignoring other aspects of the available information (1, 2). This attentional selection usually is achieved by a succession of rapid eye movements (saccades) towards the most crucial information of the visual scene (3). Interestingly, various studies demonstrated that attention does not only reach a location of interest when the gaze arrives, but already before the eyes start to move (4, 5), and it has been argued that this presaccadic attention shift is mandatory (4). However, attentional selection can also occur in the absence of eye movements (6, 7), which raised the question of whether overt (with eye movements) and covert spatial attention (without eye movements) are based on the same neurocognitive processes.

The influential premotor theory of attention (PMTA; 8–10) states that (i) both visual spatial attention and oculomotor processes rely on the same neural substrate, the oculomotor system, and that (ii) any shift of spatial attention is elicited by preceding motor activation, with motor execution being inhibited if no action is requested.

Indeed, the same brain structures are active during tasks involving overt and covert attention (11, 12), supporting the first assumption of the PMTA. These overlapping neuronal circuits include the parietal cortex, the Frontal Eye Fields (FEF) and the Superior Colliculus (SC) – oculomotor structures that form the so-called *priority maps* (13, 14). Feedback signals arising within these maps that project back to early visual areas (e.g., V1-V4) are assumed to enhance visual processing (13–15).

In support of the second assumption of the PMTA, patients who cannot perform eye movements as a result of cortical (16) or subcortical lesions (17), peripheral oculomotor palsy (18), or limited elasticity of their eye muscles (19) also seem to show attentional deficits. This is demonstrated, for example, by their inability to deploy their attention to a peripheral cue, as illustrated by a reduction of reaction time benefits normally observed when healthy participants have to detect a target at a cued compared to an uncued position (7). These results may suggest that any limitation of oculomotor processes, even at the level of the extraocular muscles, affects the proper functioning of the priority maps and consequently the deployment of attention.

Interestingly, similar effects were observed in healthy participants when using the eye abduction paradigm to limit the range of possible saccades. In this paradigm, participants rotated their heads in the opposite direction of an exogenous cue, making saccades towards it no longer possible (20–22). As a result, the exogenous cue attracted less or no attention, indicated by the lack of reaction time benefits at the cued target and smaller deviations of the saccade trajectories away from the cued location. These effects are particularly remarkable, as the absence of exogenous attention seems to demonstrate that even a temporary inability to execute saccades can affect the functioning of attentional guidance, operated by the priority maps. In this regard, these and the above effects have been considered as strong evidence in favor of the PMTA, suggesting that attention cannot be properly deployed without the possibility to pre-program an action.

It is, however, important to note that none of these studies experimentally determined and reliably monitored their participants' individual oculomotor range, nor did their paradigms include the preparation of a motor plan, two prerequisites for drawing conclusions on the interaction between the motor system and visual attention.

To test whether the deployment of visual attention is dependent on the ability to execute a saccade, we developed a paradigm that allows to disentangle these processes. For this purpose, we measured pre-saccadic orientation sensitivity at different locations within and beyond participants' oculomotor range. We reasoned that if motor programming precedes the deployment of visual attention, high sensitivity should be limited to locations reachable by the eyes.

Contrary to this assumption, we found high pre-saccadic sensitivity at cues presented both within and beyond each participant's motor range. Moreover, when participants aimed to saccade outside their oculomotor range, which resulted in considerable saccadic undershoot, sensitivity at their actual saccade endpoint was not enhanced. These results clearly demonstrate that visual attention is not limited to the oculomotor range.

## Results

Participant's rotated their heads about 35° to the left, which prevented them from performing rightward saccades larger than 8 degrees of visual angle. We assessed visuospatial attention at one of four locations on the horizontal axis (±6°, and ±10° relative to the central eye fixation) using a discrimination task based on oriented pink noise patches (23). The positions of the patches were chosen such that, due to the leftwards head rotation, the right proximal patch (+6°) lay close to the edge but still within the oculomotor range, while the right distal patch (+10°) lay beyond it (see Fig. 1*A*). A cue was briefly flashed randomly at one of the four locations (see Fig. 1*C*), which attracted exogenous attention (7) and increased visual sensitivity at the cued compared to the non-cued locations. If the deployment of attention relies on the ability to perform a saccade, a cue occurring outside their reach should not increase participants' discrimination performance at its location. Critically, and in contrast to previous studies, while trying to discriminate the orientation presented at any of the four locations, participants were also instructed to make a saccade towards the cued location. The saccade task enabled us to monitor each participant's oculomotor range during the entire experiment and to disentangle motor processes from visual attention.

We analyzed the head-tracking data to ensure that each participant maintained a consistent level of rotation across trials. While the average amount of head rotation differed between participants (Fig. 1*D* right; range: 30.2° - 43.0°; mean: 35.3°), each participant maintained a consistent rotation angle over the time of the experiment (Fig. 1*D* left) and within each block (with the exception of one participant where the rotation angle had to be lowered between the blocks to ensure that the proximal location could be reached by the eyes). To determine whether the head rotation manipulation indeed prevented saccadic eye movements to the right distal location, we analyzed the saccade landing positions. Fig. 2*A* shows the normalized spatial distribution of saccade endpoints observed across participants depending on the cued location, as well as the relative frequency of horizontal saccade endpoints. For targets within the oculomotor range (-10°, -6°, and +6°), 76.7% [73.2, 80.2] (mean [95%-CI]) of the saccades ended within a radius of 1.5° from target center. This demonstrates that,

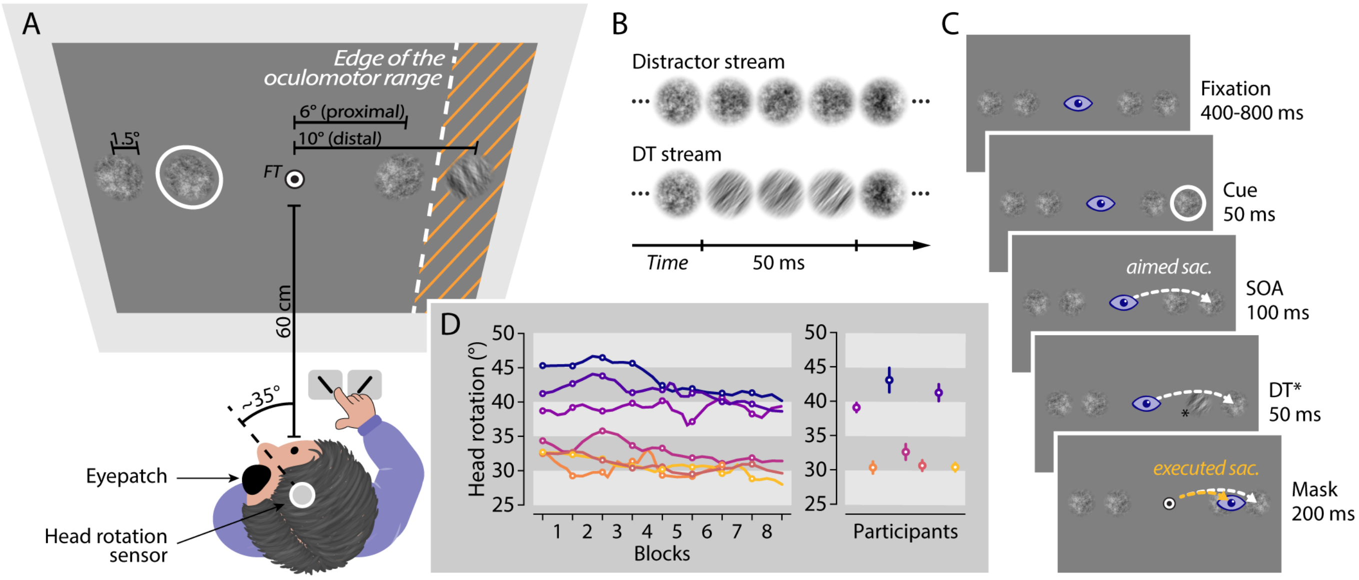

**Fig. 1.** Apparatus and procedure. (*A*) Apparatus. Participants viewed the stimuli at a distance of 60 cm, with the left eye patched and their head rotated about 35° to the left. Four pink noise patches were presented on the screen horizontal, at two eccentricities (proximal: ±6° and distal: ±10°) from the central fixation target (*FT*). The right distal patch fell outside participants' oculomotor range. (*B*) Pink noise streams. Each stream consisted of a succession of randomly generated pink noise patches, flickering at 60 Hz. The discrimination target (DT) stream included a sequence of orientation filtered noise patches (50 ms), showing a 40° clockwise or counterclockwise tilt relative to the vertical axis. (*C*) Trial sequence. After a fixation period, a circular white cue was flashed around one randomly chosen 1/f noise stream. Participants were instructed to saccade towards it and report the orientation of the DT presented before saccade onset (see Videos S1 & S2). (*D*) Head rotation angles. Different colors are used for the different participants. Left panel: Rotation angle over the time course of the experiment (8 blocks). Each dot marks the beginning of a new experimental block. Right panel: Mean rotation angle averaged over the experimental blocks for each participant. Error bars represent 95% confidence intervals.

despite the discomfortable head rotation, participants were able to saccade precisely towards these targets, as reflected by the analysis of motor errors, i.e. the distance between the target center and the saccade endpoint (-10°: 1.25° [1.11, 1.39], -6°: 0.79° [0.59, 0.99], +6°: 1.11° [0.99, 1.23]). However, when participants aimed to saccade towards the right distal target, we observed a consistent saccadic undershoot (+10°: 3.60 [3.25, 3.95]). In these cases, saccades ended about 3° too short (+6.95° [6.52, 7.38]). As the distal location could not be reached by the eyes in the majority of trials (92.5% [88.8, 96.2]), this location can be considered as falling beyond each participant's oculomotor range, which is the first requirement to investigate whether visual attention is limited to locations reachable by saccadic eye movements. Nevertheless, saccade latency did not differ depending on the saccade target location (median: 232.9 ms, 95%-CI [217.8, 248.0]; $0.715 > p > 0.111$).

The second requirement involves the simultaneous measurement of pre-saccadic visual sensitivity at different locations within and beyond the participants' oculomotor range. As we aimed to investigate pre-saccadic attention, the discrimination target (DT) was always presented during saccade preparation (DT offset on average 54.9 ms [39.0, 70.8] before saccade onset). As shown in Fig. 2*B*, when the cue occurred inside the oculomotor range visual sensitivity for DTs presented at the cued location (DT@cue) was significantly increased compared to the average sensitivity of DTs presented at the other three uncued (DT@non-cue) locations (Cue -10° and DT@cue: 1.71 [1.32, 2.10] vs. DT@non-cue: 0.10 [-0.06, 0.26], $p < 0.001$; Cue -6° and DT@cue: 1.93 [1.26, 2.60] vs.

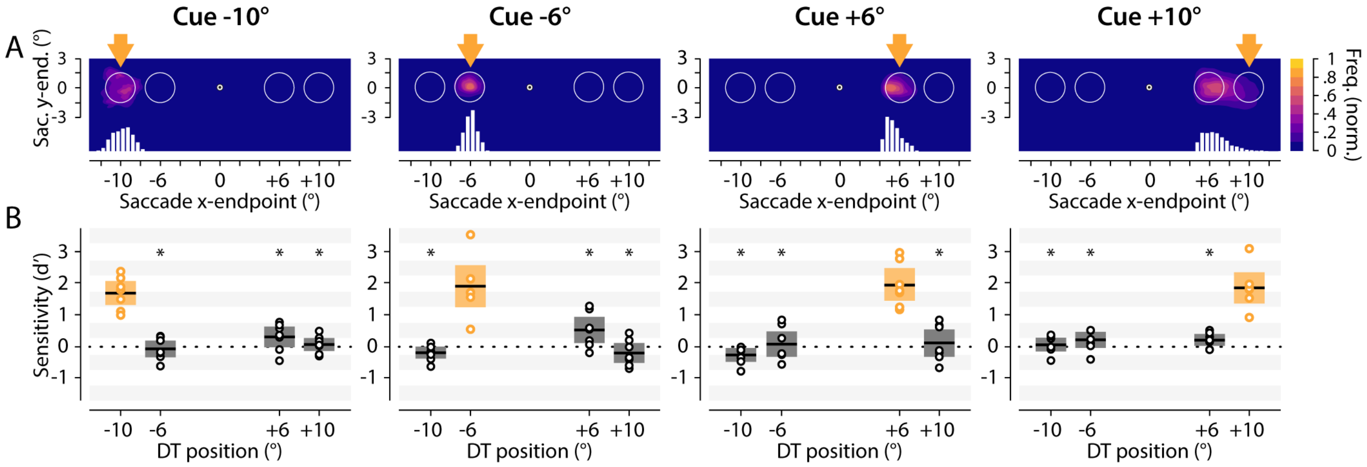

**Fig. 2.** Saccade landing and visual sensitivity as a function of cue location. (*A*) Normalized saccade landing frequency maps averaged across participants (n = 7) as a function of the cue location (-10°, -6°, +6° and +10°). Histograms illustrate the normalized frequencies of horizontal saccade endpoints per cue location. (*B*) Visual sensitivity at the cued location (orange whisker plots) and at the non-cued locations (black whisker plots) as a function of the cue location. Horizontal lines within each whisker plot indicate the averaged visual sensitivity (d') at the respective DT position. Error bars depict 95% confidence intervals, dots represent individual participant data. Dashed lines mark chance level and asterisks indicate significantly lower discrimination performance at the respective non-cued location compared to the cued location ($p < 0.001$).

DT@non-cue: 0.06 [-0.08, 0.20], $p < 0.001$; Cue +6° and DT@cue: 1.97 [1.44, 2.50] vs. DT@non-cue: -0.06 [-0.32, 0.20], $p < 0.001$). Importantly, and in contrast to a previous report using a similar design (22), we found the same attentional benefit when the cue was presented outside participants' oculomotor range (Cue +10° and DT@cue: 1.88 [1.39, 2.37] vs. DT@non-cue: 0.18 [0.06, 0.30], $p < 0.001$).

Further analysis revealed that the majority of the undershooting saccades aimed towards the distal right target actually landed at the proximal right location (within a radius of 1.5° from patch center; 62.2% [50.0, 74.4]). Crucially, for these trials, the spatial deployment of attention towards the cue at the distal location was dissociated from the actual saccade vector. If the deployment of attention is coupled to the executed saccade plan, we should observe an attentional benefit at the actual saccade endpoint. However, when participants aimed to saccade outside their oculomotor range, and landed too short, visual sensitivity at their actual saccade endpoint was not enhanced compared to the sensitivity at the other non-cued locations (DT@6°: 0.22 [0.04, 0.40] vs. DT@-10: 0.07 [-0.14, 0.28] and DT@-6: 0.23 [-0.03, 0.48]; $0.895 > p > 0.254$). Rather, we observed an unaltered deployment of attention towards the intended but not reached saccade goal (DT@10°: 1.88 [1.39, 2.37], $p < 0.001$).

# Discussion

We measured visual sensitivity both within and beyond the oculomotor range and found that an exogenous cue increased pre-saccadic visual sensitivity independently of whether it occurred inside or outside the oculomotor range. In other words, we found no evidence that attention is limited to locations reachable by gaze. This result is in direct contradiction to previous eye abduction studies reporting impaired visual attention at locations to which no eye movements can be performed (20–22), and casts some doubt on the use of oculomotor patients studies (16–19) to validate the assumptions of the PMTA.

The supposed limitation of attention to the oculomotor range was previously interpreted as a strong evidence that motor activity must precede the deployment of attention. This assumption, however, was based on limited measurements and partly inconsistent evidence. The reported attentional limitation was mainly investigated by reaction time measurements and observed for reflexive or exogenous (17–19, 21, 22), but in some studies not for voluntary or endogenous attention (19, 22). Even more puzzling, inhibition of return (an effect that follows reflexive attention shifts; 24) was observed after the presentation of exogenous cues outside the oculomotor range (22). Previous studies could also not agree on whether visual attention at locations not reachable by eye movements is only reduced (20), or eliminated (21, 22) when saccade trajectories were measured instead of reaction times (20). Last but not least, no eye abduction study recorded and monitored their participants' actual oculomotor range. We verified each participant's reach of saccades across trials and our results demonstrate that the head rotation angle required to prevent rightward saccades to the distal position differed substantially between participants (Fig. 1*D*).

Crucially, when participants aimed to saccade to a cue presented outside their oculomotor range, their saccade necessarily fell short. In this case, the spatial deployment of attention towards the distal cue was dissociated from the executed saccade vector, as the majority of saccades ended already at the proximal position. By measuring the spatial distribution of visual attention before saccade onset as a function of the actual endpoint, we directly test the link between oculomotor programming and the deployment of attention. If, as postulated by the PMTA, the deployment of attention originates from the activation of a motor plan, we should observe an attentional benefit at the actual saccade endpoint. Our data, however, reveal that visual sensitivity at the endpoint of undershooting saccades was not enhanced. Rather, we found an unaltered deployment of attention towards the intended saccade target, presented verifiably outside each participant's oculomotor range. This double dissociation—a deployment of attention towards where the eyes cannot go, paired with a lack of attention where they actually went—demonstrates that attentional orienting is not necessarily coupled to the executed motor program.

Nevertheless, these results do not necessarily exclude the possibility that spatial attention arises from a pre-motor activity, as claimed by the PMTA (8–10). Since attention shifts are assumed to arise through feedback activation from the priority maps (i.e. FEF, SC, IPS-LIP) to parietal and occipital feature maps (13–15), we propose two hypotheses accounting for our results. These hypotheses differ essentially in whether a temporary limitation of the oculomotor range, imposed by rotating the head, affects the functioning of the priority maps and consequently the deployment of attention.

The first hypothesis assumes that eye abduction affects the activity of motor neurons of the priority maps, whose movement fields, due to the head rotation, lay outside the experimentally reduced oculomotor range. Proprioceptive information about the abducted eye position available in somatosensory cortex (25) could be transferred to the priority maps, causing the suppression of activity towards locations associated with non-executable actions. In this case, given our observation that attention can be deployed outside the oculomotor range, attention shifts would arise from the activation of visual rather than motor cells within the priority maps. Indeed, the actual purpose of visual cells in the oculomotor centers may be to enable the deployment of attention without moving the eyes. Following this hypothesis, our results would directly contradict the PMTA, as attention and motor programming would neither follow nor depend on each other. This hypothesis is in agreement with electrophysiological studies demonstrating that motor cells within FEF and SC stayed silent during a covert attention task (26–28), while visual and visuomotor cells displayed sustained attention-related activity. However, as neurophysiological evidence only applies to the recorded brain areas and to the animal model used, the possibility remains that pre-motor activity emerges at another level of the brain. Our study as well as previous behavioral studies are not subject to this restriction since behavioral results necessarily reflect the activity of the system as a whole. Taking advantage of the fact that saccades naturally undershoot the aimed target, Deubel and Schneider (4) found that it is the intended saccade targets, rather than the actual saccadic landing position that receives the attentional benefit. Likewise, when investigating the spatial distribution of attention before the execution of averaging saccades, i.e. saccades unintentionally landing in between two nearby saccade targets, Wollenberg and colleagues (29) found no enhancement of visual attention at the saccade endpoint. Instead, visual attention was allocated towards the two potential saccade targets, leading the authors to conclude that saccade averaging arises from unresolved target selection. In accordance with our results, these studies show that before saccades attention is deployed to the intended location independently of the saccade plan ultimately implemented.

The second hypothesis presumes that eye abduction only imposes a muscular limitation but does not affect the neuronal activity of the priority maps. In this case, the observed deployment of attention to locations falling outside the oculomotor range could be triggered by motor cell activity within the priority maps. As oculomotor areas are retinotopically organized (30, 31), their functioning should not be affected by an abduction of the eye. Electrophysiological evidence has shown that microstimulation of motor cells within the FEF and the SC evokes saccades with certain amplitudes and directions. Although the eye abduction in our experiment artificially limited the execution of saccades to an average of 7°, motor cells still can encode larger saccades and thus trigger the attentional effects observed. According to this hypothesis, our results and in general any study based on experimental or pathologic restriction of eye-movements (16–22) could neither contradict nor speak in favor of the PMTA, as the same attentional effects (an unrestrained deployment of attention as as observed in our data) would be expected irrespective of whether an action can or cannot be executed.

Our results are consistent with both hypotheses. However, while it is conceivable that a permanent disability to perform eye movements results in functional modifications of the priority maps, it is puzzling that a induced temporary limitation of the oculomotor range would lead to the same effects. Still, our data cannot rule out the possibility that a rotation of the head modifies neuronal activity within the priority maps, and it requires an electrophysiological examination to disentangle our hypotheses.

The present results demonstrate that visual attention is not limited to the range currently accessible by eye movements. Independently of the saccade plan ultimately executed, attention is deployed to the intended saccade goal, even if it is located out of range. Visual attention is therefore not limited to the oculomotor range.

## Materials and Methods

**Participants.** 7 participants (4 females, ages 22–30 years-old, one author) completed the experiment. All participants had normal vision and except for one author (N.M.H.) were naive as to the purpose of the experiment. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München and conducted in accordance with the Declaration of Helsinki. All participants gave written informed consent.

**Apparatus.** Head rotation was recorded via a single sensor of a Polhemus Liberty 240/8 electromagnetic motion tracking device (Polhemus Inc., Colcherster, Vermont, USA) and a personal toolbox. The sensor was attached on top of participants' head, using an EEG-cap (position CZ). The exact amount of head rotation was determined individually at the beginning of the experiment, and adjusted during the experiment when necessary, to ensure that each participant's oculomotor range ended in between the right proximal (+6°) and distal locations (+10°). Gaze position of the dominant right eye was recorded using an EyeLink 1000 Tower Mount eye tracker (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The eye tracker was calibrated with the head rotated at the beginning of the experiment and whenever the head was moved. Calibration targets were presented within 8° from fixation, such that they fell within participants' oculomotor range. According to SR Research, the eye tracker used allows precise tracking of the gaze position within the range required for our paradigm (up to ~12° on the horizontal axis). Manual responses were recorded via a standard keyboard. The experimental software controlling display, response collection, as well as eye and head tracking was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (32, 33) and EyeLink toolboxes (34), running on a Dell Precision T1500 Intel Core i5 computer (Round Rock, Texas, USA). Stimuli were presented at a viewing distance of 60 cm on a 21-in SONY GDM-F500R CRT screen (Tokyo, Japan) with a spatial resolution of 1024 by 768 pixels and a vertical refresh rate of 120 Hz.

**Experimental Design.** Participants set in a dimly illuminated room, with their left eye patched and their head rotated about 35° to the left, positioned on a chin rest (Fig. 1). Each trial began with participants fixating a central fixation target (FT) comprising a black (~0 cd/m2) and white (~120 cd/m2) bull's eye (radius 0.25°) on a gray background (~60 cd/m2). Once stable fixation was detected within a 2.0° radius virtual circle centered on FT for at least 200 ms, four pink (1/f) noise streams (radius 1.5°) appeared on the horizontal axis at -10°, -6°, +6° and +10° relative to FT (positive values correspond to the right side of the screen). Each noise stream consisted of randomly generated noise patches (mean luminance ~60 cd/m2) windowed by a symmetrical raised cosine (radius 1.5°, sigma 0.5°), refreshing at 60 Hz (Fig. 1*B*). After a random fixation period between 400 and 800 ms, a cue (white annulus, radius 1.5°, ~120 cd/m2) was flashed for 50 ms around one randomly selected noise stream. Participants were instructed to perform a saccade to the cued noise stream upon cue onset. Note that cues flashed at +10° fell outside the oculomotor range due to the head rotation. 100 ms after cue onset the discrimination target (DT) was presented. The DT consisted of an orientation-filtered noise stimulus, displaying a tilt rotated 40° clockwise or counterclockwise relative to the vertical. The DT was equally likely to appear within any of the four noise streams, and was masked by the reappearance of non-oriented noise patches 50 ms later. 200 ms after DT onset the noise streams disappeared and participants reported the orientation of the DT via button press. They were informed that the DT would appear randomly at any of the four positions, and that their orientation report was non-speeded (they were instructed to take their time to rest and blink before initiating the next trial by giving their response). They received auditory negative feedback for incorrect responses.

Participants performed between 6 and 8 experimental blocks of at least 100 trials each. The trial number per block was kept low and participants took breaks after each block to ensure the maximum comfort despite the unusual head position. We controlled online for incorrect eye fixation (outside 2.0° from FT before the cue onset), too short (< 130 ms) or too long saccade latency (> 400 ms), as well as incorrect eye movements (saccade landing beyond 2.0° from a motor target within participants' oculomotor range). Incorrect trials were repeated in random order at the end of each block. Overall, participants repeated on average 23.8 [16.7, 30.9] % of the trials.

To maintain a consistent level of discrimination difficulty across participants, a threshold task preceded the experiment. The threshold task visually matched the main experiment but participants did not rotate their head and were instructed to keep their gaze on the fixation target. Furthermore, participants were informed that the DT would occur always at the cued location. We used a procedure of constant stimuli and randomly selected the orientation filter strength (corresponding to the visibility of the orientation tilt) out of five linear steps of filter widths. By fitting cumulative Gaussian functions to the discrimination performance gathered in this threshold task, we determined the filter width corresponding to 80% correct discrimination performance.

**Eye and head data pre-processing.** We scanned offline the recorded eye-position data and detected saccades based on their velocity distribution (35) using a moving average over twenty subsequent eye position samples. Saccade onset and offset was detected when the velocity exceeded or fell below the median of the moving average by 3 SDs for at least 20 ms. We included trials if a correct fixation was maintained within a 2.0° radius centered on FT until cue onset and landed within 2.0° from the cued location (or within 5.5° for the cued location outside the oculomotor range) no later than 400 ms following cue onset, and if no blink occurred during the trial. We excluded trials with head movement artifacts (rotation angle not within 3 SDs from average head rotation). In total we included 4684 trials in the analysis of the behavioral results (on average 669 [610, 729] trials per participant). To visualize the head rotation data (Fig. 1*D*), we filtered the rotation angle by using a moving average filter of 180 seconds.

**Sensitivity analysis.** We determined the sensitivity to discriminate the test orientation (d'): d' = *z*(hit rate) - *z*(false alarm rate) separately for each location, depending on the saccade target location. To do so, we took the percentage of correct signal discrimination as hit rate, the false alarm rate we computed by dividing the percentage of incorrect signal discrimination by the number of potential incorrect choices. Corrected performance of 99% and 1% were substituted if the observed proportion correct was equal to 100% or 0%, respectively. Performance below the chance level (d' = 0 corresponding to 50%) were transformed to negative d' values.

Whisker plots to visualize the data show single participant sensitivity (represented by dots) that we averaged across participants (represented by black lines), as well as the 95% confidence interval (indicated by colored bars). For all statistical comparisons we resampled our data and derived *p*-values by locating any observed difference on the permutation distribution (difference in means based on 1000 permutation resamples).

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## 2.3 Independent selection of eye and hand targets suggests effector-specific attentional mechanisms

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**Author Contributions:**

Nina M. Hanning developed the study concept, programmed the experiments, collected, analyzed, interpreted and visualized the data, and wrote the manuscript.

David Aagten-Murphy participated in programming the experiments, analyzing and interpreting the data and commented on the manuscript.

Heiner Deubel participated in interpreting the results and commented on the manuscript.

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# Independent selection of eye and hand targets suggests effector-specific attentional mechanisms

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**Both eye and hand movements bind visual attention to their target locations during movement preparation. However, it remains contentious whether eye and hand targets are selected jointly by a single selection system, or individually by independent systems. To unravel the controversy, we investigated the deployment of visual attention – a proxy of motor target selection – in coordinated eye-hand movements. Results show that attention builds up in parallel both at the eye and the hand target. Importantly, the allocation of attention to one effector's motor target was not affected by the concurrent preparation of the other effector's movement at any time during movement preparation. This demonstrates that eye and hand targets are represented in separate, effector-specific maps of action-relevant locations. The eye-hand synchronisation that is frequently observed on the behavioral level must emerge from mutual influences of the two effector systems at later, post-attentional processing stages.**

Previous research has shown that eye movements[1–3] as well as hand movements[4,5] are preceded by shifts of attention to their motor targets prior to movement onset. In everyday life, the control of these two movement types does not seem to be independent: When we interact with objects in our environment, our eye and hand movements frequently are highly coupled, both spatially and temporally. This raises the question whether eye and hand movements are attentional selected in unison, by one common mechanism, or whether they are selected individually by independent attention systems. Because of the observed interplay between both motor systems, the view that a shared, effector-agonist system underlies the selection of both eye and hand motor targets has gained wide support in numerous behavioral studies[6–11]. However, there is also psychophysiological evidence for the alternative view that eye and hand movements are selected by separate, largely independent attentional mechanisms[12].

To resolve the ambiguity, we investigated the deployment of visual attention – an index of motor target selection – during the simultaneous preparation of saccadic eye movements and hand movements. In dual movement tasks we asked our participants to either reach or look, or to simultaneously reach and look towards certain target locations, while they concurrently discriminated the orientation of briefly presented oriented patterns, embedded in noise. We took the perceptual discrimination performance at motor targets and movement irrelevant locations as a measure of the distribution of attention during motor target selection. Critically, saccade and reach movement could be either directed to the same target location, letting us examine cumulative benefits, or to different locations, allowing the detection of an attentional trade-off between the eye and the hand motor target.

Our data reveals that during the process of motor preparation attention builds up in parallel at the saccade and the reach target. Importantly, the temporal dynamics of the shift of attention to both the saccade and the reach target do not differ between single (eye or hand) and combined (eye plus hand) movements. As the different action selection mechanisms did not compete for attentional resources at any time during movement preparation, our findings demonstrate that separate, effector-specific attentional mechanisms are responsible for selecting the motor targets for eye and hand movements.

## Results

### Attentional selection in single and combined eye-hand movements.

In Experiment 1 (Fig. 1A) participants performed single or combined movements. In the single motor tasks, they made an eye or hand movement towards either a fixed ($Saccade_{Fix}$ or $Reach_{Fix}$) or a variable target ($Saccade_{Var}$ or $Reach_{Var}$), while their

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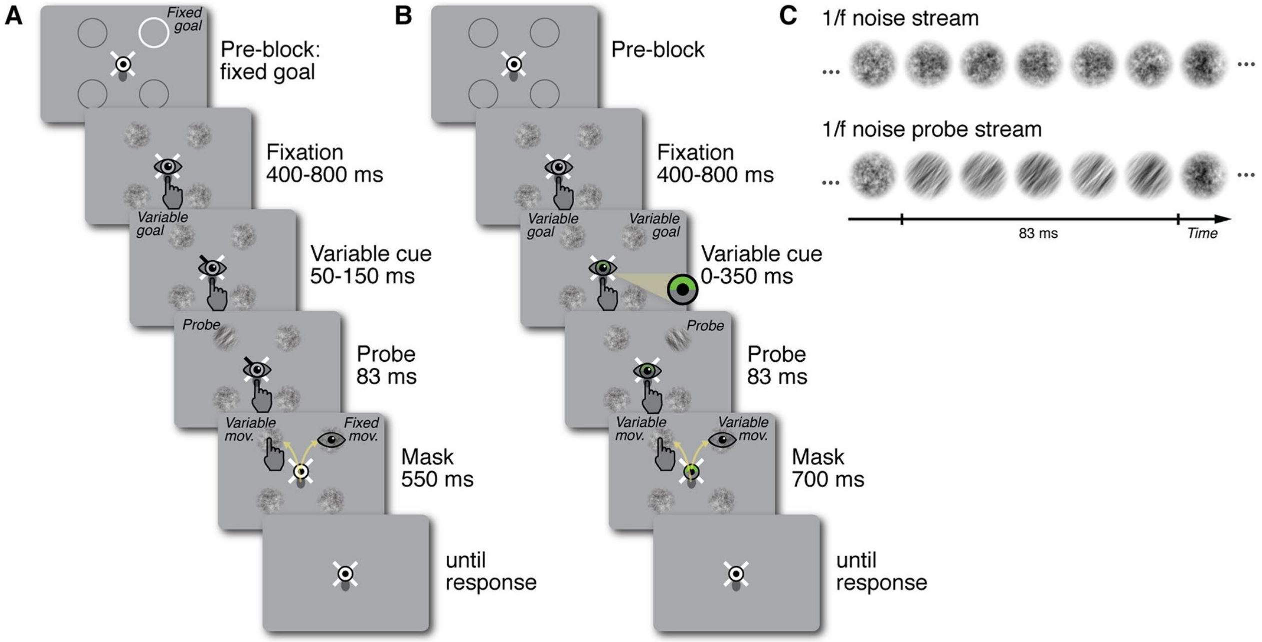

**Figure 1.** Design and stimuli. (**A**) Experiment 1, example motor task *Saccade*$_{Fix}$-*Reach*$_{Var}$: At the beginning of the block, the fixed motor target was marked by a white circle. Participants (n = 9) maintained eye and finger fixation until one of the four white direction lines pointing towards the noise patches turned black, indicating the variable motor target. Participants reached towards the variable motor target and simultaneously saccaded towards the fixed motor target. 50–150 ms after cue onset one of the noise streams showed a clockwise or counterclockwise orientation. After a masking period, participants indicated their discrimination judgement via button press. (**B**) Experiment 2, example motor task *Combined*: Participants ($n = 9$) maintained eye and finger fixation until half of the eye fixation target turned green, revealing two potential motor targets (here the two upper locations). Participants reached towards one of the two potential motor targets and simultaneously saccaded towards the other. 0–350 ms after cue onset, one of the noise streams showed a clockwise or counterclockwise orientation. After a masking period, participants indicated their discrimination judgement via button press. See also Supplementary Movie S1 (**C**) Noise streams used as discrimination stimuli. Each of the four noise streams consisted of a succession of randomly generated 1/f noise patches, flipping at 60 Hz. The probe stream comprised a 83 ms sequence of orientation filtered 1/f noise patches, showing a 40° clockwise or counterclockwise orientation.

other effector remained at fixation. In the combined motor tasks, they executed a combined eye-hand movement. One effector was consistently moved towards a fixed target, the other effector's target varied on each trial (*Saccade*$_{Fix}$-*Reach*$_{Var}$ or *Saccade*$_{Var}$-*Reach*$_{Fix}$). While the location of the variable target was unpredictable and cued centrally on each trial, the fixed target was indicated at the beginning and remained the same throughout the experimental block. The four possible motor targets were indicated by streams of 1/f noise patches separated by 90° and positioned 8° from the fixation. Participants were instructed to initiate their movement(s) as soon as the cue appeared. 50–150 ms after cue onset (within the movement latency) an orientation discrimination probe appeared at one of the four locations with equal likelihood (Fig. 1C), meaning that it could occur either at a motor target or at a non-target location. After presentation of the orientated probe, the stream of noise patches continued (acting as a mask) for another 316.6–416.6 ms, after which participants indicated whether the perceived orientation of the probe was tilted clockwise or counterclockwise.

To demonstrate that attention was allocated to each effector's target before movement onset, we first analyzed discrimination performance in the single motor tasks (Fig. 2A). All comparisons were contrasted to the non-target locations unless otherwise stated. We found that performance at the saccade target was significantly enhanced ($p < 0.01$), regardless of whether the target location varied from trial-to-trial (*Saccade*$_{Var}$; $d = 2.59$), or was consistent across the block (*Saccade*$_{Fix}$; $d = 1.66$). Similarly, discrimination performance at the variable reach target (*Reach*$_{Var}$; $d = 1.50$) was significantly improved ($p < 0.01$). However, when participants consistently reached towards the same location (*Reach*$_{Fix}$), discrimination performance was the same as at non-target locations ($P > 0.05$).

When performing combined motor tasks, we found that for a fixed reach and a variable saccade (*Saccade*$_{Var}$-*Reach*$_{Fix}$; Fig. 2B, left), discrimination performance increased only at the variable saccade target ($p < 0.01$, $d = 1.53$). Performance at the fixed reach target, however, was no different than at non-target locations ($p > 0.05$). While there was a significant enhancement in discrimination performance when the goals of variable saccade and fixed reach coincided ($p < 0.05$, $d = 1.23$), this combined target performance did not exceed that at

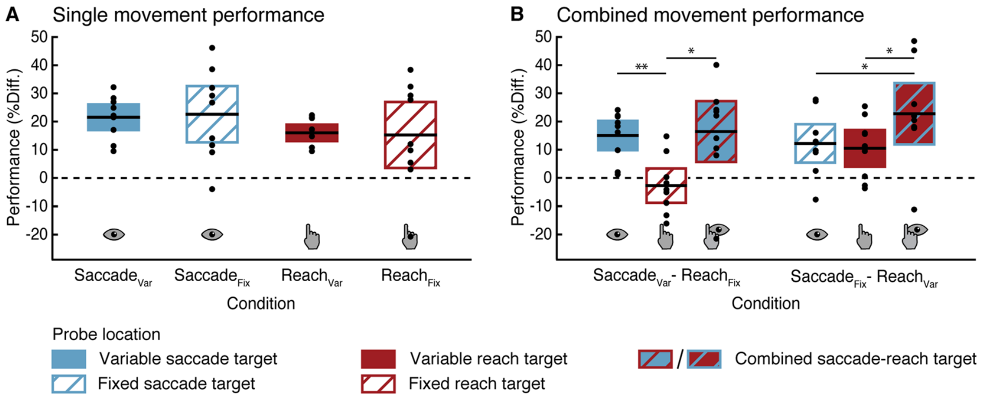

**Figure 2.** Attentional selection in single and combined movements in Experiment 1. Discrimination performance for the single eye or hand movement tasks (**A**) and the combined eye-hand movement tasks (**B**). Black lines within each whisker plot indicate the average difference in discrimination performance between each condition's motor target(s) minus the respective baseline performance at non-target locations. Coloured/striped bars show the 95% confidence interval. Dots represent individual subject data. Horizontal dashed lines mark non-target baseline performance. $^*p < 0.05$, $^{**}p < 0.01$, significant difference between two motor targets.

a spatially separate variable saccade target, when the reach was directed elsewhere ($p > 0.05$). Hence, when the reach target was fixed throughout a block, attention was no longer allocated to that location.

In contrast, when participants reached towards variable targets while making eye movements to a fixed location ($Saccade_{Fix}$-$Reach_{Var}$; Fig. 2B, right), we observed a strikingly different pattern: Discrimination performance at both the saccade ($d = 1.20$) and the reach target ($d = 0.87$) was significantly enhanced ($p < 0.05$). Importantly, when performing a combined movement to different locations, performance at the saccade (or reach) target location was approximately the same as when participants made only a single saccade (or reach). This suggests that selection mechanisms for the individual effectors operated independently and in parallel, such that the selection of one effector's motor target did not affect the attentional selection of the other.

Furthermore, when variable reach and fixed saccade target coincided, performance at this common motor target was enhanced ($p < 0.01$, $d = 1.70$), and critically it significantly exceeded the performance observed at a spatially separate fixed saccade target ($Saccade_{Fix}$; $p < 0.05$, $d = 0.77$), and at a separate variable reach target ($Reach_{Var}$; $p < 0.01$, $d = 0.77$). This suggests that saccade and reach target selection acted synergistically when both movements were directed towards a common goal, leading to a greater enhancement than would be expected from either movement alone.

### Attentional dynamics of eye and hand target selection.

To examine the degree to which saccade and reach selection were dynamically independent, Experiment 2 investigated how attentional deployment to the different motor targets developed over time. Since the results of Experiment 1 suggested that participants might utilise different attentional strategies when the reach target is fixed, both the saccade and the reach varied in Experiment 2 (Fig. 1B, see also Supplementary Movie S1). Participants either made a single movement to one of two centrally cued targets (*Saccade* or *Reach*), or performed a combined eye-hand movement (*Combined*), directing one effector to each of the cued locations at free choice. At various time points after cue onset (0–350 ms; within the movement latency), an orientation discrimination probe was presented randomly at one of the four locations. We computed the mean discrimination performance at different times after cue presentation, using a 100 ms moving average, stepping every 25 ms from test presentation 50 to 300 ms after cue onset (Fig. 3A–C).

In the single movement tasks, discrimination performance at the selected saccade or reach target increased gradually over time, while it remained near chance at the unselected location and at the non-target locations. In the *Saccade* task (Fig. 3A) discrimination performance at the saccade target was significantly superior to all remaining locations approximately 150 ms after cue onset ($p < 0.05$, $d = 1.07$). Likewise, in the *Reach* task (Fig. 3B) after 150 ms performance at the reach target was significantly better than non-target performance ($p < 0.05$, $d = 1.22$). Remarkably, in the *Combined* task performance increased simultaneously at both motor targets (Fig. 3C, and did not differ between the two locations at any point in time ($P > 0.05$), indicating that attention was dynamically allocated to both targets in parallel.

Next, we examined whether attentional dynamics differed between single and combined movements. To account for latency differences, trials were binned as a function of the time between discrimination probe offset and movement onset. Performance at the saccade target was strikingly similar throughout the entire period, regardless of whether participants were required to make a single saccade or a combined saccade and reach (*Saccade vs Combined;* $P > 0.05$, Fig. 3D). Likewise, performance at the reach target developed independently of whether participants performed only a reach or made an additional saccade *(Reach vs Combined;* $P > 0.05$, Fig. 3E).

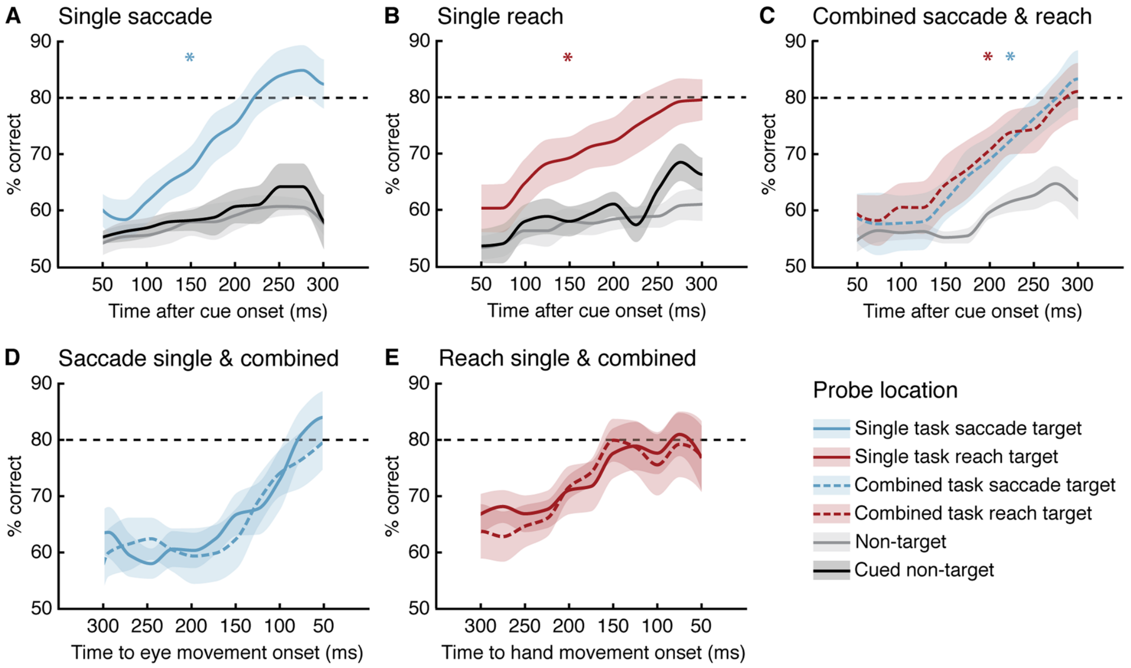

**Figure 3.** Temporal dynamics of attentional selection in single and combined movements in Experiment 2. (**A**,**B**) Discrimination performance in the single eye or hand movement tasks as a function of cue-onset to test-offset at the saccade target (blue), at the reach target (red), at the unchosen cued location (black) or at non-target locations (gray). (**C**) Performance in the combined movement task as a function of cue-onset to test-offset at the saccade target (dashed blue), at the reach target (dashed red), or at non-target locations (gray). (**D**,**E**) Performance as a function of test-offset to movement onset at the single saccade target (blue) vs. combined saccade target (dashed blue) and single reach target (red) vs. combined reach target (dashed red). Data are represented as mean, coloured areas denote the standard errors of the mean. $^{*}p < 0.05$, earliest significant difference between motor target (coloured) and non-target locations (gray).

## Discussion

In this study we not only resolve a long-standing controversy about whether eye and hand targets are selected by a unitary or by independent attentional systems, but also identify some of the reasons why previous studies have produced such divergent results. By asking our participants to perform simultaneous eye-hand movements to separate locations, we demonstrated that attention builds up at both the saccade and reach target in parallel, without any trade-off between the two motor targets. Importantly, we found no evidence that the selection mechanisms for the different effectors compete for attentional resources at any time during movement preparation, and demonstrate that eye and hand targets are represented in independent, effector-specific maps of relevant locations.

Previous studies[6,12] investigating whether different effectors are related to separate target selection mechanisms have produced mixed results, although they utilized quite similar protocols. However, our more extensive design allowed us to not only replicate their findings, but also to resolve the ambiguity in their interpretation. In accordance with earlier work[12], we observed that in combined eye-hand movements attention was allocated in parallel to both the fixed saccade and the variable reach target, with attentional performance at each target being approximately equivalent to the respective single movement condition. Moreover, we also observed a synergistic effect when hand and eye were directed towards the same location, suggesting that planning the combined movement of two effectors recruited more attentional resources than when only a single effector was engaged. Overall, our results support the previously employed broad conclusion, that separate effector-specific attentional mechanisms are responsible for the selection of eye and hand targets[12].

However, while the aforementioned study[12] investigated attention with a fixed eye target and a variable reach target, another study[6] also examined the inverse (fixed reach and variable saccade). They observed no benefit at the fixed reach target when a simultaneous saccade to a variable, different target location co-occurred, which they interpreted as evidence that the eye dominates attention in combined eye-hand movements. Yet, as we found in our first experiment, the repeated execution of a reach movement to a fixed location – even without the competition of a simultaneous saccade – did not yield a shift of attention towards the reach target. Presumably, repeated hand movements, similar to delayed hand movements[13], can be preprogrammed and therefore are not preceded by the typically reported shift of attention to the motor target[1–3]. Accordingly, our results suggest that the alleged dominance of the eye in guiding visual attention during simultaneous eye-hand movements[6] may instead be an artefact of repetitive hand movements to a fixed location ceasing to recruit reach-related attentional resources.

Our results demonstrate a difference in the premotor allocation of attention depending on the type of movement: while variably cued movements inevitably draw attention to their motor target, repeatedly performed, fixed hand actions do not cause this compulsory shift of attention. Furthermore, a comparison of the single movement data of Experiment 1 revealed a larger between-subject variance in attentional performance at the targets of fixed compared to variable eye and hand movements (Fig. 2A). In the fixed movement conditions, as one location was task-relevant throughout a whole experimental block, some participants may have endogenously attended to that location, boosting their performance, suggesting that fixed, repetitive movements are vulnerable to attentional strategies.

When investigating how attention was dynamically allocated to the movement targets in Experiment 2, we therefore ensured that both the eye and the hand target were variable and unpredictable. Furthermore, presenting the test orientation at various time points after the motor cue allowed us to study the temporal dynamics with which hand- and eye-based attentional resources were allocated to different target locations. We observed that when variable eye-hand movements were performed simultaneously, attention increased gradually at the saccade and the reach target. Remarkably, the dynamics of the shift of attention towards each effector's motor target did not depend at any time during movement preparation on whether or not a movement of the other effector was prepared simultaneously. As the gradual increase of discrimination performance at one effector's motor target was not affected by the simultaneous preparation of a movement of the other, our results demonstrate that eye and hand movement targets are selected by independent, effector-specific attentional mechanisms.

This result seems at odds with the common observation that our eye and hand movements are highly coupled, both spatially and temporally, when we interact with objects in the environment. In free-viewing tasks the eyes systematically move to reach targets before hand movement onset[10,14–16]. Because of the observed interplay between both motor systems, many behavioral studies measuring various motor parameters such as movement precision, amplitudes, velocity profiles, and latencies, have favoured the view that one shared effector-agonist system underlies the selection of eye and hand movement targets[9–11].

The interaction between the eye and the hand movement system at the behavioral level has a neurophysiological basis. Functional imaging studies in humans observed an overlap of parietal and pre-frontal cortical areas involved in eye and hand target selection[17,18]. In line with this, single-cell recording studies report that reach-related activity of neurons in the parietal cortex is modulated by eye position[19], while the activity of neurons in the primarily oculomotor-related areas like the supplementary eye field (SEF) and the frontal eye field (FEF) is modulated by hand position signals[20,21]. Furthermore, saccadic representations in the lateral intraparietal area (LIP) are influenced by a simultaneous reach movement[22], lesions of area LIP have been observed to delay the onset of reaches but only when they are accompanied by a saccade[23], and coherent spiking of neurons in this area has been suggested to coordinate eye and hand movements[24].

At first glance, the reported behavioral and neurophysiological dependencies between the two effector systems strongly argue in favour of a common, shared system serving the selection of eye and hand targets. Yet, our results demonstrate the opposite, namely that independent systems individually select eye and hand targets. We argue that the frequently reported cross-talk between the two motor systems presumably results from interactions at later processing stages, with the initial attentional selection of the motor targets being largely independent for eye and hand movements.

This conclusion is in line with imaging studies in humans which found that eye and hand movements are preceded by activity in separate parietal areas[25,26]. Furthermore, there is neurophysiological evidence that neural circuits responsible for the generation of eye and hand movements are implemented by functionally and anatomically distinct brain areas. While the brain circuit dedicated to eye movements comprises FEF and LIP[27–31], the circuit serving the production of hand movements involves more dorsal areas of the promotor cortex (PMd) and the parietal reach region (PRR) e.g[31–34]. These effector-specific neural circuits conceivably can give rise to the independent shifts of attention that we observed at the targets of eye and hand movements.

The neural mechanisms that guide the allocation of attention to salient or action-relevant locations have been referred to in the recent literature as priority maps[35,36]. In line with our assumption of separate attentional mechanisms, there is evidence that saccade and reach preparation may rely on different priority maps: While FEF and LIP are involved in saccade preparation, the PRR might code the behavioral priority for reach movements[31,37]. If a stimulus becomes relevant for a given effector, activity at the corresponding location in the respective priority map increases and triggers a feedback signal to earlier visual areas[38]. At the subcortical level, the superior colliculus (SC), for instance, receives projections from oculomotor as well as from hand-related areas and reportedly encodes priority irrespective of the effector[39–41]. The above described interaction between the eye and the hand motor system on the behavioral level, including the synergistic effect observed in our first experiment, which occurs when eye and hand movement are directed towards one common motor target, also reported in[12], can be explained by such feedback connections within saccade- and reach-related circuits converging onto earlier visual areas[42,43].

In conclusion, our findings demonstrate that motor preparation in the eye and the hand movement systems produces independent shifts of attention, suggesting that saccades and reaches are represented in separate, effector-specific maps of action-relevant locations. While previous findings have been interpreted in favour of a coupled model, or one in which a specific effector dominates the other, we here show that reach and saccade target selection can be completely dissociated at the behavioral level. Indeed, even though the frequently observed yoking of eye and hand movements indicates that eye-hand coupling is beneficial, this does not imply it is mandatory. Independent systems – which can be coupled as required – enable individual targeting when necessary, e.g. to accomplish complex tasks such as tool use and bimanual manipulation.

## Methods

**Subjects and apparatus.** Nine right handed human observers (5 females, ages 23–28 yr, one author) completed Experiment 1. Nine right handed human observers (eight of whom also participated in Experiment 1; 5

females, ages 23–28 yr, one author) completed Experiment 2. All participants gave informed consent. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München, in accordance with German regulations and the Declaration of Helsinki. Gaze position was recorded using an EyeLink 1000 Tower Mount (SR Research, Osgoode, Ontario, Canada) at a sampling rate of 1 kHz. The experimental software was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics[44,45] and EyeLink toolboxes[46]. Stimuli were presented on a 45° inclined touchscreen (Elo 2700 IntelliTouch, Elo Touchsystems, Menlo Park, CA) with a spatial resolution of 1280 × 1024 pixels and a refresh rate of 60 Hz.

**Procedure and Stimuli.** *Experiment 1.* In this experiment we investigated the deployment of visual attention in single eye, single hand and coordinated eye-hand movements, that were directed towards fixed or varying target locations. We measured attentional distribution during motor target selection by comparing orientation discrimination performance at single and combined motor targets with performance at non-target locations.

In a randomised block design, participants performed single eye movements, single hand movements, or combined eye-hand movements. In the single movement blocks, the motor target either was fixed, i.e. the eye movement was repeatedly executed towards the same location, or varied randomly between trials. Combined eye-hand movement blocks consisted of one fixed and one variable motor target. The experiment comprised six motor tasks: variable eye movement ($Saccade_{Var}$), variable hand movement ($Reach_{Var}$), fixed eye movement ($Saccade_{Fix}$), fixed hand movement ($Reach_{Fix}$), fixed eye & variable hand movement ($Saccade_{Fix}$-$\mathrm{Reach}_{\mathrm{Var}}$), and fixed hand & variable eye movement ($\mathrm{Saccade}_{\mathrm{Var}}$-$Reach_{Fix}$). Figure 1A depicts the sequence for the $Saccade_{Fix}$-$\mathrm{Reach}_{\mathrm{Var}}$ task: Participants initially fixated a central fixation target comprising a black and white bull's eye (0.5° radius) on a uniform gray background. Their right index finger remained on a gray oval (0.6° × 0.65°) slightly below the eye fixation. At the beginning of each block, four equally spaced locations were marked by gray circles (2° radius) 8° away from fixation, with four white direction lines (0.1°-width, 0.4°-length) surrounding fixation, pointing towards them. One of the four locations (randomly selected) was framed in white, indicating the fixed motor target. Participants memorized this location, as it would constitute their saccade target throughout the whole block. Once stable eye and finger fixation was detected within a 2.5° radius virtual circle centered on the fixation targets, four streams of 1/f noise patches (2° radius) appeared at the marked locations. Each noise stream consisted of randomly generated 1/f noise patches windowed by a symmetrical raised cosine (radius 2°, sigma 0.5), flipping at 60 Hz (Fig. 1C). After a delay of 400–800 ms, one of the direction lines turned black, indicating the variable motor target. The location was selected randomly and could coincide with the fixed motor target. The onset of the line cue was the go-signal for both movements. Participants reached as fast and as precise as possible to the noise stream corresponding to the black line (reach target) and simultaneously saccaded as fast and precise as possible to the fixed saccade target cued in the beginning of the block. 50–150 ms after cue onset (within the movement latency), one of the 1/f noise streams was briefly replaced by an orientation-filtered noise stimulus, showing a 40° clockwise or counterclockwise orientation. This test signal was equally likely to appear at any of the four locations and was masked by the reappearance of non-oriented 1/f noise after 83 ms. After another 1000 ms the screen turned blank and participants indicated via button press in a non-speeded manner whether they had perceived the orientation to be tilted clockwise or counterclockwise, receiving auditory negative feedback for incorrect responses.

All other motor tasks had the same timing and stimuli, but differed in cueing procedure and pre-block instruction: In the $Saccade_{Var}$-$Reach_{Fix}$ task, participants were instructed to reach towards the fixed target and saccaded according to the variable cue. In the variable single movement tasks, no fixed target was marked at the beginning of the block and participants made a saccade or a reach according to the variable line cue, while keeping fixation with the other effector. In the fixed single movement tasks, instead of one line marking the variable target all lines turned black, functioning as the go signal for the single fixed eye or hand movement. The other effector remained at fixation.

Participants performed 12 experimental blocks (4 single, 8 combined-movement) of at least 140 trials each. We controlled online for broken eye and finger fixation (outside 2.5° from fixation), too short (<100 ms) or too long (>500 ms) movement latencies, and incorrect eye or hand movements (not landing within 2.5° from target). Erroneous trials were repeated in random order at the end of each block. Overall, participants made eye movement errors in 14.8 ± 2.3 (mean ± SE) % and finger movement errors in 17.9 ± 2.8% of the trials. To maintain a consistent level of discrimination difficulty across participants, a threshold task preceded the experiment, in which we determined the individual orientation filter strength (i.e. the visibility of the tilt) corresponding to 80% correct discrimination. The threshold task matched the main experiment, but with participants maintaining eye and finger fixation and the discrimination signal predictably appearing always at the fixed cued location.

*Experiment 2.* In Experiment 2 we investigated how attentional deployment to the different motor targets developed over time. We asked participants to execute single eye or hand, or combined eye-hand movements towards two variable and simultaneously cued target locations, and presented the test orientation at various time points after the motor cue.

The experiment comprised three motor tasks: variable eye movement (*Saccade*), variable reach movement (*Reach*), and variable eye - hand movement (*Combined*). The motor tasks had the same timing and stimuli, and differed only in the pre-block instruction. Figure 1B depicts the sequence for the *Combined* task, that was identical to Experiment 1, except for the following differences: (1) No fixed motor target was marked at the beginning of the block. (2) The variable motor targets were indicated by half of the eye fixation turning green (the left, right, upper, or lower half), revealing two potential motor targets (the two left, right, upper, or lower locations, respectively). Participants reached towards either of the two potential motor targets while simultaneously making a saccade towards the other – at free choice. In the *Saccade* and *Reach* tasks, participants were instructed to make only one movement (saccade or reach, respectively) to either of the potential motor targets – again at free choice –, while keeping fixation with the other effector. The onset of the colour cue also functioned as the go signal for the movement(s). (3) The discrimination orientation within of the 1/f noise streams appeared after a variable delay of 0–350 ms after cue onset. For a demonstration of the trial sequence see also Supplementary Movie S1.

Participants performed 12 experimental blocks (three of each motor task, beginning with the single movement tasks in random order) of at least 160 trials each. Overall, participants made eye movement errors in 12.5 ± 1.4 (mean ± SE) % and finger movement errors in 14.6 ± 1.73% of trials, which were repeated in random order at the end of each block.

**Data analysis.** In both Experiments we detected saccades offline based on the eye velocity distribution[47]. We measured finger movement onset and landing time, as well as landing position. We accepted trials (1) if eye and finger fixation were maintained within 2.5° from the fixation until cue onset, (2) if movement latencies were no shorter than 100 ms and no longer than 500 ms, (3) if the saccade and/or reach landed within 2.5° from the cued target, (4) if the passive effector maintained fixation in the single movement tasks, (4) if no blink occurred during the trial, and (5) neither eye nor finger movement started before the offset of the test orientation. We took the average percentage correct orientation discrimination performance (clockwise or counterclockwise) at the four tested locations as a proxy of attentional selection. In Experiment 1 we calculated difference scores by subtracting the respective performance at non-target locations from each motor target performance. For statistical comparisons we resampled our data and derived p-values by locating any observed difference on the permutation distribution (difference in means based on 1000 permutation resamples). For the time course analysis of Experiment 2, we binned the data separately for the different locations according to the SOA between motor cue onset and orientation discrimination probe offset (from 0 to 350 ms) in 11 time bins by using a 100 ms sliding time window stepping every 25 ms (first time bin 0 to 100 ms SOA, second time bin 25 to 125 ms SOA etc.). For each location, we then computed the average discrimination performance for each time bin and interpolated the data for the visualization in Fig. 3.

**Data availability.** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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## Author Contributions

N.H., D.A.-M. and H.D. conceived the study. N.H. programmed and conducted the experiments. N.H. and D.A.-M. analyzed the data. N.H. wrote the original manuscript and visualized the results. All authors edited and revised the manuscript and approved the final version.

## Additional Information

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## 2.4 Independent effects of eye and hand movements on visual working memory

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**Author Contributions:**

Nina M. Hanning developed the study concept, programmed the experiments, collected, analyzed, interpreted and visualized the data, and wrote the manuscript.

Heiner Deubel contributed to the study design and commented on the manuscript.

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# Independent Effects of Eye and Hand Movements on Visual Working Memory

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Both eye and hand movements have been shown to selectively interfere with visual working memory. We investigated working memory in the context of simultaneous eye-hand movements to approach the question whether the eye and the hand movement systems independently interact with visual working memory. Participants memorized several locations and performed eye, hand, or simultaneous eye-hand movements during the maintenance interval. Subsequently, we tested spatial working memory at the eye or the hand motor goal, and at action-irrelevant locations. We found that for single eye and single hand movements, memory at the eye or hand target was significantly improved compared to action-irrelevant locations. Remarkably, when an eye and a hand movement were prepared in parallel, but to distinct locations, memory at both motor targets was enhanced—with no tradeoff between the two separate action goals. This suggests that eye and hand movements independently enhance visual working memory at their goal locations, resulting in an overall working memory performance that is higher than that expected when recruiting only one effector.

**Keywords: working memory, saccades, reaching movements, motor processes, attention**

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## INTRODUCTION

Eye and hand movements have been shown to bind visual attention to their goal locations during movement preparation (Kowler et al., 1995; Deubel and Schneider, 1996; Deubel et al., 1998; Rolfs et al., 2013), and it has been suggested that the underlying attentional mechanisms are effector-specific and independent (Jonikaitis and Deubel, 2011; Perry et al., 2016; Hanning et al., 2018), i.e., the attentional benefit at one effector's movement target is not affected by the concurrent movement preparation of the other effector. Furthermore, both eye (Bays and Husain, 2008; Hanning et al., 2016; Ohl and Rolfs, 2017) and hand movements (Heuer et al., 2017) selectively enhance visual working memory at their action goals, presumably due to the associated deployment of attention (Hanning et al., 2016). Given the assumption of independent mechanisms that drive attention to eye and hand targets, it is conceivable that the two effector systems also separately interact with working memory. We therefore investigated spatial working memory performance in the context of simultaneous eye-hand movements. If eye and hand movements independently of each other enhance working memory at their target locations, any memory benefit observed at the eye target should not be affected by the concurrent preparation of a hand movement, and vice versa.

# METHODS

## Participants and Apparatus

Seven right-handed observers (three females, ages 24–32) participated in Experiment 1A, five of whom also completed Experiment 1B (two females, ages 25–32). Seven right-handed observers (three females, ages 24–32) participated in Experiment 2. All participants gave written informed consent. The protocols for the study were approved by and the study was carried out in accordance with the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München, in accordance with the Declaration of Helsinki. Gaze position was recorded using an EyeLink 1000 Tower Mount (SR Research, Osgoode, ON, Canada) at a sampling rate of 1 kHz. The experiment was implemented in Matlab (MathWorks, Natick, MA, USA), using the Psychophysics (Brainard, 1997; Pelli, 1997) and EyeLink toolboxes (Cornelissen et al., 2002). Stimuli were presented on a 45° inclined touchscreen (Elo 2700 IntelliTouch, Elo Touchsystems, Menlo Park, CA, USA) with a spatial resolution of 1,280 × 1,024 pixels and a vertical refresh rate of 60 Hz.

## Procedure

### Experiment 1A: Eye and Hand Movements

At the beginning of each block, participants were instructed to perform single eye movements (*EYE*), single hand movements (*HAND*) or simultaneous eye-hand movements (*EYE-HAND*) to certain target colors (see **Figure 1A**). Participants fixated a central fixation target (FT, radius 0.5 deg; deg indicates degrees of visual angle) on gray background, their right index finger remained slightly below the eye fixation. After 400–800 ms, three colored dots (red, green and blue, radius 1 deg) appeared at random angles on an imaginary circle 8 deg around fixation for 1,000 ms. Participants memorized the locations of these dots. After 1,250–1,750 ms, in 50% of the trials (*Movement trials*) the FT turned gray and participants performed the movement(s): for example, in the *EYE* condition, they looked to the location they memorized for the blue dot, in the *HAND* condition, they pointed to the location they memorized for the red dot, and in the *EYE-HAND* condition they looked to the blue and simultaneously pointed to the red location. In this example, the green dot served as a control location that had to be memorized but was not a motor target (colors were counterbalanced across participants). In the other half of trials (*Memory trials*), the FT did not change color and participants kept fixating. Instead, one of the dots reappeared and participants indicated via button press whether its location had changed clockwise or counterclockwise on the imaginary circle. They were instructed to perform the movement(s) as fast and precise as possible, the spatial memory task was not speeded. As *Memory trials* and *Movement trials* were randomly interleaved, participants always prepared the instructed movement(s), even though they actually moved in only half of the trials. This allowed us to investigate the effect of movement preparation on working memory, avoiding potential confounds induced by movement execution. We took location change discrimination performance as a proxy of working memory performance. See **Supplementary Information S1** for details about the procedure.

### Experiment 1B: Fixation Control

To disentangle the influence of attentional load from movement-related effects on working memory in Experiment 1A, we conducted a control experiment in which, instead of performing one or two movements, participants attended to one or two items. At the beginning of each block they were informed which of the memory items would be tested with a higher probability. To resemble the single and combined motor tasks of Experiment 1A, in separate experimental blocks either one (*1TAR*) or two targets (*2TAR*) received an increased likelihood to be tested. Memory task, timing and visual input were equivalent to the *Memory trials* of Experiment 1A (see **Figure 1B**), but we biased the test likelihood according to the pre-block instruction: in a *1TAR* block, only one item, e.g., the blue one, would re-occur in 80%, while the other two items re-occurred in 20%. In a *2TAR* block the blue or red item would re-occur in 80% of the cases (*2TAR*), while the green item only re-occurred in 20%. See **Supplementary Information S1** for details about the procedure.

### Experiment 2: Double Eye and Double Hand Movements

To assess whether the effects of eye and hand movements are effector-specific and independent of each other, in Experiment 2 we contrasted the effects of two movements—either one of each effector system or two movements within the same system. At the beginning of each block, participants were instructed to perform an eye movement (*EYE*), a hand movement (*HAND*), simultaneous eye-hand movements (*EYE-HAND*), double eye (*2EYE*), or double hand (*2HAND*) movements. After 400–800 ms of fixation, three colored dots (red, green and blue, radius 0.75 deg) appeared at randomly selected angles 8 deg around fixation for 1,000 ms (see **Figure 1C**). During the first 100 ms of the following 300 ms delay, the items were masked by a circular arrangement of multiple colored dots. Afterwards, the FT turned gray and participants performed the instructed movement(s). In the *2EYE* condition, for example, they could first look to the red, and immediately afterwards to the green location, at free choice. In the *2HAND* condition they instead performed double hand movements. After their movement(s), one of the dots reappeared and participants performed the location change discrimination task. See **Supplementary Information S1** for details about the procedure.

## Data Analysis

We detected saccades offline based on the eye velocity distribution (Engbert and Mergenthaler, 2006). In all Experiments we took location change discrimination performance (clockwise or counterclockwise) as a proxy of working memory performance. We initially computed the mean single subject performance for the different locations of each motor condition. For statistical comparisons we

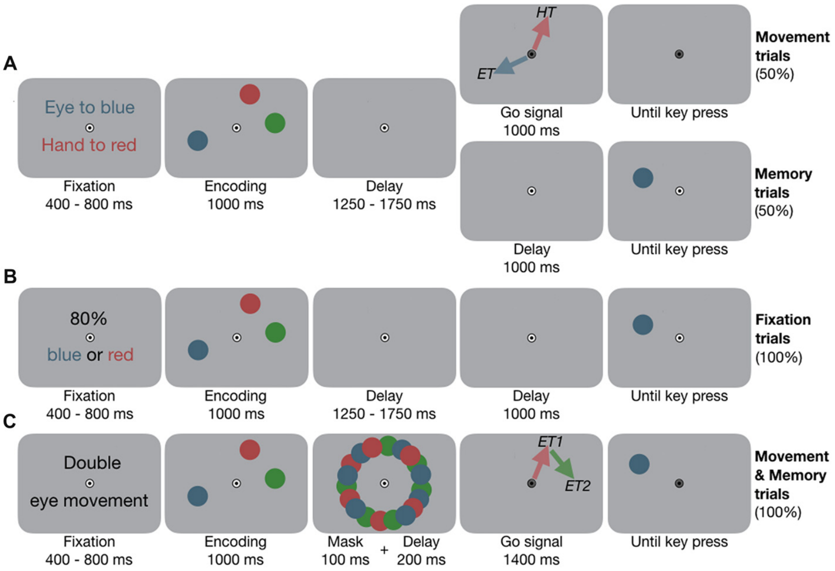

**FIGURE 1 |** Experimental design. **(A)** Experiment 1A, example condition eye-hand movements (EYE-HAND). Participants fixated the central bull's eye and placed their index finger slightly below. They encoded the locations of the three colored dots. In *Movement trials*, once the fixation target (FT) changed color, they performed the movements according to pre-block instruction. Red and blue arrows visualize the motor targets (*ET*, eye target; *HT*, hand target) and were not shown in the experiment. In *Memory trials*, the FT did not change color, instead one dot reappeared, and participants performed a location change discrimination task. **(B)** Experiment 1B, example condition two targets (2TAR). At the beginning of each block, participants were informed about which color(s)—either one or two—would be tested in 80% of the cases at the end of the trial. **(C)** Experiment 2, example condition double eye (2EYE). Participants encoded the locations. Once the FT changed color, they performed two successive eye movements towards any two of the memorized locations, e.g., first eye movement (*ET1*) to red, second eye movement (*ET2*) to green. Afterwards, any of the dots reappeared, and participants performed the memory task.

conducted permutation tests. We resampled the respective mean individual subject data pairs and derived *p*-values by locating any observed difference on the permutation distribution (difference in means based on 1,000 permutation resamples), next to which we report effect sizes (Cohen's *d*). To visualize group performance we averaged the individual means across participants.

# RESULTS

## Experiment 1A

Results are based on the analysis of the *Memory trials* (see **Figure 2A**). When participants prepared only an eye movement during the maintenance interval (*EYE*), we observed a clear memory benefit for items memorized at the eye target ($p = 0.001$, Cohen's $d = 3.364$). Likewise, when only a single hand movement was required (*HAND*), memory at the hand target was superior to motor irrelevant locations ($p = 0.001$, $d = 2.658$). Importantly, when participants simultaneously performed an eye and a hand movement towards different target locations (*EYE-HAND*), we found a memory benefit both at the eye ($p = 0.039$, $d = 2.240$) and the hand target ($p = 0.001$, $d = 2.578$) compared to non-target locations. Importantly, we observed no tradeoff compared to the respective single movement conditions, i.e., performance at each motor target was approximately as high as if just a single eye or hand movement was performed.

## Experiment 1B

In Experiment 1B (**Figure 2B**), when one item was attended, memory performance for this item was superior to the unattended items ($p = 0.001$, $d = 3.839$). Crucially, when participants payed attention to two items, we observed increased working memory performance for both attended items compared to the one unattended item ($p = 0.001$, $d = 1.941$), however—unlike the *EYE-HAND* condition of Experiment 1A—we also observed a tradeoff: the benefit at two attended items was significantly smaller than the benefit at a single attended item ($p = 0.001$, $d = 2.723$).

## Experiment 2

In Experiment 2 (**Figure 2C**), we again observed a memory benefit at the motor targets of single *EYE* ($p = 0.001$, $d = 4.309$) or *HAND* movements ($p = 0.001$, $d = 4.467$), as well as at both targets of simultaneous *EYE-HAND* movements (eye target: $p = 0.001$, $d = 3.159$; hand target: $p = 0.001$, $d = 3.362$), again without any tradeoff between the two. When participants performed two eye movements (*2EYE*), we observed a memory benefit at both eye targets compared to the non-target (first target: $p = 0.042$, $d = 1.254$; second target: $p = 0.013$, $d = 2.623$), but

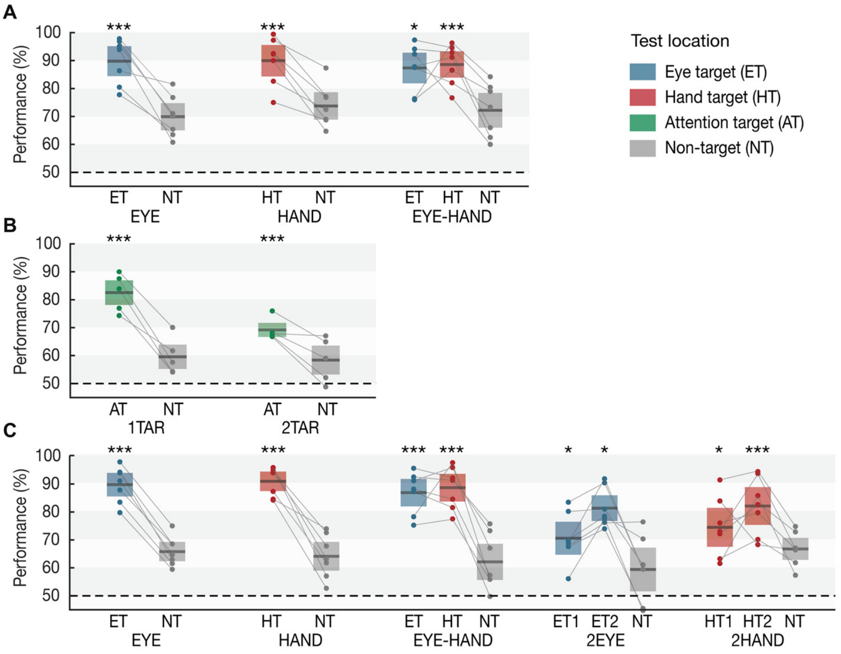

**FIGURE 2 |** Working memory performance in **(A)** Experiment 1A, **(B)** Experiment 1B and **(C)** Experiment 2 as a function of condition and test location. Horizontal lines within each whisker plot indicate the mean discrimination performance for each condition's motor targets, attention targets, and non-targets. Colored bars (eye: blue, hand: red, attention target: green, non-target: gray) show 95% confidence intervals. Dots connected by lines represent averaged individual subject data. Asterisks indicate significant differences between targets and the respective condition's non-targets (*$p < 0.05$, **$p < 0.01$, ***$p = 0.001$).

memory performance at both was significantly lower compared to the eye target in the *EYE-HAND* condition, i.e., when the eye movement was accompanied by a hand movement instead of a second eye movement. Likewise, in the *2HAND* condition, performance at both hand targets was increased compared to the non-target (first target: $p = 0.023$, $d = 0.747$; second target: $p = 0.001$, $d = 1.754$), but at both targets was significantly lower compared to the hand target in the *EYE-HAND* condition.

## DISCUSSION

When an eye and a hand movement were performed while maintaining spatial information, working memory performance at both motor targets was improved—approximately as much as if just a single eye or hand movement was made. This is surprising, as it is well established that our working memory capacity is limited (e.g., Luck and Vogel, 1997), and current working memory models assume that memory for one item can only be enhanced at the expense of memory for other items stored (e.g., Bays et al., 2009). We observed such typical memory tradeoff when participants attended to one or two items instead of performing movements: the average memory for two attended items was significantly lower than for one attended item—in contrast to what we found for one (eye or hand) compared to two (eye and hand) motor targets, in which case no tradeoff occurred. As the memory benefit at one effector's movement target was unaffected by the concurrent movement preparation of the other effector, we conclude that eye and hand movements independently of each other enhance working memory.

This finding mirrors the reported independent attentional enhancements at eye and hand targets (Jonikaitis and Deubel, 2011; Hanning et al., 2018), which are thought to result from effector-specific feedback loops between frontoparietal and posterior areas (Perry et al., 2016; Perry and Fallah, 2017). Likewise, visuospatial working memory is assumed to rely on recurrent feedback between prefrontal and posterior cortices (Hale et al., 1996; Chafee and Goldman-Rakic, 2000), and it has been hypothesized that this feedback activity is influenced by motor actions like eye or hand movements (Lawrence et al., 2001). Our data suggest that these movement-evoked effects on working memory are effector-specific: separate feedback signals from the frontoparietal networks serving eye and hand movement preparation may, independently of each other, improve the maintenance of visuospatial information, similar to their effects on visuospatial attention. In consistence with this hypothesis, we found a memory tradeoff between the motor targets of double eye or double hand movements, demonstrating that two movements originating from the same feedback network do not elicit independent memory benefits.

Our results challenge current working memory models that assume an overall limit, be it capacity or resource: contrary to the widespread belief, improved memory for a subpart of the stored content does not necessarily burden memory for the remaining content. Eye and hand movements independently of each other enhance visuospatial memory at their motor targets, resulting in overall memory performance that is higher than that expected when recruiting only one or no effector.

## AUTHOR CONTRIBUTIONS

NH developed the study concept and wrote the manuscript. HD contributed to the study design and provided critical revisions. Data collection and data analysis were performed by NH. Both authors interpreted the data and approved the final version of the manuscript for submission.

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## ACKNOWLEDGMENTS

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fnsys.2018.00037/full#supplementary-material

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## 2.5 Oculomotor selection underlies feature retention in visual working memory

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**Author Contributions:**

Nina M. Hanning participated in designing the study concept, programmed the experiment, collected, analyzed, interpreted and visualized the data, and drafted the manuscript.

Donatas Jonikaitis participated in designing the study concept, interpreting the results and in drafting the manuscript.

Heiner Deubel participated in designing the study concept, interpreting the results and commented on the manuscript.

Martin Szinte participated in designing the study concept, helped programming the experiment and analyzing the data, and participated in interpreting the results and drafting the manuscript.

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Rapid Report

# Oculomotor selection underlies feature retention in visual working memory

**Nina M. Hanning,[1,2] Donatas Jonikaitis,[1] Heiner Deubel,[1] and Martin Szinte[1]**
[1]*Allgemeine und Experimentelle Psychologie, Department Psychologie, Ludwig-Maximilians-Universität München, Munich, Germany; and* [2]*Graduate School of Systemic Neurosciences, Department Biologie, Ludwig-Maximilians-Universität München, Planegg-Martinsried, Germany*

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**Hanning NM, Jonikaitis D, Deubel H, Szinte M.** Oculomotor selection underlies feature retention in visual working memory. *J Neurophysiol* 115: 1071–1076, 2016. First published November 18, 2015; doi:10.1152/jn.00927.2015.—Oculomotor selection, spatial task relevance, and visual working memory (WM) are described as three processes highly intertwined and sustained by similar cortical structures. However, because task-relevant locations always constitute potential saccade targets, no study so far has been able to distinguish between oculomotor selection and spatial task relevance. We designed an experiment that allowed us to dissociate in humans the contribution of task relevance, oculomotor selection, and oculomotor execution to the retention of feature representations in WM. We report that task relevance and oculomotor selection lead to dissociable effects on feature WM maintenance. In a first task, in which an object's location was encoded as a saccade target, its feature representations were successfully maintained in WM, whereas they declined at nonsaccade target locations. Likewise, we observed a similar WM benefit at the target of saccades that were prepared but never executed. In a second task, when an object's location was marked as task relevant but constituted a nonsaccade target (a location to avoid), feature representations maintained at that location did not benefit. Combined, our results demonstrate that oculomotor selection is consistently associated with WM, whereas task relevance is not. This provides evidence for an overlapping circuitry serving saccade target selection and feature-based WM that can be dissociated from processes encoding task-relevant locations.

saccade; working memory; task relevance; visual feature

THE EFFICIENT INTERACTION with our visual environment depends on multiple processes working in parallel: selection and prioritization of parts of the visual scene, execution of rapid eye movements (saccades) to sample task information effectively, and keeping track of what is where in visual environment, even when the sensory input is not present anymore (Franconeri et al. 2013). However, the understanding of the links between those processes, visual selection, oculomotor selection, and visual working memory (WM), is limited, because they appear to be hard to dissociate from each other under experimental conditions.

It is established that the oculomotor system biases sensory processing during saccade preparation. Saccade target selection improves the detection of visual features such as shape and orientation (Deubel and Schneider 1996; Rolfs et al. 2011). The benefit at the saccade target comes at the expense of visual processing at other task-relevant locations (Deubel and Schneider 1996). These effects arise due to the oculomotor system enhancing processing in visual sensory cortex at saccade target locations (Ekstrom et al. 2008; Moore and Armstrong 2003).

The oculomotor system not only selects the immediate saccade target location but also maintains information about upcoming saccade targets (Gregoriou et al. 2012; Umeno and Goldberg 2001). Because this maintenance of spatial information can be observed in the absence of any visual input, the oculomotor system may at least partially underlie representations in spatial WM (Umeno and Goldberg 2001). This linkage also has been suggested by behavioral studies (e.g., Baddeley 1986). However, whether the oculomotor system also biases the retention of feature representations (in a similar way as it affects the perception of readily available visual information) remains unclear.

Evidence of links between oculomotor selection and visual WM is limited for several reasons. First, a location that has to be selected as saccade target is by definition also task relevant. Thus interactions between WM and saccade target selection could be driven by the task requirement to prioritize a certain location in space over the others, rather than by oculomotor selection per se. Furthermore, the oculomotor system represents task-relevant locations even during periods of fixation, when no saccade is made (Clark et al. 2012). Typical WM tasks made under fixation conditions therefore cannot distinguish whether the effects are due to visual or oculomotor selection. In the current study we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. We designed a task in which a memorized location was encoded as task relevant for one of two reasons: either to plan a delayed saccade to it (task relevant and saccade target) or to avoid making a saccade to it (task relevant but not saccade target). This allowed us to manipulate the involvement of the oculomotor system in WM. Our results demonstrate that the oculomotor system biases feature retention at saccade target locations, which is achieved by mitigating the loss of feature representations at locations to which saccades are prepared. This effect of oculomotor selection does not rely on saccade execution. We also show that information maintenance in visual WM is not mediated by mere task relevance.

## MATERIALS AND METHODS

*Subjects and apparatus.* Eight human observers (6 females, ages 24–26 yr, 1 author) completed the experiment. The protocols for the study were approved by the ethical review board of the Faculty of Psychology and Education of the Ludwig-Maximilians-Universität München, in accordance with German regulations and the Declaration of Helsinki. Gaze position was recorded using an EyeLink 1000 Tower Mount (SR Research, Osgoode, ON, Canada) at a sampling rate of 1 kHz. The experiment was controlled by an Apple Mac mini

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computer (Cupertino, CA) with an Intel Core i5 processor (Santa Barbara, CA), and the experimental software was implemented in MATLAB (The MathWorks, Natick, MA) using the Psychophysics and Eyelink toolboxes (Brainard 1997; Cornelissen et al. 2002). Stimuli were presented at a viewing distance of 60 cm on a 21-in. gamma-linearized LaCie Electron 21/108 CRT screen (Paris, France) with a spatial resolution of 1,024 × 768 pixels and a vertical refresh rate of 120 Hz.

*Stimuli and procedure.* The experiment comprised three types of blocked tasks (look, avoid, and fixate) that were visually identical but differed in the pre-block instruction (Fig. 1*A*). Subjects initially fixated a central black and white bull's eye (0.35° radius) on a gray background (60 cd/m$^2$). The trial started once stable fixation was detected within a 2.5° radius virtual circle centered on the fixation target. Two WM items appeared peripherally at randomly selected locations (7° away from fixation, separated by an angle of 60°, 120°, or 180°). The items were black (0.5 cd/m$^2$)-outlined (~0.4° width) radial frequency patterns (adapted from Wilkinson et al. 1998). Each pattern (Fig. 1*B*) had a mean radius of 1.4°, a randomly selected radial frequency of 3, 4, or 5 cycles, and an angular phase (rotation angle) of 1° to 360°. The amplitude was chosen randomly between 20% and 80% of the radius. After 950 ms, the items were masked by the brief presentation (50 ms) of 4 overlaid radial frequency patterns with random amplitude, radial frequency, and angular phase. After 200 ms, a red cue (0.8° radius dot, 20 cd/m$^2$) was flashed for 50 ms at the location of one of the two WM items. The cue did not indicate which of the items would be probed at the end of the trial. After a delay of 800–1,200 ms, in 75% of the trials (main trials), two blue response dots (radius 0.8°, 12 cd/m$^2$) were presented for 1,000 ms, separated from each other by an angle of 60°, 120°, or 180°. One of the blue dots appeared at the previously cued location. In the look task, subjects saccaded toward the dot presented at the previously cued location and subsequently back to the fixation target. In the avoid task, subjects instead saccaded to the noncued dot and back to the fixation target. Subject were instructed to perform the saccade task as fast and as precisely as possible. In the fixate task, subjects ignored the blue response dots and maintained fixation, allowing us to evaluate bottom-up attentional effects induced by the presentation of the cue. Although all tasks were visually identical, task load was increased in the look and avoid tasks, because subjects additionally had to maintain the cued location to correctly perform the saccade task. In 25% of trials in all 3 tasks, catch trials were randomly interleaved in which no blue response dots appeared and subjects maintained fixation. We probed WM by presenting one of the radial frequency patterns at its former location, which could be the cued or a noncued location. In 50% of trials the item reappeared with a changed radial amplitude. Subjects reported in a nonspeeded manner whether or not a change had occurred (same/different response). To avoid edge effects across the range, the amplitude of the probe never exceeded the range of the items to be memorized. After an initial training phase, subjects performed 30 randomly arranged blocks in 4 to 5 sessions on different days. Altogether they completed 900 trials of the look task, 900 trials of the avoid task, and 450 trials of the fixate task. To maintain a consistent level of difficulty, a threshold task (WM change detection task without eye movements) was performed before each session to determine the amplitude change corresponding to 80% correct change detection.

*Data analysis.* We detected saccades based on the gaze position velocity distribution (Engbert and Mergenthaler 2006). We accepted saccade trials in which we detected the saccade landing within 2.5° to the target and a return saccade to the fixation no later than 1,000 ms following target onset. We excluded trials with erroneously broken fixation (not within 2.5° from the fixation target). In total, we included 5,637 trials (78.3%) of the look task, 5,743 trials (79.8%) of the avoid task, and 3,001 trials (83.4%) of the fixate task. We computed WM performance as a percentage of correct change detection. For statistical comparisons we computed the mean values of 10,000 bootstrap samples that we drew with replacement from each condition's data set. We calculated the difference of their means and derived two-tailed *P* values from the distribution of these differences. We determined within-subject bootstrapped 95% confidence intervals (CIs) by normalizing each subject's mean across conditions and scaling the variance of the bootstrap distribution by $M/(M - 1)$, where $M$ is the number of within-subject conditions in the analysis before the bootstrap (Morey 2008).

## RESULTS

Subjects correctly saccaded to the instructed response dot in 91.3 ± 1.8% (mean ± SE) of trials in the look task and in 90.6 ± 1.3% in the avoid task. WM performance at cued and neutral locations combined did not differ between the look and avoid task (look: 67.9 ± 0.8% vs. avoid: 67.5 ± 1.1%, $P > 0.05$) but was significantly higher in the fixate task (71.0 ±

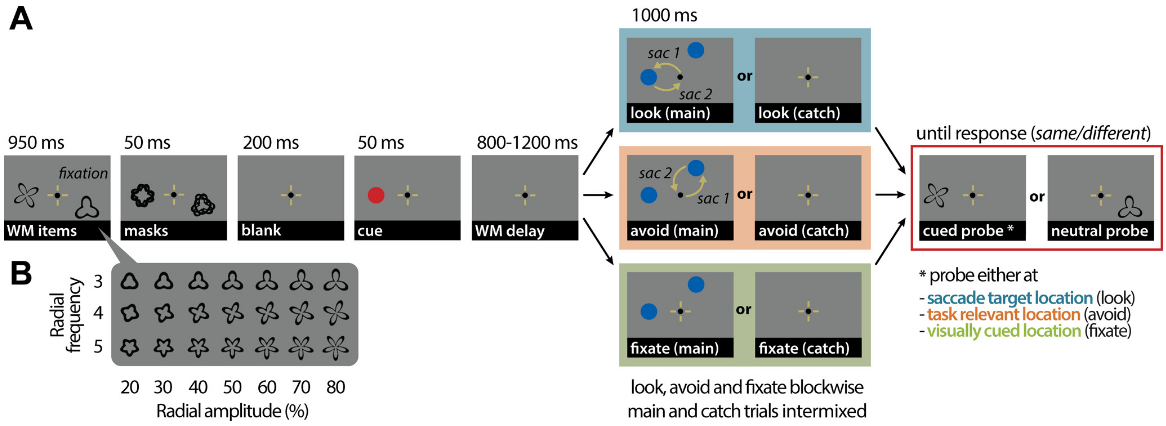

Fig. 1. Design and stimuli. *A*: task design. Subjects memorized 2 randomly chosen radial frequency patterns. Shortly afterward, a cue (red dot) was presented at the location of one of the working memory (WM) items. After a delay period, in 75% of the trials (main trials) 2 response targets (blue dots) appeared, one at the cued location and another at a new location. Subjects saccaded to the cued location and back to the center in the look task, or saccaded to the uncued location and back to the center in the avoid task. In the fixate task, subjects maintained fixation. Within all tasks, in 25% of the trials (catch trials) no response targets appeared and subjects kept central fixation. We probed WM by presenting one WM item at its former location with the same or a changed amplitude. *B*: WM items. The probe amplitude was either identical or increased/decreased relative to the pattern shown previously. Radial frequency was task irrelevant.

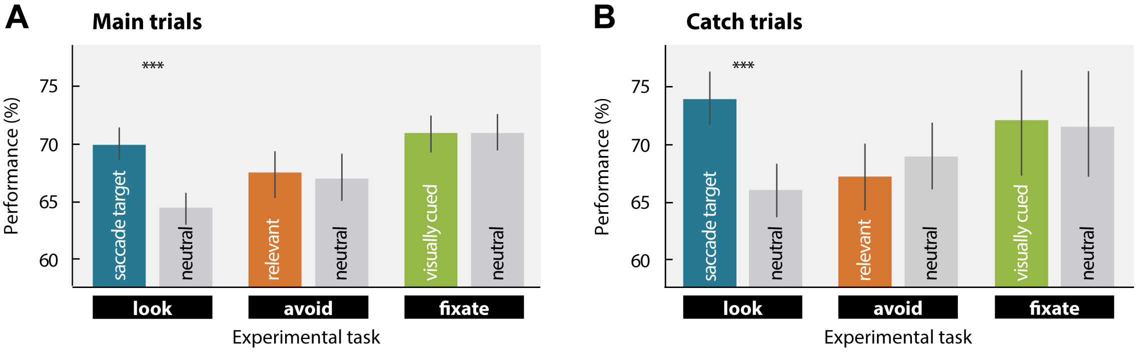

Fig. 2. WM performance for the different tasks and cueing conditions in the main trials (*A*) and the catch trials (*B*). Error bars indicate within-subject 95% confidence intervals (CIs). $^{***}P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

1.1%, $P < 0.001$). This suggests a comparably increased task load in both eye movement tasks. Average saccade latencies did not differ between look and avoid task (look: 272 ± 18 ms vs. avoid: 272 ± 14 ms, $P > 0.05$), which furthermore suggests a comparable task load in the two eye movement tasks. We compared WM performance at cued and neutral locations. In the main trials of the look task, that is, when subjects prepared and executed a saccade toward the cued location, WM performance was superior at the saccade target compared with neutral locations (Fig. 2*A*; saccade target: 69.8 ± 5.7% vs. neutral: 64.3 ± 6.2%, $P < 0.001$). In contrast, WM performance at task-relevant vs. neutral locations (avoid task) did not differ (Fig. 2*A*; task relevant: 67.4 ± 5.7% vs. neutral: 66.9 ± 5.1%, $P > 0.05$). The absence of a performance difference between cued and neutral locations in the fixate task rules out that attentional effects due to bottom-up attentional cueing induced the benefit at the saccade target in the look task (Fig. 2*A*; visually cued: 70.9 ± 7.0% vs. neutral: 70.8 ± 6.0%, $P > 0.05$). Thus, with identical visual input in all three tasks, the cued location was only superior when a saccade was prepared toward it.

The question arises whether saccade execution per se can account for the WM advantage at the saccade target. Analysis of the catch trials in the look task, in which subjects prepared a saccade but finally kept fixation, showed a very similar pattern of results (Fig. 2*B*; saccade target: 74.1 ± 5.3% vs. neutral; 66.1 ± 6.4%, $P < 0.001$), indicating that oculomotor selection was sufficient for the WM advantage. The decisive role of oculomotor selection as opposed to saccade execution also was observed in the avoid task. In 15% of the trials, the saccade target appeared at the uncued location, which was later probed for WM (to increase statistical power, we doubled the likelihood of the appearance of a response dot at the location of the uncued WM item). Simply executing a saccade (that could not be prepared over the WM delay) did not lead to a WM advantage at the saccade target (avoid task: memory probe at saccade target: 65.8 ± 5.6% vs. memory probe elsewhere: 67.0 ± 5.1%, $P > 0.05$). This demonstrates that the advantage was mediated by oculomotor selection rather than saccade execution.

To investigate the temporal dynamics of the effect, we binned the trials according to their WM delay duration in a 150-ms moving average. If oculomotor selection actually is the underlying factor, we hypothesized that the advantage at the saccade target would vary with the time allocated to oculomotor selection. Indeed, the analysis of the look task showed a decline of WM performance over time at nonsaccade targets (Fig. 3*A*; 800–950 ms: 66.7 ± 2.1% vs. 1,050-1,200 ms: 62.0 ± 2.3%, $P < 0.001$). In contrast, WM performance at the saccade target remained stable between the shortest and the longest delay (Fig. 3*A*; 800–950 ms: 69.5 ± 2.1% vs. 1,050-1,200 ms: 72.3 ± 2.3%, $P > 0.05$). Maintaining a location as a motor target thus seems to diminish the decay of feature representations held at the intended motor goal.

Our previous analysis suggested that oculomotor selection mediates the advantage at the saccade target. We reasoned that a poor selection should result in a slower saccade execution,

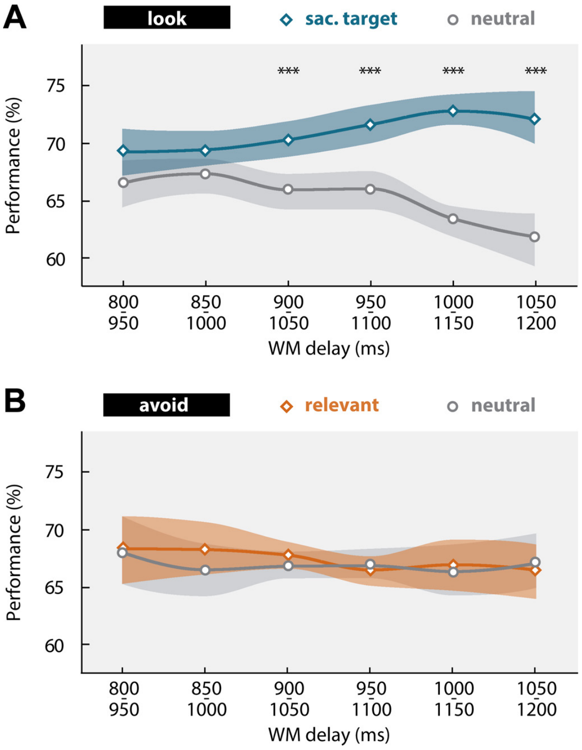

Fig. 3. WM performance as a function of memory delay (binned in 5 time windows) in the look task (*A*) and the avoid task (*B*) for main and catch trials combined. Colored areas indicate within-subject 95% CIs. $^{***}P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

hence longer saccade latencies. Therefore, we split the data according to the latency of the first saccade into three latency terciles. Indeed, the WM advantage at the saccade target disappeared in the last latency tercile, that is, for the slowest initiated saccades (Fig. 4*A*; saccade target: 66.6 ± 4.7% vs. neutral: 66.3 ± 4.7%, $P > 0.05$), confirming the need of an effective oculomotor selection for the improved retention of feature information at the saccade target. Importantly, saccade latencies did not differ between short and long WM delays in either the look task (800–950 ms: 270 ± 19 ms vs. 1,050-1,200 ms: 266 ± 15 ms, $P > 0.05$), nor in the avoid task (800–950 ms: 272 ± 15 ms vs. 1,050-1,200 ms: 268 ± 14 ms, $P > 0.05$). This rules out the possibility that the pronounced benefit for well-prepared saccades can be explained in terms of a longer WM delay, and thus preparation time.

## DISCUSSION

In the current study we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. In contrast to the saccade target location in the look task, the task-relevant location in the avoid task did not entail a saccade plan toward it, and any mechanisms actively maintaining that location did not interact with WM representations. Our results thus demonstrate that oculomotor selection, and not task relevance per se, mediates the retention of feature information at the saccade target. This is achieved by mitigating the loss of feature representations at locations marked as saccade targets, an effect due to saccade target selection, even without concomitant saccade execution.

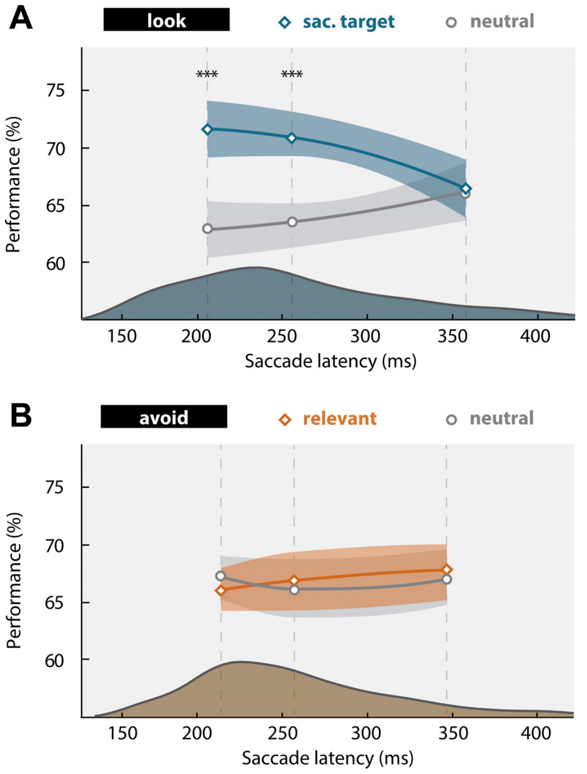

Fig. 4. WM performance as a function of saccade latency (binned in 3 terciles) for the main trials of the look task (*A*) and the avoid task (*B*). Histograms at *bottom* illustrate pooled (cued and uncued) distributions of saccade latencies. Colored areas indicate within-subject 95% CIs. $^{***}P < 0.001$, significant difference between cued (colored) and uncued (gray) locations.

Earlier studies have demonstrated links between task relevance and WM. In particular, asking subjects to select one of several objects maintained in WM was shown to increase the probability of its correct retrieval (e.g., Griffin and Nobre 2003; Souza et al. 2014). However, this work cannot dissociate effects of task relevance and oculomotor selection. Because the oculomotor system also represents spatial selection during periods of fixation (Clark et al. 2012), the reported beneficial effects of visual selection on WM could be mediated not only by the selection of task-relevant locations but also by the covert oculomotor selection of these task-relevant locations. In our study, the measurement of WM performance at the cued location in the avoid task allowed us to disentangle task relevance and oculomotor selection. In the avoid task, the cue only informed the subjects about where not to look but did not provide information about the future saccade target location. However, the cued location still was task relevant, because the selection of the correct saccade target after the delay was not possible without maintaining it in spatial memory. Therefore, this task uniquely provides a paradigm in which a stimulus is task relevant but to which it can be safely assumed that oculomotor selection does not occur. Because we did not find a WM benefit at these task-relevant nonsaccade targets, the frequently reported link between task relevance and WM is likely based on oculomotor programs.

The impact of oculomotor programming on feature WM has been investigated by earlier work (Bays and Husain 2008; Melcher and Piazza 2011; Shao et al. 2010). In line with our results, improved WM performance at the saccade target compared with neutral locations has been reported. However, by cueing the saccade target location before or together with the presentation of the WM material, these studies investigated encoding rather than retention. Because in visually guided saccade tasks sensory discrimination is best at the saccade target and worse at nontarget locations (Deubel and Schneider 1996; Rolfs et al. 2011), the observed WM benefits and costs in earlier studies cannot be clearly attributed to links between oculomotor selection and WM. They also could arise due to subjects being able to discriminate, perceive, and thus encode features at saccade target locations better than at nontarget locations. For this reason, we cued the saccade target location only after the WM items disappeared and were masked, ruling out any sensory explanation of oculomotor selection on feature-based WM. Furthermore, those earlier studies again cannot distinguish between task relevance and oculomotor selection, since in their designs selected saccade target locations also were task relevant.

Our findings from the fixate task are important for the interpretation of earlier work linking task relevance, oculomotor selection, and WM. We observed that performance decreased at both cued and noncued locations in the avoid task compared with the fixate task (Fig. 2). This suggests that adding a further task (preparing/executing saccades vs. keeping fixation) increases the task difficulty, leading to the overall decrease in WM performance. Therefore, earlier work cannot rule out that the impaired WM performance in saccade vs. fixation tasks is due to a general increase in task load instead of oculomotor selection (Hale et al. 1996; Lawrence et al. 2001; Lawrence et al. 2004; Pearson and Sahraie 2003; Postle et al. 2006). Our results, in contrast, are unbiased from task-load effects, because we compared WM at saccade target vs. neutral locations within the same task. The look and avoid tasks, furthermore, were matched in terms of visual input and task load. Thus the preserved WM performance at saccade goal locations (but not at task-relevant locations) can only be explained by the beneficial effect of saccade target selection. It is interesting to note that the WM benefit at the saccade target became pronounced only with longer WM delays. Figure 3*A* shows that the performance difference between saccade goal and neutral locations was significant only for delays of 900 ms and longer. Given the predictable WM delay of 800 to 1,200 ms, this may indicate that subjects delayed their saccade preparation until shortly before the temporal interval where the saccade target could be expected. Alternatively, the time course of our effect may rely on slow memory processes: as shown by previous work, the effect of postcues on WM necessitates time to evolve (e.g., Souza et al. 2014).

We observed that oculomotor selection consistently interacts with feature WM, whereas task relevance per se does not. In line with this finding, there is evidence that processes associated with maintaining task relevant locations that are not encoded as saccade targets differ from those maintaining saccade targets. A neurophysiological study reported that separate neuronal populations in the frontal eye fields (FEF) encode allowed (look task) and avoided (avoid task) locations (Hasegawa et al. 2004). Human functional magnetic resonance imaging (fMRI) data also suggest that different areas might represent these locations, with the FEF encoding saccade target locations in the look task and the parietal cortex encoding task-relevant locations in the avoid task (Curtis et al. 2004, 2005). This has led to suggestions of two distinct selection processes: prospective selection, involving oculomotor selection, and retrospective selection, which does not involve oculomotor selection (Curtis et al. 2004, 2005). Our findings suggest that only prospective selection interacts with feature-based WM representations.

In support of different mechanisms underlying representations of saccade target and task-relevant locations, an earlier study with a design similar to ours also observed different effects of oculomotor selection and spatial selection in look and avoid tasks (Dhawan et al. 2013). This study reported improved perceptual discrimination at saccade target locations in the look task and reduced discrimination at task-relevant locations in the avoid task. In the current study we did not observe a corresponding reduction in WM performance at task-relevant locations. However, our effects on WM are hard to compare with this earlier study, which focused on spatial selection during the presaccadic period close to saccade execution. Nevertheless, both studies likewise reveal a different pattern of processing associated with task-relevant locations and saccade targets, which is in line with the proposal that location maintenance differs in look and avoid tasks (Curtis et al. 2005).

In summary, we dissociated different variables interacting with WM: task relevance, saccade target selection, and saccade execution. Our findings suggest that oculomotor selection, and not execution, biases both visual selection and WM benefits at saccade target locations, with a corresponding cost at nonsaccade target locations. We show that oculomotor selection is consistently associated with WM, whereas task relevance is not. This effect is presumably mediated by an overlapping circuitry serving saccade target selection and spatial WM maintenance, and it is likely dissociable from circuits maintaining target locations that do not constitute saccade targets.

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## DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the authors.

## AUTHOR CONTRIBUTIONS

N.M.H., D.J., H.D., and M.S. conception and design of research; N.M.H. performed experiments; N.M.H. and M.S. analyzed data; N.M.H., D.J., H.D., and M.S. interpreted results of experiments; N.M.H. and M.S. prepared figures; N.M.H. and D.J. drafted manuscript; N.M.H., D.J., H.D., and M.S. edited and revised manuscript; N.M.H., D.J., H.D., and M.S. approved final version of manuscript.

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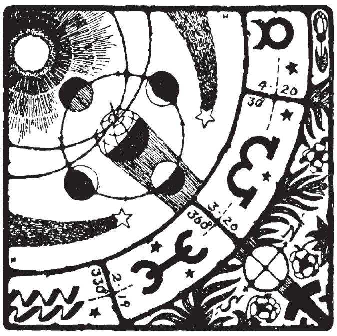

# General Discussion

The central aim of this thesis was to combine and extend current knowledge about the interplay of goal-directed actions with visual attention and visual working memory. The following sections will briefly summarize the five experimental studies that constitute the present thesis and discuss how their outcomes advance our understanding of how motor actions shape what we perceive and remember.

## 3.1 Summary of findings

The first study (**Chapter 2.1:** Hanning, Deubel, & Szinte, *in preparation*) compared the strength and weaknesses of a set of stimuli frequently used to investigate visuospatial attention: *Digital letters* (e.g., Deubel & Schneider, 1996), *Gabors* (e.g., Rolfs & Carrasco, 2012), *Crosses* (e.g., Born et al., 2012), *Pink noise* (Hanning et al., 2018), and *Random Dot Kinematograms* (e.g., Szinte et al., 2015). Using a dual-task paradigm that combines a discrimination task with a saccade task, we evaluated these stimuli regarding temporal and spatial specificity, along with their dependence on the tested set-size, and their influence on saccade metrics. Since it is well established that attention and oculomotor programming are tightly coupled (Kowler et al., 1995; Deubel & Schneider, 1996; Deubel & Schneider, 2003; Montagnini & Castet, 2007; Deubel, 2008), it is crucial to choose a measurement that does not perturb saccade programming when investigating attention. Otherwise, the applied method might affect precisely what it is supposed to measure, the deployment of attention, and thus bias the findings.

Results revealed that irrespective of the stimulus type, visual sensitivity increased at the cued location (i.e., the saccade target). The time course, spatial specificity, and magnitude of the detected pre-saccadic shift of attention, however, were specific to each stimulus. Most importantly, stimuli that rely on a sudden onset of the discrimination target systematically prolonged saccade latencies, while dynamically changing stimulus streams with embedded discrimination signals had no effect on oculomotor programming. The latter should thus be favored when investigating visual attention. Based on the results of this comparison study, we chose a novel pink noise stimulus (Hanning et al., 2018) to approach the subsequent research questions.

Having established the methodological basis to investigate visuospatial attention, the second study (**Chapter 2.2**: Hanning, Szinte, & Deubel, *submitted*), aimed to resolve a highly controversial topic concerning the interplay between oculomotor programming and visual attention. Motivated by the claim that attention can only be allocated to locations that are reachable by saccadic eye movements (Rafal et al., 1988; Craighero et al., 2001; Smith et al., 2004; Smith et al., 2010; Smith et al., 2012;

Boon et al., 2017), we measured the sensitivity to discriminate oriented noise patterns – a proxy for visual attention – within or beyond the oculomotor range. Using an eye abduction paradigm, participants performed saccadic eye movements to an exogenous cue, which occasionally appeared outside of their oculomotor range.

Contrary to previous findings, we found high visual sensitivity at cues presented both within and beyond each participant's oculomotor range. Even when participants aimed at a saccade cue outside of their oculomotor range, which resulted in considerable saccadic undershoot, we observed an unaltered deployment of attention to the cued location, with no attentional advantage at the actual saccade endpoint. This double dissociation – attention deployment to where the eyes cannot move, yet an absence of attention where they actually land – demonstrates that spatial attention is not necessarily coupled to the implemented motor program. Instead, attention can be shifted without restriction to locations to which saccades cannot be executed and is therefore not limited by the oculomotor range.

The third study (**Chapter 2.3**: Hanning, Aagten-Murphy, & Deubel, 2018) investigated whether eye and hand targets are attentionally selected in unison by a common mechanism (Bekkering et al., 1995; Song & McPeek, 2009; Huestegge & Adam, 2011; Khan et al., 2011; Huestegge et al., 2014; Nissens & Fiehler, 2017) or individually by independent attention systems (Jonikaitis & Deubel, 2011). We examined visual attention in coordinated eye-hand movements by taking visual sensitivity at the motor targets as a proxy for motor goal selection. Crucially, the two movements could be either directed to the same location, letting us investigate cumulative benefits, or to different locations, allowing the detection of an attentional trade-off between the eye and the hand target.

Here, results revealed that during simultaneous eye and hand movement preparation attention was allocated in parallel to the saccade and the reach targets, increasing at both until movement onset. When eye and hand movements were directed towards the same target, we observed a significantly greater attentional enhancement at the shared target than would be expected from either movement alone. Importantly, the attentional dynamics at both motor targets did not differ depending on whether one single eye or hand movement, or a combined eye-hand movement was prepared. Since the motor target selection mechanisms did not compete for attentional resources at any time during movement preparation, our findings demonstrate that separate, effector-specific attentional mechanisms select eye and hand movement targets.

The fourth study (**Chapter 2.4**: Hanning & Deubel, 2018) tested the conjecture of independent, effector-specific selection mechanisms in the framework of visual working memory. We based our study on previous work investigating working memory in the context of single movements (either eye or hand). These studies showed that both eye movements (Bays & Husain, 2008; Shao et al., 2010; Melcher & Piazza, 2011; Hanning et al., 2016; Ohl & Rolfs, 2017) and hand movements (Heuer et al., 2017) selectively enhance working memory at their motor targets. Since the memory benefits at action goals have been argued to arise from the shifts of attention associated with movement preparation (Hanning et al., 2016), and given the evidence of effector-specific systems for the attentional selection of saccade and reach targets (Jonikaitis & Deubel, 2011; Hanning et al., 2018), we hypothesized that eye and hand movements likewise may independently affect working memory.

To test this assumption, we asked participants to memorize several locations and perform eye, hand, or simultaneous eye-hand movements during the maintenance interval. Subsequently, we tested spatial working memory at the eye or the hand motor goal as well as at action-irrelevant locations. Results showed that memory at the motor targets of a single eye or hand movement was significantly improved compared to action-irrelevant locations. Remarkably, when participants performed an eye and a simultaneous hand movement to distinct locations, memory at both motor targets was enhanced – with no tradeoff between the two. This suggests that the two effector systems enhance working memory at their selected motor targets independently.

The final study (**Chapter 2.5**: Hanning, Jonikaitis, Deubel, & Szinte, 2016) dissociated the different variables interacting with working memory in the context of motor actions. In particular, we contrasted the impact of task relevance and oculomotor selection, two parameters that are interdependent and thus difficult to disentangle experimentally. In a modified version of the oculomotor delayed match- and nonmatch-to-sample task, participants maintained the shapes of radial frequency patterns in working memory while simultaneously either avoiding or selecting a specific location as a (delayed) saccade target. Critically, the avoided location in this paradigm was task-relevant but did not constitute a potential motor target.

We found dissociable effects of task relevance and oculomotor selection on working memory: While oculomotor selection was consistently associated with an increased working memory performance at the motor target, mere task relevance – without the usually coupled effect of oculomotor selection – did not yield a memory advantage. This indicates that the frequently reported memory benefit for task-relevant items (e.g., items with an increased likelihood of being tested) might, in fact, be caused by oculomotor selection.

## 3.2 How our actions shape what we perceive

Converging evidence ranging from single cell recordings to psychophysics has demonstrated that goal-directed actions like eye or hand movements massively shape sensory processing. The increased sensitivity at targets of upcoming motor actions – the so-called pre-motor shift of attention – has been observed with such consistency that it is considered a reliable marker of motor target selection.

The tight coupling of visual attention and saccadic eye movements led researchers to propose that any shift of spatial attention is contingent on pre-motor activation arising within the oculomotor system. Notable evidence in favor of this so-called *premotor theory of attention* (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Craighero et al., 1999) comes from studies in which the ability to execute eye movements is pathologically (Rafal et al., 1988; Craighero et al., 2001*;* Smith et al., 2004) or experimentally (Smith et al., 2010; Smith et al., 2012; Boon et al., 2017) restricted. Both lines of research report that visual attention, measured as expedited reaction times, could not be deployed unrestrictedly towards locations where the eyes could not move, and therefore may depend on oculomotor programming.

Approaching this hypothesis by using a sensitivity measure to assess visual attention (Hanning, Szinte, & Deubel, *submitted*), we obtained a strikingly different result: Visual attention can not only shift towards locations unreachable by saccadic eye movements but is also not necessarily linked to the executed saccade plan, i.e., its endpoint.

Our first observation – the unlimited deployment of attention outside the oculomotor range – contradicts previous studies with similar experimental designs (Rafal et al., 1988; Craighero et al., 2001; Smith et al., 2010; Smith et al., 2012). In contrast to our method, however, these studies rely on reaction time measurements to assess visual attention. It has been hypothesized that visual sensitivity and reaction time measures indicate different aspects of attention-modulated visual processing; while sensitivity is understood as a direct index of early visual processing (Bashinski & Bacharach, 1980; Luck et al., 1994), reaction times are thought to reflect these early processes and additional later decision and response-dependent operations (Santee & Egeth, 1982). Taking this distinction into account, our results may indicate that the previously reported attentional deficits observed outside the oculomotor range (Rafal et al., 1988; Craighero et al., 2001; Smith et al., 2010; Smith et al., 2012) reflect decision- and response-related limitations rather than the ability to shift attention per se.

By combining the measurement of visual sensitivity with a saccade task, our paradigm furthermore allowed us to dissociate the deployment of attention from the executed oculomotor plan. When participants attempted to saccade outside their oculomotor range, which necessarily resulted in considerable saccadic undershoot, sensitivity at their actual saccade endpoint was not enhanced, demonstrating that attention is not coupled to the executed motor program. Our observation is consistent with previous work reporting the absence of an attentional enhancement at the endpoint of undershooting saccades (Deubel & Schneider, 1996) or averaging saccades, i.e., saccades unintentionally landing in between two nearby saccade targets (Wollenberg et al., 2018). Both studies found that instead of being linked to the motor output, attention was deployed towards the intended target. Our study demonstrates that this link between attention and motor intention even exists when the target is out of reach.

Our finding may suggest that, unlike what is proposed by the premotor theory (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Craighero et al., 1999), visual attention is not the consequence of motor programming but rather its antecedent: Only once we have attentionally selected the prioritized motor target – based on "bottom-up" salience and "top-down" behavioral goals (Fecteau & Munoz, 2006) – the associated movement towards that location is executed. Vitally, attentional selection is not limited by the accessible motor range. That is to say, if the prioritized target is out of reach (e.g., when we intend to shift gaze outside the oculomotor range), visual attention still gets deployed to the targeted location, and only the associated motor execution fails (in the saccade example, due to limitations by the eye muscle system).

While this assumption directly contradicts, or rather reverses, the premotor theory of attention (Rizzolatti et al., 1987; Rizzolatti et al., 1994; Craighero et al., 1999), it is well in line with another established theoretical framework – the *visual attention model* (VAM; Schneider, 1995). VAM assumes a tight linkage between *selection-for-action* and *selection-for-object-recognition* and, importantly, postulates that motor programming is a consequence of attentional selection. Moreover, and similarly relevant for the present thesis, VAM suggests that visual attention (as a common mechanism) serves the selection of motor targets across different effector-systems. In other words, eye and hand motor targets are attentionally selected by the same shared system. This assumption not only complies with the eye-hand synchronization observed when we interact with objects in our environment (Neggers & Bekkering, 2000; Land & Hayhoe, 2001; Horstmann & Hoffmann, 2005), but also seems to be supported by the mutual influence of eye and hand movements detectable in various movement parameters (Bekkering et al., 1995; Song & McPeek, 2009; Huestegge & Adam, 2011; Khan et al., 2011; Huestegge et al., 2014; Nissens & Fiehler, 2017).

The results of our third study (Hanning et al., 2018), however, contradict this hypothesis. When investigating the spatiotemporal deployment of visual attention while preparing combined eye-hand movements, we found that attention was allocated in parallel to both targets – critically without any trade-off between the two. Our observation that the allocation of attention to one effector's motor target was unaffected by the concurrent preparation of the other effector's movement speaks against the assumption of a shared mechanism, and instead implies that effector-specific selection mechanisms independently drive attention to eye and hand motor targets. Though at first glance, independent attention mechanisms seem implausible and uneconomical in light of the frequently reported eye-hand coupling (Neggers & Bekkering, 2000; Land & Hayhoe, 2001; Horstmann & Hoffmann, 2005), they do allow flexibility: Independent systems – which can be coupled as required – enable individual targeting when necessary, e.g., to accomplish complex tasks such as tool use and bimanual manipulation.

## 3.3 How our actions shape what we remember

Several studies have demonstrated that goal-directed motor actions such as eye or hand movements – whether coupled to one another or performed independently – massively shape ongoing sensory processing. The active engagement with our environment, selecting motor targets and executing motor actions according to our current goals, requires our cognitive system to maintain representations of past sensory events.

Consistent with previous work investigating active visual working memory (Bays & Husain, 2008; Shao et al., 2010; Melcher & Piazza, 2011; Heuer et al., 2017; Ohl & Rolfs, 2017), the present thesis demonstrates that our cognitive system not only effectively copes with the sensory changes resulting from motor actions, but that our own movements selectively bias memory towards behavioral relevance (Hanning et al., 2016; Hanning & Deubel, 2018). Crucially, the motor-elicited memory enhancements at action goals appear to be effector specific and largely independent of each other. When we simultaneously perform an eye and a hand movement while memorizing spatial information, memory for content maintained at both motor targets is improved without any tradeoff between the two (Hanning & Deubel, 2018).

The observation that during combined eye-hand movements memory performance can be enhanced at two locations without any cost is remarkable given that working memory is widely considered to be limited in capacity. The precise nature of this limitation is still under debate. Some classic models posited that only a fixed, small number of items can be stored, such as *Miller's magical number seven* (Miller, 1956) or *Cowan's four* (Cowan, 2001). Others proposed that working memory information is retained in three or four independent "slots" (Luck & Vogel, 1997; Luck & Vogel, 2013). According to *slot models*, an item is either stored in one of these memory slots with high precision, or not, in which case it is not remembered at all. Such all-or-none conceptualization is rejected by *resource models* which assume that the capacity of working memory is determined by the overall quality or precision with which the information is maintained, rather than by an upper limit of objects that can be stored (Palmer, 1990; Wilken & Ma, 2004; Bays & Husain, 2008). According to this view, a limited overall working memory resource is flexibly distributed among the various elements of a scene. The more resources allocated to a particular item, the more precisely it can be recalled.

In our memory studies, participants only memorized two (Hanning et al., 2016) to three (Hanning & Deubel, 2018) items or locations – a number well below the proposed slot limit (Luck & Vogel, 1997). According to the original slot model, all information should thus be memorized with high precision. Since we still observed a pronounced modulation of memory performance (close to perfect memory at motor targets, significantly lower performance at action-irrelevant locations), our results, at first glance, seem to be rather consistent with a resource view of visual working memory; the execution of a goal-directed movement led to an increased allocation of memory resources to the corresponding motor target.

According to a model that assumes a limited memory resource, a prioritized assignment of processing capacities to a particular item should inevitably result in deteriorated memory of the remaining stored content. This, however, is not what we observed in the context of combined eye-hand movements: Memory performance at both motor targets was considerably enhanced, remarkably at no cost. Thus, contrary to the widespread belief, improved memory for a subpart of the memorized information does not necessarily burden memory of the remaining content. Instead, the simultaneous recruitment of two effector-systems leads to a higher memory performance than when programming only one movement.

In this regard, our finding challenges current perspectives on visual working memory: While resource models would not have predicted the observed independent memory enhancements at eye and hand movement goals, slot models fail to explain why action-irrelevant locations could not access memory despite available memory slots.

## 3.4 Conclusion and future perspectives

The present thesis investigated how eye and hand movements interact with visual attention, visual working memory, and with each other. We conducted a series of experiments in which participants performed eye movements, hand movements, or combined eye-hand movements, either towards different or the same motor target, while we simultaneously tested attention or working memory performance. In summary, we found a strikingly similar pattern both in the attention and working memory domains: Eye and hand movements independently of each other affect our perception as well as our memory representations. This similarity may suggest a shared neurophysiological basis for the observed motor-induced attention and memory modulations.

The link between goal-directed movements and visual perception is rather well understood. Each layer of our hierarchical visual system encodes certain aspects of the available information in retinotopic coordinates, i.e., adjacent locations in the actual visual scene are represented by adjacent populations of neurons in the layer. While early processing stages encode specific stimulus features (e.g., orientation in V1, contour in V2), layers at the top of the hierarchy, frequently referred to as *priority maps*, are agnostic to feature details. Instead, they integrate “bottom-up” saliency information across various feature dimensions with the current behavioral relevance for each part of the visual scene. Activity within these priority maps is tightly linked to motor preparation (Fecteau & Munoz, 2006; Bisley & Goldberg, 2010; Zelinsky & Bisley, 2015; Rolfs & Szinte, 2016) and in line with the assumption of separate, effector-specific attentional mechanisms (Deubel & Jonikaitis, 2011; Hanning et al., 2018), there is evidence that saccade and reach preparation rely on different priority maps (**Figure 2**). While FEF and LIP are involved in saccade preparation, PRR encodes the behavioral priority for reach movements (Snyder et al., 1997; Bisley & Goldberg, 2003; Lawrence & Snyder, 2009). If a stimulus becomes behaviorally relevant for a given effector, activity at the corresponding location in the respective priority map increases and triggers a feedback signal to earlier visual areas (Schall, Morel, King, & Bullier, 1995; Stanton, Bruce, & Goldberg, 1995). The back-projected signal enhances the responsiveness of early visual neurons (Moore & Armstrong,

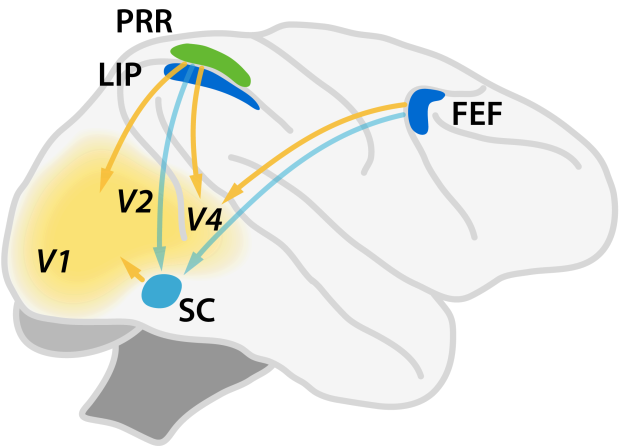

**Figure 2**. Effector-specific feedback connections associated with motor-related attention modulations. Lateral surface of a macaque brain showing parts of the eye and hand motor control networks comprising the frontal eye fields (FEF), the lateral intraparietal area (LIP), the parietal reach region (PRR) and the superior colliculus (SC), as well as their feedback projections onto earlier visual processing regions (V1, V2, V4).

2003; Armstrong, Fitzgerald, & Moore, 2006) and accounts for the multitude of attentional modulations observed within the visual cortex.

Our findings demonstrate that motor preparation in the eye and the hand movement systems produces independent shifts of attention (Hanning et al., 2018), supporting the idea that eye and hand movement targets are represented in separate, effector-specific priority maps, such as FEF, LIP or PRR (Perry, Amarasooriya, & Fallah, 2016; Perry & Fallah, 2017). At the subcortical level, the SC receives projections both from oculomotor as well as from hand-related areas and reportedly encodes priority regardless of the effector (Song et al., 2011; Borra et al., 2012; Song & McPeek, 2015), enabling this site to mediate eye-hand coordination and account for the frequently observed coupling of the two effector systems.

The effector-specific working memory enhancements that we observed at eye and hand movement targets (Hanning & Deubel, 2018) might indeed be based on on similar back-projections. Comparable to the attention domain, visuospatial working memory is assumed to rely on recurrent feedback between prefrontal and posterior cortices (Hale, Myerson, Rhee, Weiss, & Abrams, 1996; Chafee & Goldman-Rakic, 2000). Moreover, it has been hypothesized that this feedback activity is influenced by motor actions like eye or hand movements (Lawrence et al., 2001). Our data suggest that these movement-evoked effects on working memory are effector-specific; separate feedback signals from the frontoparietal networks serving eye and hand movement preparation may, independently of each other, improve the maintenance of visuospatial information – similar to their effects on perception.

The observation of effector-specific, independent attention and memory advantages raises the obvious question as to whether the simultaneous recruitment of the oculomotor and the hand movement systems increases overall cognitive capacity. Although during combined eye-hand movements, attention was simultaneously enhanced at both motor targets without any trade-off – possibly indicating an overall increase in attention capabilities (Hanning et al., 2018) – our paradigm does not allow us to determine whether the parallel allocation of processing resources towards the motor targets was detrimental to attentional deployment towards the remaining action irrelevant locations (since visual sensitivity at those locations was close to chance level already when performing only a single movement). Only if such decline at non-motor targets can be ruled out, the simultaneous sensitivity enhancement at separate effectors' motor targets can be interpreted as an increased attentional capacity, achieved by motor preparation within separate effector systems. A framework suitable to test this hypothesis is the *theory of visual attention* (TVA; Bundesen, 1990; see Bundesen & Habekost, 2008 for a more recent review), which is designed to reveal differences in attention capacity. A future line of research should apply this established TVA paradigm to combined eye-hand movements in order to determine whether the simultaneous programming of multiple actions within separate effector systems actually increases the overall attention capacity.

Moreover, the neurophysiological basis of our observed independent sensitivity improvements at eye and hand targets requires further investigation. For the oculomotor system, it has been shown that subthreshold microstimulation of FEF transiently enhances visual responses in extrastriate area V4 (Moore & Armstrong, 2003; Moore et al., 2006) and likewise improves performance in attention tasks (Moore & Fallah, 2004). This has been taken as evidence that priority map-generated feedback signals project back from FEF to early visual areas, and in turn sharpen perception. To test our assumption that effector-specific feedback projections separately enhance visual processing, single-cell recording studies should clarify whether the simultaneous stimulation in effector-specific priority maps (e.g., LIP and PRR) leads to spatially separated enhanced responses in early visual areas.

Another question arises pertaining to the *visual attention model* (VAM; Schneider, 1995). How does *selection-for-action* – which, as we demonstrate is effector-independent – interact with *selection-for-object-recognition*? In other words, is the voluntary deployment of attention likewise independent of the observed effector-specific pre-motor attention? Future research should investigate how attention shifts towards eye and hand targets are affected by the simultaneous requirement to endogenously focus attention to yet another location. These results would provide insights into whether our cognitive system possesses yet another independent selection mechanism, and if not, how our ability to voluntarily prioritize particular locations or features is obstructed by motor selection – or vice versa.

Finally, the most pressing question concerning visual working memory is whether the effector-independent enhancements we observed regarding spatial memory (Hanning & Deubel, 2018) also apply to the feature domain. Previous work investigating memory in the context of single movements (either eye or hand) has already reported increased memory at the motor targets of goal-directed eye or hand movements for various visual features (Bays & Husain, 2008; Melcher & Piazza, 2011; Hanning et al., 2016; Heuer et al., 2017; Heuer & Schubö, 2017; Ohl & Rolfs, 2017). In light of our results, it seems plausible that these feature memory benefits likewise arise separately for each effector. This would further challenge current perspectives on visual working memory by demonstrating that the overall memory capacity can be improved through the recruitment of multiple effectors.

To conclude, both visual attention and visual working memory are finely tuned to meet the challenges of active behavior. While we engage with the environment, our eye and hand movements selectively enhance our visual processing of the currently most relevant aspects of the scene and likewise bias our memory capacities according to behavioral priority. This allows us to process relevant items in detail while precisely keeping track of what is where despite the constant changes in the visual environment caused (in part) by our own actions. To ensure maximum flexibility, the motor-induced attention and memory modulations are effector-specific and largely independent. In this way, our cognitive system makes optimal use of its attention and memory resources in the service of goal-directed and intelligent behavior.

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# List of Publications

## Published Articles

Hanning, N. M., & Deubel, H. (2018). Independent effects of eye and hand movements on visual working memory. *Frontiers in Systems Neuroscience*, *12*, 37.

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), 9434.

Hanning, N. M., Jonikaitis, D., Deubel, H., & Szinte, M. (2016). Oculomotor selection underlies feature retention in visual working memory. *Journal of Neurophysiology*, *115*(2), 1071-1076.

## Published Abstracts

Hanning, N., & Deubel, H. (2018). Measuring presaccadic attention without distorting it: A novel dynamic noise paradigm to investigate visuospatial attention. *Journal of Vision*, *18*.

Hanning, N., Deubel, H., & Szinte, M. (2017). Sensitivity measures of visuospatial attention. *Journal of Vision*, *17*(10), 673.

Hanning, N., Aagten-Murphy, D., & Deubel, H. (2016). Attentional competition between reach target and saccade target selection. *Journal of Vision*, *16*(12), 1034.

Hanning, N., Dhawan, S., Jonikaitis, D., Deubel, H., & Szinte, M. (2015). Maintenance of saccade goals boosts working-memory. *Journal of Vision*, *15*(12), 539.

# Eidesstattliche Versicherung / Affidavit

Hiermit versichere ich an Eides statt, dass ich die vorliegende Dissertation “Visual attention and working memory in action: How eye and hand movements shape what we perceive and remember” selbstständig angefertigt habe, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und stets nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

I hereby confirm that the dissertation “Visual attention and working memory in action: How eye and hand movements shape what we perceive and remember” is the result of my own work and that I have only used sources or materials listed and specified in the dissertation.

München, den 25.10.2018
Munich, 25.10.2018

Nina M. Hanning

Unterschrift / signature