Graduate School of
Systemic Neurosciences

LMU Munich

ATTENTIONAL DYNAMICS BEFORE COORDINATED EYE AND HAND MOVEMENTS

Donatas Jonikaitis

Dissertation

at the Graduate School of Systemic Neurosciences

of Ludwig-Maximilians-University Munich

Munich, October 2010

Supervisor: prof. Heiner Deubel

Second expert appraiser: prof. Torsten Schubert

Date of the oral defense: February 1st, 2011

ACKNOWLEDGMENTS

I would like to thank Heiner Deubel for his supervision, guidance and advice, which helped to shape the present work. I also thank him for sparking my interest in pursuing the research path. I must also thank Torsten Schubert and Andreas Straube for their advice and discussions during my PhD. I thank Patrick Cavanagh for an invitation to his lab which proved extremely useful. Many of the ideas and directions of the work presented here were affected by discussions with my fellow friends, Martin Rolfs, Michael Hegenloh, Dragan Rangelov and Saurabh Dhawan. I also wish to express my gratitude to GRK 1091 and Graduate School of Systemic Neuroscience, without whose financial support this work would not have been possible, to participants JP, SB, VS & BT who did almost every single experiment presented in this thesis and Birgitt Assfalg who helped with data collection. Last, but not least, I thank family in Lithuania and my friends in Munich who made my stay here enjoyable - Jasmine Su Yi Huang, Lana Ilankovic, Christian Stoessel, Georgiana Juravle, Constanze Hesse, Jose David Perez & Boris Tchitchanov. Those were great three years!

TABLE OF CONTENTS

CHAPTER I

GENERAL INTRODUCTION AND DISCUSSION

INTRODUCTION

As opposed to typical laboratory paradigms, the natural scenes that we must negotiate with daily contain a wealth of potential movement targets. Hence, a selection process that selectively delivers the spatial coordinates of the intended movement target is crucial for the accuracy of both eye and hand movements. While it is well known that the motor systems of eye and hand are coordinated with each other, it remains a matter of debate whether the goal selection system and the resulting representations of the target location underlying eye and hand movement planning are shared or separate. So far, both psychophysical and neurophysiological evidence related to this question have been inconsistent. For instance, some studies have observed that saccade and reach locations are selected in parallel systems (Sailer et al., 2000; Snyder, Batista & Andersen, 1997), whereas others reported evidence for shared movement goal location selection (Bekkering et al., 1994; 1995; Song & McPeek, 2009).

Several lines of evidence have shown that attention is shifted to goals of future movement targets as a direct consequence of movement planning (e.g., Deubel & Schneider, 1996; Moore & Fallah, 2004). In the work described in this thesis, we used the deployment of visuospatial attention as an index of target selection in early movement planning. We found striking evidence, consistent across a variety of paradigms and situations, that goal selection for eye and hand movements is done in a parallel and independent manner. However, a number of possible interactions have to be taken into account to correctly interpret these results. For example, the reliance of the reaching system on gaze-centered representations suggests that this could be one of the potential sources leading to the interactions observed between saccade and reach planning. Another source of interaction could be that attentional signals related to saccade and reach planning might be represented on a common attentional priority map.

I will first present a detailed discussion of the various findings related to the debate on common versus parallel eye-hand movement goal selection systems in movement planning. This will be followed by a discussion of studies that demonstrate a close coupling between movement planning and attentional shifts, and how this coupling could be used to investigate saccade and reach movement planning. Lastly, I will introduce the five studies constituting this PhD thesis which while suggesting that eye and hand movement goal selection relies on parallel, independent systems, also demonstrate considerable cross-talk between the two systems.

EYE AND HAND MOVEMENTS ARE COUPLED

Two recent studies (Land, Mennie, & Rusted, 1999; Hayhoe, 2000) looked into how eye and hand are coordinated in everyday situations such as making a sandwich or preparing a cup of tea. The results were similar in both studies: participants usually looked at the object first, then reached for it or manipulated that object. The generated movements were coupled – saccades and reaches started almost simultaneously, and they were directed to the same object. The authors suggested that such coupling might be functional – looking at the object which is to be manipulated by the hand helps to gather the spatial information necessary for the manipulation (Land & Hayhoe, 2001). For example, participants would look at the sugar bowl before reaching for it, or look at the water tap before opening it.

However, such observations also raise the question of what cognitive and neural mechanisms are behind this coordination. One possibility is that this behavior arises simply because it is advantageous to coordinate eye and hand movements. Definitely, it is an optimal scenario when both effectors – the eye collecting visual information and the hand acting upon it – are geared towards the same goal. Alternatively such a behavior may reflect a basic limitation of eye and hand movement planning. That is, the underlying processing mechanism might have a limited capacity and can not plan multiple movements at a time. In other words, do we coordinate our eye and hand movements the way we do because it is the best strategy, or because we can not do otherwise?

One of the most influential studies about the processing of visual information before coordinated eye-hand movements was done by Prablanc and colleagues (1979). The authors observed that reaching accuracy declined if participants had to reach for the object, but were not allowed to look at it, or if the reaching movement goal disappeared with saccade onset. Removing vision of the subject’s hand increased reaching errors further. The results of this study seem to agree with the just discussed observations – looking at the object that we reach for produces the most precise reaching – and this is why it could be the preferred mode of coordinating eye and hand movements. Additionally, the authors concluded that after the initial visual processing “commands sent to oculomotor system and to the hand motor system seem to be organized more in parallel than in series” (page

123). A moderate correlation (coefficients in the range of 0.4-0.5) between eye and hand movement errors led to this conclusion. These results initiated a line of research trying to answer the following questions: does the planning of eye and hand movements rely on single, shared mechanism, or do these processes run in parallel at some stages (and at which stages)?

SHARED REPRESENTATIONS

There is, thus, ample psychophysical evidence that we usually look where we reach, and that reaches are most precise when we do so. One line of research claims that this eye-hand coupling originates from a shared, limited capacity mechanism. Bekkering and colleagues have demonstrated this coupling in two different experimental situations. First, the authors observed that eye movement latencies were longer if participants reach for the same object simultaneously (Bekkering et al., 1994; Bekkering et al., 1995; also reported by Sailer et al., 2002; but see Lünenburger, Kutz & Hoffmann, 2000). Target localization seemed to be a determining factor for this effect: saccade latencies increased only if a simultaneous reach to an object was required, but not when a button had to be pressed. Eye movement latencies also increased if participants did not know in advance where they will have to reach. Importantly, these results suggest that goal selection for eye and hand movements might be coupled at visual processing stages as early as object localization. This coupling could also be "associated with selective, attentional processes of where to look and point (Bekkering et al, 1995; page 482)". This last interpretation underscores the fact that a shared, limited-capacity mechanism underlies eye and hand movement goal selection.

Additional evidence for these suggestions came from a series of studies on "gaze anchoring" by Neggers and Bekkering (2000, 2001, 2002). They demonstrated that participants were unable to start a saccade to a newly appeared object while they were reaching for the object they were currently looking at. Moreover, participants' saccade latencies were not shorter when the new object was shown during the hand movement – in other words, the saccadic system did not benefit from the prolonged preview of the new saccade goal. This seems to indicate that the analysis of the new stimulus by the saccadic system is delayed till the ongoing reach is executed.

On the other hand, Song and colleagues have demonstrated that reaching trajectories could also reflect eye and hand movement coupling (Song & McPeek, 2009; Song & Nakayama, 2009; Song & Nakayama, 2008). In a number of visual search tasks participants (both, humans and monkeys) had to reach for a unique colored target among differently colored distractors. As eye movements in those tasks were not constrained, participants usually looked at the target first, and only then reached for it. Frequently participants made two or three saccades before fixating the target. The trials in which the reach to the target started after participants had looked at it, reaches were directed straight to that target. On the other hand, when participants started reaching while they looked at the distractor, their reach trajectories deviated towards that distractor. Song and colleagues interpreted these results as a demonstration for a common mechanism that selects targets for both reaches and saccades.

However, as we will discuss in some detail later, the findings of Bekkering and colleagues could also be given an alternative interpretation. Also, the findings of Song and colleagues could reflect a different effect than shared eye-hand movement target selection. It is known that reach trajectories are affected by any targets present in the visual field that are attended, regardless of whether simultaneous saccades are executed or not (Howard & Tipper, 1997; Song & Nakayama, 2006; Song, Takahashi & McPeek, 2008). The same has also been demonstrated for saccades deviating away from distractors that need to be suppressed (Tipper, Howard & Paul, 2001; van der Stigchel, 2010; van Zoest, van der Stigchel, & Barton, 2008). Thus, it is debatable how much movement trajectory deviations can really tell us about the shared or independent nature of representations used for eye and hand movement planning.

PARALLEL REPRESENTATIONS

Contrary to the aforementioned claims, a number of studies have instead suggested that eye and hand movement planning is based on parallel processes and representations. First, this position was supported by a series of studies showing low correlations between saccade and hand movement end-point errors (Biguer et al., 1982; Gielen et al., 1984; Prablanc et al., 1979; Sailer et al., 2000; but high correlations were reported by Herman et al., 1981). If both, eye and hand, used identical spatial information before initiating the movements, then correlations should have been high. However, correlation level does not necessary imply independent or shared target selection mechanism. These high correlations could alternatively be explained by shared perceptual input, without the need to invoke shared target selection for reaches and saccades. Similarly, low correlations could be attributed to independent noise appearing before saccade and reach generation (Sailer et al., 2000).

An alternate way of investigating parallel or shared processing before eye and hand movements is to provide a stimulus for an action, and to observe whether target selection for saccades differs from that for reaches. This approach has recently been used in a study by Stritzke and Trommershäuser (2007). Their participants had to quickly point to a rewarded target and to avoid pointing to a more salient, but forbidden object. It was observed that while the hand went immediately to the highly rewarded object, the eyes fixated the more salient object at that time. Usually the next saccades were directed to the hand target only once the reaches had started. This suggests that different objects were selected at the same time for reaches and saccades. Furthermore, Sailer and colleagues (2002) showed that the global effect – the tendency to reach and look in between target and distractor, as if averaging the location of both of them – affects eye and hand movements differently. Interestingly, the global effect observed for saccades and reaches was different even when both actions were performed simultaneously.

But even if we consider eye and hand movement target selection as parallel, some signs of cross-talk were found . Eventually saccades were directed to the reach object in the Stritzke and Trommershäuser (2007) study, and the global effect (Sailer et al., 2002) showed cross-talk when combined saccades and reaches were planned as compared to single eye or hand movements. However, these two studies elegantly reveal different representations used for eye and hand movement, based on different aspects of the same visual stimulation.

Naturally, that is not the end of the debate whether saccade and reach movement goal selection depends on common or parallel mechanisms, as neurophysiological studies present an even more complex picture.

PARALLEL ACTION SELECTION SYSTEMS

Posterior parietal cortex (PPC), centered on the intraparietal sulcus, is known to be involved in movement goal selection for saccades and reaches. Anatomically this area is situated between visual processing areas in occipital and parietal cortex and motor areas in the central sulcus, making it a good candidate to be involved in transformations from vision to action. It can be subdivided in a number of separate areas, such as lateral intraparietal area (LIP), medial intraparietal area, anterior, caudal and ventral intraparietal areas (Grefkes & Fink, 2005). Even though these areas are interconnected, they have different sets of outgoing connections. LIP (which is often linked to saccade planning) is connected to the frontal eye fields in prefrontal cortex, whereas the medial intra-parietal area (linked to reach planning) is heavily connected to the dorsal premotor cortex (Andersen & Buneo, 2002; Snyder, Batista & Andersen, 2000).

One of the most influential single cell recording study on monkeys in the field was carried out by Andersen and colleagues (Snyder, Batista & Andersen, 1997). They discovered that neurons in LIP and parietal reach region (PRR, which encompasses medial intraparietal area, but also includes a posterior portion of intraparietal sulcus) respond differently depending on whether an animal planned a saccade or a reach movement to a memorized location. Therefore, these findings go beyond the interpretation that these neurons simply represent memorized target locations. This activity was interpreted as intention-related – intention would be like a statement “I will reach for this particular apple”, but it is not yet a plan that describes the muscle set and forces needed to reach for that apple, nor is it necessary that the reach will ever happen. Intention specifies the object, the spatial location of the intended action, and the effector to be used. This concept of movement intention seems to coincide with early movement planning stages, that are involved in object localization and effector selection, but not in motor command specification.

Following the seminal study by Andersen and colleagues, a number of studies were published supporting the proposal that LIP and PRR are involved in saccade and reach goal selection, respectively. For instance, it was demonstrated that neural activity associated with visual stimulus alternates in PRR and LIP if the instruction to make a saccade or a reach is changed a couple of times before the action is allowed (Snyder, Batista & Andersen, 1998). Also, the activity in these areas differs when the monkey makes an autonomous choice to make a saccade or a reach (Cui & Andersen, 2007; Scherberger & Andersen, 2007). Furthermore, specifying only the effector before revealing the location of the movement leads to effector-specific activity in these two areas (Chang, Dickinson & Snyder, 2008; Calton, Dickinson & Snyder, 2002; Dickinson, Calton & Snyder, 2003). And finally, PRR and LIP also respond during the delay period before movements to sound stimuli, without any accompanying visual information (Cohen & Andersen, 2000).

All these studies demonstrate that separate regions in parietal cortex (PRR and LIP) are involved in selecting objects for saccades and reaches. This selection happens after the visual input has already passed through a number of visual information processing stages, specifying object features and location. However, in parietal cortex this visual information is represented and selected in parallel for different actions. This could be interpreted as early parallel processing of visual information for action, as there is still a way to go before visual stimuli are represented in coordinate frames relevant for the specific action (Pesaran, Nelson & Andersen, 2006), and before particular actions are planned.

In addition to LIP and PRR other parietal areas are also known to show activity related to visuo-motor transformations. The anterior intraparietal area has been found to selectively respond to objects that can be grasped (Murata et al., 2000; Sakata et al., 1995). The ventral intraparietal area is especially responsive to stimuli indicating motion close to or towards the observer's head, such as sound, visual, tactile, or vestibular stimulation (Bremmer et al., 1997; Colby, Duhamel & Goldberg, 1993; Duhamel, Colby & Goldberg, 1998; Klam & Graf, 2003). Stimulation in this area leads to head avoidance behaviors (Cooke et al., 2003). These studies suggest that multiple parallel modules are present within PPC, subserving different actions and effectors.

Furthermore, imaging studies with human participants have confirmed that PPC is involved in visuo-motor transformations. Saccade-related activity has been described in parietal cortex (Brignani et al., 2010; Connolly et al., 2005; Corbetta et al., 1998 Curtis & Connolly, 2008). Activity related to reach planning has also been observed in the intraparietal sulcus (Fernandez-Ruiz et al., 2007; Filimon et al., 2009; Medendorp et al., 2005;). Dissociation studies that asked participants to plan either saccades or reaches have demonstrated that distinct regions in PPC are more responsive before the saccades or the reaches (Astafiev et al., 2003; Beurze et al., 2009; Levy et al., 2007; Simon et al., 2002). It has also been shown that reach and saccade-related activity originates in different regions of parietal cortex and results in different gamma band oscillations in EEG (Van Der Werf et al., 2010). Patient studies have reported lesions in parietal cortex leading to specific impairments in saccade or reach amplitudes (Pierrot-Deseilligny, Milea & Muri, 2004; Trillenberg et al., 2007). One interesting investigation traced perceptual decisions leading to saccades or reaches to distinct regions in parietal cortex (Tosoni et al., 2008).

To summarize, these studies demonstrate that separate regions in parietal cortex are involved in processing information related to saccade and reach planning. However, these imaging studies showed a significant overlap between parietal regions in most of the above mentioned tasks. Hence it remains debatable how specialized these areas are for the kind of movement for which they show enhanced activity.Typically, one region responded more than others to either saccades or reaches, but this region was also active when the non-preferred action was planned. One possible explanation could be that not all studies activate reach related regions strongly enough, as due to physical constraints of scanning many of these imaging studies used pointing instead of reaching. A second possibility could be that tasks requiring to plan a reach might (inadvertently) co-activate saccade planning to the same object, even if participants are not instructed to make a saccade (observed by Snyder, Batista & Andersen, 1997). And lastly, as is discussed in the next section, these results could be confounded by attention allocation.

Other neurophysiological studies have shown that specificity to saccade and reach planning extends beyond parietal cortex. For instance, the frontal eye fields (FEF), an area located in arcuate sulcus in monkeys and in pre-motor cortex in humans, show activity related to saccade planning (Connolly et al., 2007; Connolly et al., 2005; Curtis & Connolly, 2008; Lawrence & Snyder, 2006; Schall, 2000). Saccade planning activity is also observed in supplementary eye fields (Connolly et al., 2005; Histed & Miller, 2006; Luna et al., 1998), as well as in superior colliculus (King, 2004). Dorsal and ventral parts of premotor cortex also show reach planning related activity (Beurze et al., 2009; Medendorp et al., 2005), before the action is represented in the motor cortex. All of these areas form a fronto-parietal network involved in action planning (Pesaran, Nelson & Andersen, 2008). While, as previously noted, dissociations between saccade and reach planning are not absolute, they do not form a shared and common movement planning system either.

INTENTION OR ATTENTION?

Allied to the discussion of whether movement targets are selected by separate or by shared systems is another important issue which concerns the relationship between action planning and shifts of attention. In one of the first studies investigating the relationship between saccades and attention (Deubel & Schneider, 1996; see also, Kowler et al, 1995), Deubel and Schneider asked participants to make saccades instructed by a central cue, and during the time when participants were preparing the required eye movement (it takes about 200-300 ms to prepare a saccade), a probe letter was briefly presented at either the saccade target or at another, saccade-irrelevant location. The authors observed that discrimination of the probe was the best if it was presented at the saccade location. This was the case even if participants knew in advance that the probe would appear elsewhere. Thus, it seems that attention shifted to the saccade target location even if participants were encouraged to attend elsewhere (Deubel & Schneider, 2003; Godijn & Pratt, 2002; Montagnini & Castet, 2007). This suggests a tight coupling between attention and saccades – attention goes where the eyes go.

One possible explanation for this coupling is that attention originates in the saccadic system. In their premotor theory of attention Rizzolatti and colleagues (Rizzolatti, Riggio & Sheliga, 1994; Rizzolatti et al., 1987) proposed that saccade programming results in attention shifts to the saccade target. According to this theory, planning a saccade leads to an attentional shift, thus when the saccade plan is executed, coupling between saccades and attention is observed. The theory also states that covert shifts of attention without saccades result from planned but not executed saccades. Additionally, the theory proposes that attention shifts could originate in any action system – be it for saccades, reaches or for other actions.

Further studies have confirmed this close and obligatory relationship between saccades and attention. For example, it has been shown that stimuli that capture attention usually elicit involuntary saccades to these stimuli (Theeuwes et al., 1999; Theuwes et al., 1998). Also, attended stimuli – such as the ones kept in working memory or just flashed objects – affect saccadic trajectories: saccades typically veer away from the potentially distracting stimulus (Theeuwes, Olivers & Chizk, 2005; van der Stigchel, 2010). Such saccade deviations have been explained in the light of competing saccadic plans – if a potential saccade goal is suppressed, then saccade trajectories deviate away from it (Tipper, Howard & Houghton, 1998). Interestingly it has been shown that participants think that they are already looking at the object even though they are still just planning a saccade to the object (Deubel, Irwin & Schneider, 1999; Hunt & Cavanagh, 2009).

This close relationship between attention and saccades has also factored into the debate of whether the parietal cortex is involved in movement goal selection, or whether it is a part of the system responsible for attentional shifts. LIP, which as discussed before, might be involved in saccade goal selection, could alternatively represent important or attended objects. These objects could grab attention in a bottom-up way, or they might be attended due to the top-down set. Such attended object might eventually become a goal of the saccade, which could lead to the mistaken assumption that LIP is directly involved in saccade selection. In fact LIP is known be involved in selection of any visual information which is intrinsically important or salient in the outside world (Bisley & Goldberg, 2010; Goldberg et al., 2006; Colby & Goldberg, 1999). One striking observation to support this proposal is that LIP activity during delayed match-to-sample tasks represents attended objects instead of the ones to which saccades will be directed after the delay (Bisley & Goldberg 2006; 2003). Additionally, only attended or novel stimuli, but not unattended and static stimuli elicit LIP activity, even though saccades are never made to those stimuli (Kusunoki, Gottlieb & Goldberg, 2000). While it has not been resolved whether the parietal activity observed in these studies represents attentional shifts or saccadic planning, both of these interpretations are compatible with the premotor theory of attention. In cases when saccades are executed, pre-saccadic activity in LIP would reflect both, saccade planning and attention. In cases when saccades are not executed, attention shifts could reflect initiated, but not executed saccade plans.

Another area that shows both, saccade- and attention-related activity is FEF. Electrical current stimulation of neurons in FEF evokes fixed-amplitude saccades directed to specific locations, and this area, together with its counterpart, the superior colliculus (SC), is accepted as being directly involved in saccade planning (Schall, 2002; Thompson, Biscoe & Sato, 2005). A series of experiments has demonstrated that activity of visuo-motor neurons in FEF is also related to performance in visual search tasks and may represent attended stimulus and potential saccade goals (Bichot et al., 2001; Murthy et al., 2009; Schall & Hanes, 1993). However, dissociation between attention-related and saccade-related activity in FEF has also been observed. Schall and colleagues (Schall, 2004; Sato & Schall, 2003) described two groups of visuo-motor neurons in a task where the monkey performed an anti-saccade task. While one group of neurons selected a target first, and then represented a location to which an anti-saccade would be directed, another group of neurons represented only the anti-saccade goal, and not the visual stimulus. Thus, there is some dissociation between the selection of visual stimuli for action, and the specification of the final saccade goal. However, this dissociation actually underscores the fact that there is indeed a close linkage between attention and saccades – neurons in the same area seem to represent both, attention and saccades simultaneously. Like area LIP, which has been proposed to be either an attentional map or a saccade selection area, FEF has also been proposed to be a site of an attentional map (Thompson & Bichot, 2005). Recently it has been shown that SC is also involved in attentional selection (Lovejoy & Krauzlis, 2010; Cavanaugh & Wurtz, 2004).

Thus a substantial body of evidence exists in favour of a close relationship between the systems involved in saccade planning and attention shifts. Similarly, behavioral studies have also demonstrated that attention shifts to goals for other motor actions as well, for instance to reaching goals (Bekkering & Pratt, 2004; Deubel, Schneider & Paprotta, 1998; Linnell et al., 2005), or to grasping targets (Fischer & Hoellen, 2004; Schiegg, Deubel & Schneider, 2003). While it is not clear whether the areas involved in selection for reaching or grasping are associated with attentional allocation, some imaging studies suggest that there is an overlap between the areas that are active in pointing and in attentional tasks (Astafiev et al., 2003; Simon et al., 2002). The idea that other action-related areas – for reaching or grasping, for example – might also be involved in attention shifting also fits nicely with the premotor theory of attention, which also specified that attention shifts could originate in any action system (Rizzolatti, Riggio & Sheliga, 1994).

ATTENTIONAL MAPS

In the current context, one aspect of the relationship between attention and action planning needs to be emphasized, namely that areas that are involved in action goal selection are also thought to represent attentional or priority maps (Bisley & Goldberg, 2010; Colby & Goldberg, 1999; Thompson & Bichot, 2005). Such priority maps combine different sources of information – physically distinct features such as stimulus color, orientation, movement and luminance – which results in an activity map representing salient stimuli (Fecteau & Munoz, 2006; Itti & Koch, 2000). They are also assumed to take into account "top-down" information – information which can make even an indistinct visual stimulus important, such as task rules, expectations or reward contingencies. Thus, an "uninteresting" stimulus might become interesting if there is a reward associated with it. On the other hand, activity to a distractor could be diminished if task instructions specify to focus on a different stimulus (Bisley & Goldberg, 2010). Thus, such priority maps combine information about different visual object properties, about different task rules and rewards. Saccade or reach planning could also serve as inputs to such a priority map, as planning an action to a specific object singles this object out from others.

However, it remains to be debated where such a general priority map is implemented. While it has been proposed that LIP in parietal cortex or FEF in frontal cortex could represent such a priority map, it is equally likely that attention-related signals in those areas represent only specific inputs to the combined priority map. As the behavioral tasks that have been used to study FEF and LIP in most cases involved saccades as responses, it could be that these areas represent only attended potential saccade goals. To my knowledge, there is no direct evidence for attention-related signals before hand movements. Instead it is possible that priority information from different sources is combined in lower visual processing areas that show attention-related modulations (Moran & Desimone, 1985; Moore & Fallah, 2004). For example, signals related to saccade planning in FEF can modulate activity in other visual processing areas, like V4 (Moore & Fallah, 2001, 2004). Parietal cortex also seems to modulate activity in earlier visual areas (Lauritzen et al., 2009).

In summary, two important conclusions could be derived from these links between attention and action planning. First, attention is closely linked to saccade and reach planning. This has been supported by a number of psychophysical studies, and in the case of saccade planning by neurophysiological evidence as well. Second, attentional shifts related to saccade or reach planning could serve as inputs to a more general priority map – an attentional map which represents all currently relevant objects. However, as most of these studies focused on the relationship between priority map and saccade planning only, evidence for the latter conclusion is relatively scarce.

INTERPRETING INTERACTIONS

We have discussed a number of studies, some of them subscribing, others objecting to the idea that early movement planning for saccades and reaches is carried out in parallel. While there is a large number of neurophysiological studies supporting parallel processing for reaches and saccades, interactions between the two systems have also been observed. Psychophysical studies have emphasized shared movement planning for reaches and saccades more than neurophysiological studies, even though I highlighted some examples which support parallel movement planning. However, the findings in psychophysical studies are not necessarily incompatible with the idea that reach and saccade planning could be carried out in parallel systems. There are a number of interactions that could offer alternative explanations for the observed overlap between goal selection in these two systems. In the following discussion I will outline three such possibilities. One possibility is that gaze is kept stable, as each eye movement would change the retinotopic visual representations. Another possibility is that the need to update information across saccades could also lead to overlap in eye-hand goal selection. And third, it is possible that the observed interactions might instead result from interactions between the attentional processes linked to both reach and saccade planning.

To date, numerous interactions between eye and hand movement planning have been reported. It has been shown that people usually look at the locations they will reach to (Hayhoe, 2000; Johansson et al., 2001; Land, Mennie & Rusted, 1999; Pelz, Hayhoe & Loeber, 2001), that during reaches gaze is fixed to the target (Neggers & Bekkering, 2000; 2001; 2002), and that reaches are more accurate when directed to the foveated targets, even if the hand is not visible (Prablanc et al., 1979). Concurrent reaches reduce inhibition of return which is observed in saccade latencies (Pratt & Neggers, 2008). Presence of the hand in the workspace – even when it's not visible – affects saccade latencies (Thura, Boussaoud & Meunier, 2008), and reaches directed to the same location as the saccade affect both, saccade latencies (Bekkering et al., 1994, 1995) and saccade velocity (Snyder et al., 2002).

Neurophysiological literature offers insight about how some of those interactions could arise during saccade and reach planning. One interesting observation is that activity of the PRR cells selective to reaches is modulated by the position of the eye (Batista et al., 1999); similar observations have also been reported in FEF, an area associated with saccade planning (Thura et al., 2008), and even in SC (Reyes-Puerta et al., 2010). The last result is especially interesting. It was observed that neurons in rostral SC, involved in fixation holding, also respond more strongly during the reach movements, suggesting that SC is involved in holding fixation during reaches. This finding could explain the observed gaze-anchoring effect (Neggers & Bekkering, 2000; 2001). It could also explain why saccade latencies are delayed if concurrent reaches are planned (Bekkering et al., 1994, 1995). Thus, it seems that there are neural mechanisms which favour eye and hand movement coupling.

The reason why gaze stability might be favoured has been illustrated in a recent study by Gaveau and colleagues (2008) on optic ataxia patients. Optic ataxia, which results from lesions in superior parietal lobule in humans, is characterized by impaired reach movements. Specifically, patients with optic ataxia are unable to reach for locations if they are not allowed to fixate the reach target (Carey, Coleman & Della Sala, 1997). Gaveau and colleagues asked participants to reach towards targets, and eye movements were not restricted. Naturally, participants looked at the reach target before their reaches started. On some trials though, the reach target jumped to a new position after the eye movement was completed, but before the hand movement started. The authors observed that healthy control participants could quickly foveate the changed reach target location, and their reach latencies were relatively unaffected by the target jump. Optic ataxia patients, on the other hand, showed a striking impairment. Instead of quickly foveating the misplaced stimulus and then reaching of it, they made a sequence of hypometric saccades aiming at the new target location, and their hand movements never started before they managed to finally foveate the shifted target. This finding was interpreted as reflecting the failure to update visual information quickly after the movement of the reach target. Similar results have been obtained using trans-cranial magnetic stimulation over parietal cortex with healthy participants, who failed to reach for the new reach target location if the target was shifted during the saccade (Desmurget et al., 1999).

It is well known that visual representations are affected by intervening eye movements: after each eye movement, a stationary object falls on different locations on the retina and different sets of neurons are processing the visual information from these locations. In other words, neurons in a number of visual processing areas represent visual information in retinotopic coordinates – their receptive fields represent specific parts of retina. This is true in early visual processing areas like V1, V2, V3 and V4 (Sereno et al., 1995), and even in later processing areas such as parietal cortex (Hagler, Riecke & Sereno, 2007; Silver & Kastner, 2009; Sereno, Pitzalis & Martinez, 2001). Even though the visual input changes after each eye movement, we still perceive a stable visual world – and updating of visual information across saccades has been proposed to be at the heart of this perceived stability. Updating – or remapping – works by taking into account saccade planning: as each saccade amplitude is specified, the visual system takes into account where objects are, as represented in retinotopic coordinates, before the saccade, and anticipates where these objects would be after the saccade (reviewed in Cavanagh et al., 2010).

The remapping of object representations could offer one link where saccades and reaches would have to share information. There is evidence that during early stages of movement planning, reach goals are represented in eye-centered coordinates (Cohen & Andersen, 2002; Beurze, Van Pelt & Medendorp, 2006; Desmurget et al., 1998). This means that reach planning would have to take into account intervening saccades, and update those representations to reflect changed gaze position. One recent fMRI study has demonstrated that reach target locations are indeed updated across saccades (Medendorp et al., 2008). Taken together, some of the observed eye-hand interactions could be reinterpreted as follows: it is advantageous to hold the gaze stable during reach planning and execution, so as to keep visual information stable and this could result in such effects as "gaze anchoring". Additionally, in case a saccade is made, reach target locations have to be updated to take into account changed gaze direction, which could prolong movement latencies (both, eye and hand movement latencies) in tasks requiring eye movements.

Another possible reason for interactions to occur could be the close relationship between attention and movement planning. It is accepted that saccade and reach planning leads to attention shifts to movement goal locations (Bekkering & Pratt, 2004; Deubel & Schneider, 1996; Kowler et al, 1995; Deubel, Schneider & Paprotta, 1998; Linnell et al., 2005). Additionally, shifting attention to objects might lead to movement planning to those objects (Theeuwes et al., 1999; Theuwes et al., 1998). Given this close relationship between attention shifts and movement planning, attention allocation to saccade targets could affect reach planning, and vice versa. These attentional effects on saccade and reach planning could arise at the level of general priority map. While both, saccade and reach planning could be parallel, both systems are likely to share inputs from the general priority map. Therefore, if saccade planning results in representation of a saccade goal as salient on a priority map, then this representation could affect reach target selection, which is carried out in reach planning system. This could explain the interactions reported previously by Song and colleagues (Song & McPeek, 2009; Song & Nakayama, 2009; Song & Nakayama, 2008).

OVERVIEW OF OUR EXPERIMENTAL STUDIES

Rationale

There has been little direct exploration of the plausible causes, offered in the preceding section, that might explain the overlap between goal selection mechanisms for eye and hand movements. Additionally, even though it may be likely that saccade and reach planning are carried out in overlapping but parallel, largely independent systems, there is relatively little psychophysical evidence supporting this hypothesis. In the following five studies we explored whether separate systems are involved in saccade and reach planning, and at which stages interactions between the two systems may occur.

Study 1: Remembering where not-to-look: Attention is suppressed at task-relevant locations forbidden to saccades

First we explored whether the proposed coupling between attention and saccadic planning will also be true when a response needs to be suppressed. In particular, we were interested in how varying saccadic instructions (make a saccade or suppress it) would affect attentional allocation. We used a classic oculomotor delayed response task with two conditions – Match and Nonmatch. In the Match condition, subjects had to remember the location of a sample cue and after a delay make a response (e.g. a saccade or a manual reaching) to that location. In the Nonmatch condition, on the other hand, subjects were instructed to remember the location of a sample cue as a marker of where not-to-respond and after a delay, when it reappears along with a new stimulus, make a response to the one at the nonmatching location. We measured whether attention was allocated to the memorized location by briefly presenting a discrimination probe during the delay and observed a very close coupling between attention allocation and saccades, regardless of opposing working memory demands. Participants could discriminate probes at the location to which they would make a saccade in the Match task. This shows that their attention shifted to the location held in working memory (which was also a potential saccade location; Awh, Vogel & Oh, 2006; Awh & Jonides, 2001). However, in the Nonmatch task probe discrimination at that location was worse than at other, non-memorized locations. In other words, visual processing at the location forbidden to the saccades was suppressed, even though that location had to be maintained in working memory. Note that suppressing a location is disadvantageous for performing the probe discrimination task, as participants can discriminate fewer probes. This finding highlights the fact that saccadic instructions (allowed or forbidden saccades) can alter the attentional representation of the environment, regardless of what demands other, simultaneous tasks involve. Thus, this study further emphasizes the close link between attention and saccade planning. Additionally, these results provide first direct evidence that participants can maintain the inhibition of a forbidden motor goal throughout a delay and in the absence of the goal itself besides also being a notable example of the local suppression of visuospatial attention (as opposed to that of object or feature based attention).

Study 2: Independent allocation of attention to eye and hand targets in coordinated eye-hand movements

While neurophysiological data suggest that parallel systems are involved in selecting targets for reaches and saccades, the findings are less clear in a number of psychophysical experiments. In order to investigate this question more closer, we took advantage of the previously described link between attention and movement planning. If movement planning results in attention shifts, we could use attentional allocation as an index to measure movement planning. In a series of experiments we presented two different sets of tasks: saccade-only and reach-only tasks, in which participants made either saccade or reach to a cued location; and combined-movement task, in which participants looked and pointed simultaneously to the same or to different objects. A probe discrimination task was used to measure how movement goals are selected before saccades and reaches. While participants performed a saccade or a reach, we briefly presented a probe letter at either the saccade target, the reach goal, or at any other, movement-irrelevant location. We found that when participants made simultaneous eye and hand movements to separate locations, attention was allocated in parallel at both locations, with no cost arising from the need to plan two movements instead of one. Therefore, even if eye and hand movements are linked, this is not likely to be due to attentional limits in selecting the targets for both movements. Moreover, we found that delaying the eye movement delayed the attentional shift to the saccade target while leaving attentional deployment to the reach goal unaffected. These results demonstrate that attentional resources are allocated independently to eye and hand movement targets and suggest that the goals for these effectors are selected by separate attentional mechanisms. Additionally, the finding that attentional allocation for each of the two movements interacts synergistically (discrimination performance was better if saccades and reaches were directed to the same location as compared to making two movements to two different locations) is also compatible with the interpretation that attentional signals from saccade and reach planning could serve as inputs to a general priority map (see the previous section on “Attentional maps”).

Study 3: Preparing coordinated eye and hand movements: Dual task costs are not attentional

Our Study 2 argues against the proposal that eye and hand movement goal selection is shared. It is possible that the difference between the arguments for parallel, independent movement goal selection for reaches and saccades as observed in our study and those for a common mechanism in other previously described studies is due to different methodologies: while we measured movement goal selection directly by measuring how much attention was allocated at the movement goal at different points of time *during* action planning, previous studies have instead measured movement latencies and movement errors, relying on the *final result* of action planning and execution (f.e. Bekkering et al., 1994, 1995; Biguer et al., 1982; Gielen et al., 1984; Prablanc et al., 1979; Sailer et al., 2000). In a series of experiments presented in Study 3 we demonstrate that different conclusions can be potentially derived if movement goal selection mechanisms were inferred from latencies, instead of attentional allocation. We asked participants to reach and look at different or same locations, while we varied the time delay between the cues instructing each of the movements. This variable delay is typically used in multi-tasking paradigms in order to investigate whether two tasks (like performing a saccade or a reach) share some processing stages, or whether these processes run in parallel (Schubert, 2008; Pashler, 1994). When a cue is presented to plan a reach movement, and then shortly after a second cue is shown to make a saccade, then one of two effects should be observed. If saccade planning relies on the same resources that are used for the reach movement planning, saccades would be delayed. Alternatively, if the resources used for reach and saccade planning are separate, saccade planning would start immediately after the saccade cue, regardless of the reach movement planning. In other words, if two actions compete for shared resources, whatever action comes later will be delayed due to the resources being used up by the first action while if they don’t then the execution of one will not interfere with that of the other We found that saccades were indeed delayed if a reach movement was planned at the same time, and vice versa – reaches were delayed if a saccade was planned at that moment. However, importantly, attention shifts to the saccade locations were not affected by simultaneous reach planning (Experiment 3 in Study 3). This demonstrates a striking contrast between the ability to select movement goals (which was not affected by reach planning), and the actual initiation of the movements (which was delayed). Thus, it seems clear that a coupling between saccades and reaches indeed occurs at some stage, but it is likely to occur at a stage after the movement goals have been selected.

Study 4: Reach decisions are affected by saccade preparation

After having found support for parallel saccade and reach goal selection, we next looked at the extent to which the two systems overlap and interact with each other. As already discussed in the section “Interpreting interactions”, visual representations during early reach planning stages are affected by gaze position (Beurze, Van Pelt & Medendorp, 2006; Cohen & Andersen, 2002; Desmurget et al., 1998), which could lead to one possible way for interactions between eye and hand movement planning systems to occur. We reasoned that if reach goal selection is indeed represented in gaze centered coordinates, then the reach planning system should take into account the planned saccades, since the eye movement would result in the need to determine the new retinotopic position of the reach goal after the saccade. While it has been shown previously that reach target locations are updated across eye movements (Medendorp et al., 2008, review in Crawford, Medendorp & Marotta, 2004), we asked whether this updating process is predictive. In other words, does reach planning take into account planned saccades? We used a free-choice reaching task in which participants are asked to choose one out of two reach targets. This task has previously been used to investigate the reference frames involved in reach planning (Scherberger, Goodale & Andersen, 2003), and to study the function of eye movements during combined eye-hand movements (Horstmann & Hoffmann, 2005). In our experiments we presented two potential reach targets while participants were planning their saccade to a specified location. We found that the preferences of where to reach changed as a function of the saccade plan. The closer the reach objects appeared in time to the saccade onset, the more likely participants were to choose the target on that side of the visual field where the saccade was directed. It is important to note that reach targets were presented while participants looked at the center of the display, and reaches happened while participants were looking at the center as well – ruling out that it was eye position that affected those preferences. Rather, this effect depended on how close to the saccade onset the reach objects were shown. Additionally, we did not observe a reversed effect – reach execution did not affect saccade target selection. This finding supports the hypothesis that one of factors causing interactions between saccade and reach planning could be the need for reach planning to keep track of the impeding eye movements.

Study 5: Predictive remapping of attention across eye movements

In this set of experiments we further investigated how movement goal location is updated – or remapped – before saccades. Single cell recording studies and imaging studies have demonstrated that visual information is remapped across saccades to take into account that every eye movement results in a change of object positions in retinotopic representations (Duhamel et al., 1992; Medendorp et al., 2005). Here we looked into predictive nature of this remapping – that the future retinotopic location of an object is known before saccade onset. In particular, in the experiments described in Study 5 we investigated whether attention is remapped before saccade onset. We asked participants to make a single saccade or a sequence of two saccades and measured attention allocation at different locations. We found that before saccade onset, attention shifted to the saccade target locations (be it single target or two targets in double saccade task). Additionally, before the onset of the first saccade, attention also shifted to the retinal locations that the saccade targets would occupy once the eye movement was finished. In other words, we demonstrated an attentional remapping before saccades – shifts of attention predicting where objects would be represented in a retinotopic reference frame after the saccade.

In a pilot study we applied the same logic to reach movement planning. In the following task participants were asked to point and look to two separate targets at the same time. We observed the expected behavior – participants started the saccade first, and the reach later. As saccade and reach targets were at different locations, participants shifted their attention to both, saccade and reach goals in parallel. This is in line with findings described in Study 2. Interestingly, we also observed that, before saccade onset, discrimination also increased at the post-saccadic retinotopic location of the reach target. In other words, before the saccade started, attention shifted to the (retinal) location representing the reach target with respect to the future eye position. Additionally, when we analyzed the trials separately for slow and fast saccades, we found that this visual updating started in the last 100 ms before the saccade, regardless of the saccade latency. If the saccade started later, attentional shift to the remapped location of the hand target was also delayed (but within the last 100 ms before the saccade onset), and if the saccade started sooner, the remapping also happened sooner before saccade onset. While this observation is just correlational, one straightforward interpretation is that saccades did not start as long as the reach target location was not remapped. This experiment supports the idea that retinotopic representations of reach targets are also updated across saccades. This could be another possible cause that might contribute to the previously reported interactions between saccade and reach planning.

SUMMARY

The work described in this thesis primarily addresses the question whether the goal selection system and the resulting representations of the target location underlying eye and hand movement planning are separate or shared. So far, psychophysical and neurophysiological evidence related to this question remains equivocal and exists for both sides of the debate. The results we present here clarify this controversy in two different ways. Firstly, by showing evidence in support of the former view that target selection for eye and hand movements indeed result from separate and parallel systems instead of being shared. Secondly, by offering alternative explanations for results that have so far been taken as evidence for the contrary position.

We exploited the fact that movement planning results in attention shifts to investigate the temporal and spatial dynamics of target selection for motor goals. The deployment of attention at intended targets was used as an index of target selection in early movement planning. Consistent across a variety of situations we found clear evidence that goal selection for the eye and for the hand movement is done in a parallel and independent manner. We further demonstrated a striking dissociation between measuring saccade and reach target selection using direct measures (such as attention) and indirect measures (such as movement latencies). These findings reveal that different measures of movement planning could provide different interpretations with respect to whether saccade and reach planning proceeds in parallel or not.

Next, using two different tasks we investigated whether movement targets are updated across saccades. In one type of task, we observed predictive remapping of saccade goals – attention allocated to planned saccade locations also shifted to retinal locations that the planned saccade targets would cover once the eyes have moved. Moreover, we were able to demonstrate that planned reach locations were also remapped to future retinotopic locations before saccades, in a way very similar to the updating of saccade tar-

gets. In the other task, we used free-choice reaching selection paradigm and observed that saccade planning affected which targets were selected for reaches. These two findings complement the observation that movement goals for saccades and reaches are selected in parallel by suggesting potential cross-talk mechanisms between saccade and reach target selection. Our results thus show that psychophysical studies that argued for a common selection system could instead be explained as results of a parallel but highly coordinated and interactive systems.

In summary, our results shown that while we tend to look and reach for objects at the same time, these actions are planned in parallel systems, which dynamically allocate resources for movement goal selection, separately for each effector. These systems also keep track of the planned actions, in order to allow for fast updating of movement goal representations across the eye movements. The flexibility allowed by such parallel but coordinated systems then results in a perfectly orchestrated repertoire of eye and hand movements contributing to cognitive flexibility that primates are known for.

REFERENCES

Andersen, R.A., & Buneo, C.A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience, 25*, 189-220.

Astafiev, S.V., Shulman, G.L., Stanley, C.M., Snyder, A.Z., van Essen, D.C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *The Journal of Neuroscience, 23*, 4689-4699.

Awh, E., Vogel, E.K., & Oh, S.-H. (2006). Interactions between attention and working memory. *Neuroscience, 139*, 201-208.

Awh, E., & Jonides, J. (2001). Overlapping mechanisms of attention and spatial working memory. Trends in Cognitive Science, 5, 119-126.

Batista, A.P., Buneo, C.A., Snyder, L.H. & Andersen, R.A. (1999). Reach plans in eye-centered coordinates. *Science, 285*, 257-260.

Bekkering H., Adam, J.J., Kingma, H., Huson, A., & Whiting H.T. (1994). Reaction time latencies of eye and hand movements in single- and dual-task conditions. *Experimental Brain Research, 97*, 471-476.

Bekkering, H., Adam, J.J., van den Aarssen, A., Kingma, H., & Whiting H.T. (1995). Interference between saccadic eye and goal-directed hand movements. *Experimental Brain Research, 106*, 475-484.

Bekkering H., & Pratt J. (2004). Object-based processes in the planning of goal-directed hand movements. *The Quarterly Journal of Experimental Psychology, 57*, 1345-1368.

Beurze, S.M., de Lange, F.P., Toni, I., & Medendorp, W.P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. Journal of Neurophysiology, 101, 3053-3062.

Beurze, S.M., Van Pelt, S., & Medendorp, W.P. (2006). Behavioral reference frames for planning human reaching movements. *Journal of Neurophysiology, 96*, 352-362.

Bichot, N.P., Thompson, K.G., Chenchal Rao, S. & Schall, J.D. (2001) Reliability of macaque frontal eye field neurons signaling saccade targets during visual search. *Journal of Neuroscience, 21*, 713–725.

Biguer, B., Jeannerod. M., & Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research, 46*, 301-304.

Bisley, J.W., & Goldberg, M.E. (2010). Attention, intention, and priority in the parietal lobe. *Annual Review of Neuroscience, 33*, 1-21.

Bisley, J.W., & Goldberg, M.E. (2006). Neural correlates of attention and distractibility in the lateral intraparietal area. *Journal of Neurophysiology, 95*, 1696-1717.

Bisley, J.W., & Goldberg, M.E. (2003). Neuronal activity in the lateral intraparietal area and spatial attention. *Science, 299*, 81-86.

Bremmer, F., Klam, F., Duhamel, J.R., Ben Hamed, S., & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP). *European Journal of Neuroscience, 16*, 1569–1586.

Brignani, D., Bortoletto, M., Miniussi, C., & Maioli, C. (2010). The when and where of spatial storage in memory-guided saccades. *NeuroImage, 52*, 1611-1620.

Beurze, S.M., de Lange, F.P., Toni, I. & Medendorp, W.P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology, 101*, 3053-3062.

Calton, J.L., Dickinson, A.R., & Snyder, L.H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. *Nature Neuroscience, 5*, 580-588.

Carey, D.P., Coleman, R.J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex, 33*, 639-652.

Cavanagh, P., Hunt, A.R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences, 14*, 147-153.

Cavanaugh, J., & Wurtz, R.H. (2004). Subcortical modulation of attention counters change blindness. *Journal of Neuroscience, 24*, 11236-11243.

Chang, S.W.C., Dickinson, A.R., & Snyder, L.H. (2008). Limb-specific representation for reaching in the posterior parietal cortex. *Journal of Neuroscience, 28*, 6128-6140.

Cohen, Y.E., & Andersen, R.A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience, 3*, 553-562.

Cohen, Y.E., & Andersen, R.A. (2000). Reaches to sounds encoded in an eye-centered reference frame. *Neuron, 27*, 647–652.

Colby, C.L., Duhamel, J.R., & Goldberg, M.E. (1993). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology, 69*, 902–914.

Colby, C.L., & Goldberg, M.E. (1999). Space and attention in parietal cortex. *Annual Review of Neuroscience, 22*, 319-349.

Connolly, J.D., Goodale, M.A., Cant, J.S., & Munoz, D.P. (2007). Effector-specific fields for motor preparation in the human frontal cortex. *NeuroImage, 34*, 1209-1219.

Connolly, J.D., Goodale, M.A.,Goltz, H.C., & Munoz, D.P. (2005). fMRI activation in the human frontal eye field is correlated with saccadic reaction time. *Journal of Neurophysiology, 94*, 605-611.

Cooke, D.F., Taylor, C.S., Moore, T., & Graziano, M.S. (2003). Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of Sciences of the United States of America, 100*, 6163-6168.

Corbetta, M., Akbudak, E., Conturo, T.E., Snyder, A.Z., Ollinger, J.M., Drury, H.A., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*, 761-773.

Crawford, J.D., Medendorp, W.P., & Marotta, J.J. (2004). Spatial transformations for eye-hand coordination. *Journal of Neurophysiology, 92*, 10-19.

Cui, H., & Andersen, R.A. (2007). Posterior parietal cortex encodes autonomously selected motor plans. *Neuron, 56*, 552-559.

Curtis, C.E., & Connolly, J.D. (2008). Saccade preparation signals in the human frontal and parietal cortices. *Journal of Neurophysiology, 99*, 133-145.

Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E., & Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience, 2*, 563-567.

Desmurget, M., Pélisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: planning goal-directed movements. N*euroscience and Biobehavioral Reviews, 22*, 761-788.

Deubel, H., Irwin, D.E. & Schneider, W.X. (1999). The subjective direction of gaze shifts long before the saccade. In: W. Becker, H. Deubel & Th. Mergner (eds) *Current Oculomotor Research: Physiological and Psychological Aspects*. New York, London: Plenum, pp. 65-70.

Deubel, H. & Schneider, W.X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals New York Academy of Sciences, 1004*, 289-296.

Deubel, H., & Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research, 36*, 1827-1837.

Deubel, H., Schneider, W.X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81-107.

Dickinson, A.R., Calton, J.L., & Snyder, L.H. (2003). Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. *Journal of Neurophysiology, 90*, 2460-2464.

Duhamel, J.R., Colby, C.L., & Goldberg, M.E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *Journal of Neurophysiology, 79*, 126–136.

Duhamel, J.R., Colby, C.L., & Goldberg, M.E. (1992) The updating of the representation of visual space in parietal cortex by intended eye movements. *Science, 255*, 90-92.

Fecteau, J.H., & Munoz, D.P. (2006) Salience, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences, 10*, 382-390.

Fernandez-Ruiz, J., Goltz, H.C., Desouza, J.F., Vilis, T., & Crawford, J.D. (2007). Human parietal "reach region" primarily encodes intrinsic visual direction, not extrinsic movement direction, in a visual motor dissociation task. *Cerebral Cortex, 17*, 2283-2292.

Filimon, F., Nelson, J.D., Huang, R-S., & Sereno, M.I. (2009). Multiple parietal reach regions in humans: cortical representations for visual and proprioceptive feedback during online reaching. *Journal of Neuroscience, 29*, 2961-2971.

Fischer, M.H., & N. Hoellen (2004). Space- and object-based attention depend on motor intention. *Journal of General Psychology, 131*, 365-377.

Gaveau, V., Pélisson, D., Blangero, A., Urquizar, C., Prablanc, C., Vighetto, A., & Pisella, L. (2008). Saccade control and eye-hand coordination in optic ataxia. *Neuropsychologia, 46*, 475-486.

Gielen, C., van den Heuvel, P.J., & van Gisbergen, J.A. (1984). Coordination of fast eye and arm movements in a tracking task. *Experimental Brain Research, 56*, 154-161.

Godijn, R., & Pratt, J. (2002). Endogenous saccades are preceded by shifts of visual attention: evidence from cross-saccadic priming effects. *Acta Psychologica, 110*, 83-102.

Goldberg, M.E., Bisley, J.W., Powell, K.D. & Gottlieb, J. (2006). Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Progress in Brain Research, 155*, 157–175.

Grefkes, C., & Fink, G.R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy, 207*, 3-17.

Hagler, D.J., Riecke, L., & Sereno, M.I. (2007). Parietal and superior frontal visuospatial maps activated by pointing and saccades. *Neuroimage, 35*, 1562-1577.

Hayhoe, M. (2000). Vision using routines: a functional account of vision. *Visual Cognition, 7*, 43-64.

Herman, R., Herman, R., Maulucci, R. (1981). Visually triggered eye-arm movements in man. *Experimental Brain Research, 42*, 392-398.

Howard, L.A. & Tipper, S.P. (1997). Hand deviations away from visual cues: indirect evidence for inhibition. *Experimental Brain Research, 113*, 144-152.

Histed, M.H., & Miller, E.K. (2006). Microstimulation of frontal cortex can reorder a remembered spatial sequence. PLoS: Biology, 4, e134.

Horstmann, A., & Hoffmann, K.-P. (2005). Target selection in eye-hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research, 167*, 187-195.

Hunt, A.R., & Cavanagh, P. (2009). Looking ahead: the perceived direction of gaze shifts before the eyes move. *Journal of Vision, 9*, 9:1-7.

Itti, L. & Koch, C. (2000) A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research, 40*, 1489-1506.

Johansson, R.S., Westling, G., Backstrom, A., & Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience, 21*, 6917-6932.

King, A.J. (2004). The superior colliculus. *Current Biology, 14*, R335-R338.

Klam, F., & Graf, W. (2003). Vestibular signals of posterior parietal cortex neurons during active and passive head movements in macaque monkeys. *Annual New York Academy of Science, 1004*, 271–282.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*, 1897-1916.

Kusunoki, M., Gottlieb, J., & Goldberg, M.E. (2000). The lateral intraparietal area as a salience map: the representation of abrupt onset, stimulus motion, and task relevance. *Vision Research, 40*, 1459-1468.

Land, M.F., & Hayhoe, M.M. (2001). In what ways do eye movements contribute to everyday activities? *Vision Research, 41*, 3559-3565.

Land, M.F., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception, 28*, 1311-1328.

Lauritzen, T.Z., D'Esposito, M., Heeger, D.J., & Silver, M.A. (2009). Top-down flow of visual spatial attention signals from parietal to occipital cortex. *Journal of Vision, 9*, 18:1-14.

Lawrence, B.M., & Snyder, L.H. (2006). Comparison of effector-specific signals in frontal and parietal cortices. *Journal of Neurophysiology, 96*, 1393-1400.

Levy, I., Schluppeck, D., Heeger, D.J., & Glimcher, P.W. (2007). Specificity of human cortical areas for reaches and saccades. *The Journal of Neuroscience, 27*, 4687-4696.

Lovejoy, L.P., & Krauzlis, R.J. (2010). Inactivation of primate superior colliculus impairs covert selection of signals for perceptual judgments. *Nature Neuroscience, 13*, 261-266.

Linnell, K.J., Humphreys, G.W., McIntyre, D.B., Laitinen, S., & Wing, A.M. (2005). Action modulates object-based selection. *Vision Research, 45*, 2268-2286.

Luna, B., Thulborn, K.R., Strojwas, M.H., McCurtain, B.J., Berman, R.A., Genovese, C.R., & Sweeney, J.A. (1998). Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. *Cerebral Cortex, 8*, 40-47.

Lünenburger, L., Kutz, D.F., & Hoffmann, K.P. (2000). Influence of arm movements on saccades in humans. *European Journal of Neuroscience, 12*, 4107-4116.

Medendorp, W.P., Beurze, S.M., Van Pelt, S., & Van Der Werf, J. (2008). Behavioral and cortical mechanisms for spatial coding and action planning. *Cortex, 44*, 587-597.

Medendorp, W.P., Goltz, H.C., Crawford, J.D., & Vilis, T. (2005). Integration of target and effector information in human posterior parietal cortex for the planning of action. *Journal of Neurophysiology, 93*, 954-962.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*, 8:1-16.

Moran, J., & Desimone, R. (1985). Selective attention gates visual processing in the extrastriate cortex. *Science, 229*, 782-784.

Moore, T., & Fallah, M. (2001). Control of eye movements and spatial attention. *Proceedings of the National Academy of Sciences of the United States of America, 98*, 1273–1276.

Moore, T., & Fallah, M. (2004). Microstimulation of the frontal eye field and its effects on covert spatial attention. *Journal of Neurophysiology, 91*, 152–162.

Murata, A., Gallese, V., Luppino, G., Kaseda, M., & Sakata, H. (2000). Selectivity for the shape, size, and orientation of objects for grasping in neurons of monkey parietal area AIP. *Journal of Neurophysiology, 83*, 2580-2601.

Murthy, A., Ray, S., Shorter, S.M., Schall, J.D., & Thompson, K.G. (2009).Neural control of visual search by frontal eye field: effects of unexpected target displacement on visual selection and saccade preparation. *Journal of Neurophysiology, 101*, 2485-2506.

Neggers, S.F.W., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. J*ournal Neurophysiology, 86*, 961–970.

Neggers, S.F.W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*, 639–651.

Neggers, S.F.W., & Bekkering, H. (2002). Coordinated control of eye and hand movements in dynamic reaching. *Human Movement Science, 21*, 349-376.

Pashler, H.E. (1994). Dual-task interference in simple tasks: data and theory. *Psychological Bulletin, 116*, 220-244.

Pelz, J., Hayhoe, M.M., & Loeber, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research, 139*, 266-277.

Pesaran, B., Nelson, M.J., & Andersen, R.A. (2008). Free choice activates a decision circuit between frontal and parietal cortex. *Nature, 453*, 406-409.

Pesaran, B., Nelson, M.J., & Andersen, R.A. (2006). Dorsal premotor neurons encode the relative position of the hand, eye, and goal during reach planning. *Neuron, 51*, 125-134.

Pierrot-Deseilligny, C., Milea, D., & Muri, R.M. (2004). Eye movement control by the cerebral cortex. *Current Opinion in Neurology, 17*, 17-25.

Prablanc, C., Echallier, J.F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at visual target. *Biological Cybernetics, 35*, 113-124.

Pratt, J., & Neggers, B. (2008). Inhibition of return in single and dual tasks: examining saccadic, keypress, and pointing responses. *Perception and Psychophysics, 70*, 257-265.

Rizzolatti, G., Riggio, L., & Sheliga, B.M. (1994). Space and selective attention. In C. Umilta & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 231–265). Cambridge, MA: MIT Press.

Rizzolatti, G., Riggio, L., Dascola, I., & Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. *Neuropsychology, 25*, 31-40.

Reyes-Puerta, V., Philipp, R., Lindner, W., Hoffmann, K.-P. (2010). Role of the rostral superior colliculus in gaze anchoring during reach movements. *Journal of Neurophysiology, 103*, 3153-3166.

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2002). Global effect of a nearby distracter on targeting eye and hand movements. *Journal of Experimental Psychology: Human Perception and Performance, 28*, 1432-1446.

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. *Experimental Brain Research, 134*, 163-173.

Sakata, H., Taira, M., Murata, A., & Mine, S. (1995). Neural mechanisms of visual guidance of hand action in the parietal cortex of the monkey. *Cerebral Cortex, 5*, 429-438.

Sato, T.R., & Schall, J.D. (2003). Effects of stimulus-response compatibility on neural selection in frontal eye field. *Neuron, 38*, 637-648.

Schall, J.D. (2004). On the role of frontal eye field in guiding attention and saccades. *Vision Research, 44*, 1453-1467.

Schall, J.D. (2002). The neural selection and control of saccades by the frontal eye field. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 357*, 1073-1082.

Schall, J.D. (2000). On the role of frontal eye field in guiding attention and saccades. *Vision Research, 44*, 1453-1467.

Schall, J.D., & Hanes, D.P. (1993). Neural basis of saccade target selection in frontal eye field during visual search. *Nature, 366*, 467-469.

Scherberger, H., & Andersen, R.A. (2007). Target selection signals for arm reaching in the posterior parietal cortex. *Journal of Neuroscience, 27*, 2001-2012.

Scherberger, H., Goodale, M.A., & Andersen, R.A. (2003). Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *Journal of Neurophysiology, 89*, 1456-1466.

Schiegg, A., Deubel, H., & Schneider, W.X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition, 10*, 409-431.

Schubert, T. (2008). The central attentional limitation and executive control. *Frontiers in Bioscience, 13*, 3569-3580.

Sereno, M.I., Dale, A.M., Reppas, J.B., Kwong, K.K., Belliveau, J.W., Brady, T.J., Rosen, B.R., Tootell, R.B. (1995). Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science, 268*, 889-893.

Sereno, M.I., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science, 294*, 1350-1354.

Silver, M.A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences, 13*, 488-495.

Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., & Dehaene, S. (2002). Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron, 33*, 475-487.

Snyder, L.H., Batista, A.P., & Andersen, R.A. (2000). Intention-related activity in the posterior parietal cortex: a review. *Vision Research, 40*, 1433-1441.

Snyder, L.H., Batista, A.P., Andersen, R.A. (1998). Change in motor plan, without a change in the spatial locus of attention, modulates activity in posterior parietal cortex. *Journal of Neurophysiology, 79*, 2814-2819.

Snyder, L.H., Batista, A.P., & Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167-170.

Snyder, L.H., Calton, J.L., Dickinson, A.R., Lawrence, B.M. (2002). Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology, 87*, 2279-2286.

Song, J.-H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Sciences, 13*, 360-366.

Song, J.-H., & Nakayama, K. (2008). Target selection in visual search as revealed by movement trajectories. *Vision Research, 48*, 853-861.

Song, J.-H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Joural of Vision, 6*, 982-995.

Song, J.-H., & McPeek, R.M. (2009). Eye-hand coordination during target selection in a pop-out visual search. *Journal of Neurophysiology, 102*, 2681-2692.

Song, J.-H., Takahashi, N., & McPeek, R.M. (2008). Target selection for visually guided reaching in macaque. *Journal of Neurophysiology, 99*, 14-24.

Stritzke, M., & Trommershauser, J. (2007). Eye movements during rapid pointing under risk. *Vision Research, 47*, 2000-2009.

Theeuwes, J., Kramer, A.F., Hahn, S., Irwin, D.E., & Zelinsky, G.J. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Pscyhology: Human Perception and Performance, 25*, 1595-1608.

Theeuwes, J., Kramer, A.F., Hahn, S., & Irwin, D.E. (1998). Our eyes do not always go where we want them to go: Capture of eyes by new objects. *Psychological Science, 9*, 379-385.

Theeuwes, J., Olivers, C.N.L., & Chizk, C.L. (2005). Remembering a location makes the eyes curve away. *Psychological Science, 16*, 196-199.

Thompson, K.G., & Bichot, N.P. (2005). A visual salience map in the primate frontal eye field. *Progress in Brain Research, 147*, 251-262.

Thompson, K.G., Biscoe, K.L., & Sato, T.R. (2005). Neuronal basis of covert spatial attention in the frontal eye field. *Journal of Neuroscience, 25*, 9479-9487.

Thura, D., Boussaoud, D., & Meunier, M. (2008). Hand position affects saccadic reaction times in monkeys and humans. *Journal of Neurophysiology, 99*, 2194-2202.

Thura, D., Hadj-Bouziane, F., Meunier, M., & Boussaoud, D. (2008)

Tipper, S.P., Howard, L.A., & Houghton, G. (1998). Action-based mechanisms of attention. *Philosophical Transactions of the Royal Society of London: Series B, Biological Sciences, 353*, 1385-1383.

Tipper, S.P., Howard, L.A., & Paul, M.A. (2001). Reaching affects saccade trajectories. *Experimental Brain Research, 136*, 241-249.

Tosoni, A., Galati, G., Romani, G.L., & Corbetta, M. (2008). Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nature Neuroscience, 11*, 1446-1453.

Trillenberg, P., Sprenger, A., Petersen, D., Kömpf, D., Heide, W., & Helmchen, C. (2007). Functional dissociation of saccade and hand reaching control with bilateral lesions of the medial wall of the intraparietal sulcus: implications for optic ataxia. *NeuroImage, 36*, T69-76

Van der Stigchel, S. (2010). Recent advances in the study of saccade trajectory deviations. *Vision Research, 50*, 1619-1627.

Van Der Werf, J., Jensen, J., Fries, P., & Medendorp, W.P. (2010). Neuronal synchronization in human posterior parietal cortex during reach planning. *Journal of Neuroscience, 30*, 1401-1412.

van Zoest, W., Van der Stigchel, S., & Barton, J.J.S. (2008). Distractor effects on saccade trajectories: A comparison of prosaccades, antisaccades, and memory-guided saccades. *Experimental Brain Research, 186*, 431-442.

CHAPTER II

STUDY 1: Remembering where not-to-look: Attention is suppressed at task-relevant locations forbidden to saccades

Manuscript for submission

Remembering where not-to-look: Attention is suppressed at task-relevant locations forbidden to saccades

Saurabh Dhawan, Heiner Deubel, Donatas Jonikaitis[1]

Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität, München, Germany.

Contribution: The author of this PhD thesis designed and ran experiments, analysed the results and wrote the manuscript (introduction, methods and results sections).

ABSTRACT

Several lines of evidence have shown visuospatial attention to be coupled to both saccadic planning and working memory. A key question that remains, however, is whether these couplings are truly obligatory or are they malleable to task demands. In this study, we investigated an oculomotor delayed response task that required a location to be forbidden to saccades but to be maintained in working memory through a delay – the two systems thus making conflicting demands on attentional modulation. We found that visuospatial attention, at a location under such a conflict, is modulated along with the saccadic signal and is suppressed. The extent of suppression was found to be correlated to success or failure in making the correct saccadic response. Our results, while confirming and complementing the claims for a selective coupling between attention and saccades, show that working memory interacts with attentional resources in a task-dependent rather than obligatory manner. Additionally, the results constitute a notable example of the local suppression of visuospatial attention (as opposed to that of object or feature based attention).

---

[1] Correspondence should be addressed to D.J. (djonikaitis@gmail.com).

INTRODUCTION

Visuospatial attention has been shown to be coupled to and deployed according to the demands of both saccades (Deubel and Schneider, 1996; Awh et al., 2006b) and working memory (Smyth and Scholey, 1994; Awh et al., 2006a). However, both these couplings have mostly been studied independently of each other and it is not clear what happens in cases where both working memory and saccades are involved and make conflicting demands on attentional resources. The oculomotor delayed nonmatch-to-sample task presents a unique experimental situation to help investigate this issue – subjects are instructed to remember the location of a sample cue as a marker of where not-to-look and after a delay, when it reappears along with a new stimulus, make a saccade to the one at the nonmatching location (Figure 1). Hence, even though a saccadic response to the memorized location needs to be suppressed, the location remains task relevant and must be maintained in working memory. In the present study, we tested how such a suppression of saccades to a memorized location would affect visual discrimination performance, a frequently used diagnostic measure of visual attention (Deubel and Schneider, 1996; Carrasco and Yeshurun, 2009).

Recent studies offer different predictions concerning the strategy by which the target-nontarget distinction in this task is achieved. In a neurophysiological study using this task, Hasegawa and colleagues (2004) identified a group of neurons in the frontal eye fields and the caudal prefrontal cortex that fire selectively when a stimulus appears at a specific location in the visual field ‘and’ when saccades to that location are forbidden, that is, to the memorized location in the Nonmatch task. Their findings suggest that the strategy used to identify the Nonmatch target is by actively suppressing a response to the memorized location so that the desired saccade could be made to the other location. Curtis et al. (2004, 2005, 2006), on the other hand, proposed that the Nonmatch task is solved by keeping sustained covert attention at the sample location to help sustain it in the working memory to be able to later identify the target that does not match. Based on this assumption the authors claim that the specific pattern of activation seen during the delay in the posterior parietal cortex and the dorsolateral prefrontal cortex represents a retrospective sensory code. However, neither of these studies directly investigated the role attention might have in performing this task.

Additionally, directly studying attentional allocation in this task should also allow us to inquire whether spatial attention can mediate response suppression, since only location and not objects or features are relevant during the delay. Most of the previous studies investigating the role of attention in response suppression have relied on either the suppression of a specific object or else of a particular feature of the stimulus (Ipata et al., 2006; Zanto & Gazzaley, 2009; Snyder and Foxe, 2010), while the studies that did address suppression of a location relied on indirect measures of suppression like movement trajectories (Van der Stigchel and Theeuwes, 2006). Thus, it remains unclear whether a task requiring the suppression of a response to a specific location is solved by actively suppressing spatial attention at that location, by simply ignoring it, or else by actively attending to that location but suppressing the response.

METHOD

Participants. Ten participants (5 males and 5 females, aged between 18 and 28) took part in the experiments. They had normal or corrected-to-normal vision and all but two were naïve as to the purpose of the study.

Experimental setup and stimuli. Observers sat in a silent and dimly lit room with the head positioned on a chin rest, 70 cm in front of a computer screen. Stimuli were presented on a 22" Lacie Electron 22 Blue screen with a spatial resolution of 1280x1024 pixels running at 85 Hz vertical refresh rate. Gaze position of the dominant eye was recorded using an EyeLink 1000 Desktop Mount (SR Research, Osgoode, Ontario, Canada) with an average spatial resolution of 15 to 30 min-arc and a sampling rate of 1000 Hz. The experiment was controlled through a desktop computer; manual responses were recorded through a standard keyboard. The software controlling stimulus presentation and response collection was implemented in MATLAB (MathWorks, Natick, Massachusetts, USA), using the Psychophysics and EyeLink toolboxes.

Experimental design and data analysis. The experiment comprised 5 blocks of the Match and 5 blocks of the Nonmatch task, each block consisting of 50 trials. The task order was determined randomly for each subject. The experiment was preceded by a single

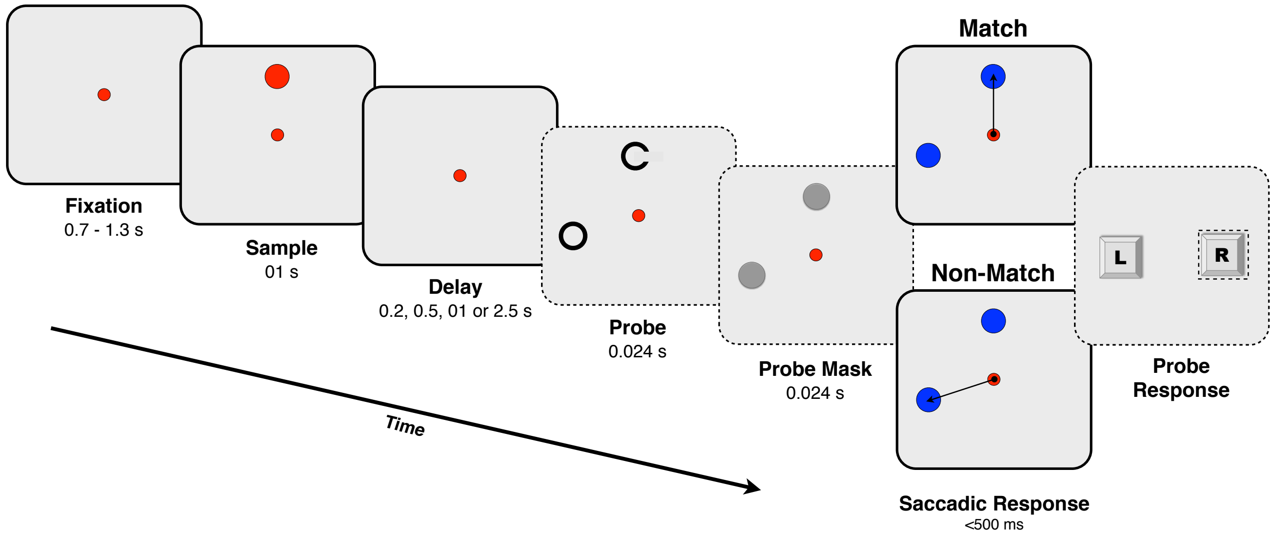


Figure 1. Schematic depiction of the sequence of stimuli and experimental conditions. See *Stimuli and tasks* under *Methods* for details.

practice block of 50 trials. The blocks were administered consecutively with short periods of rest (determined by participants; 1-2min on an average). A two-way ANOVA was used for statistical analyses.

Stimuli and tasks. **Figure 1** provides a schematic illustration of the sequence of stimuli and the experimental conditions. Each trial on both tasks comprised 6 phases: (i) Fixation: Each trial started with the presentation of a fixation point (a red circle of radius 0.3º) in the center of the screen on which subjects were instructed to fixate all through the trial except when making the saccade response. (ii) Sample: After a fixation delay selected randomly between 700 and 1300 ms, a sample (a red circle of radius 0.8º) appeared for 1s at one of 10 possible positions along a circular array of radius 5º centered at the fixation point. Subjects were told to memorize the location of the sample (hereafter referred to as the memorized location). (iii) Delay: When the sample disappears, subjects continue to fixate at the center for 4 different delay durations – 0.2s, 0.5s, 1s and 2.5s. (iv) Probe presentation: At the end of the delay period, a Landolt ring (the discrimination probe with either a left or a right orientation) and a complete ring of identical luminance flashed for two video frames (~24 ms), one at the memorized location (position 0) and the other at one of nonmemorized locations at a distance of 36º, 72º or 108º (positions 1, 2 and 3 respectively) from the other ring followed by a mask image for the same duration. Probability of the discrimination probe appearing at position 0, 1, 2 or 3 was equal, which means 25% for memorized location and 75% for nonmemorized locations. (v) Saccade Response: Immediately after that, two blue circles identical in size and luminance to the sample appeared as test stimuli for 600 ms at the same locations as the two rings presented before (one at the memorized location and another at position 1, 2 or 3). In the Match task subjects had to make a saccade to the target at the memorized location, while in the Nonmatch task they had to make a saccade to the target at the nonmemorized location. (vi) Probe Response: Upon the disappearance of the test stimuli, subjects had to indicate by pressing a button, the left or right orientation of the Landolt ring that was shown in step (iv). The next trial started immediately upon the button press.

RESULTS

Discrimination performance at the memorized location (Figure 2A). In the Match task, probe discrimination was found to be better at the memorized location (to which a saccade was planned) than at the nonmemorized locations (repeated measures two-way ANOVA; F=14.57, p<0.005), which shows that memorizing a location as a future saccade target in the Match task leads to a deployment of attention to that location. In the Nonmatch task, on the other hand, probe discrimination at the memorized location (to which saccades were forbidden) was worse as compared to nonmemorized locations (F=13.40, p<0.006) showing that memorizing it as a marker of 'where not to look' leads to a suppression of attentional performance at that location. This clearly demonstrates that attentional deployment at the memorized location depends on the contextual condition preceding the appearance of the probe, that is, whether later a saccade has to be made (Match task) or avoided (Nonmatch task) at the location that was memorized. Additionally, no significant effect was found when we compared the discrimination performance at the nonmemorized locations to which saccades were neither planned nor suppressed (dashed lines; standard errors are not shown for graphic clarity) in the Match task with those in the Nonmatch task (F=2.28, p>0.1). The data points at the nonmemorized locations, in our view, can be treated as a baseline performance where there was neither attentional benefit nor suppression.

Attentional benefits and costs. **Figure 2B** presents relative probe discrimination obtained by subtracting the performance at the memorized location from that at the nonmemorized locations, separately for both Match (blue bars) and Nonmatch trials (red bars)

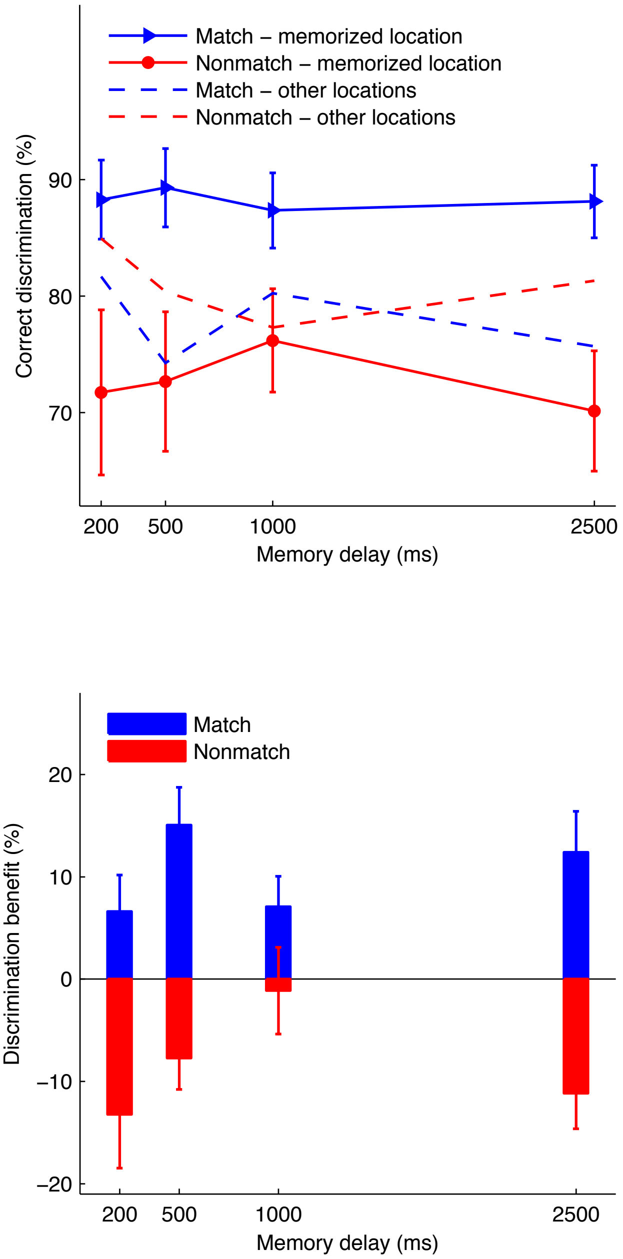


Figure 2. **(A)** Perceptual performance in identifying the discrimination target as a function of the delay condition. **(B)** Attention benefit at memorized vs. nonmemorized locations. Blue and red bars show the relative discrimination performance for each delay condition, respectively for match and nonmatch trials, obtained by subtracting the performance at the memorized locations from that at the nonmemorized locations.

at each delay condition. The data show that memorizing a location as a saccade target binds attention to that location giving it all the local processing benefits compared to non-memorized locations. On the other hand, memorizing a location to which saccades are forbidden, leads to an attentional cost at that location compared to the nonmemorized locations that are not forbidden to saccades.

Effect of probe distance from the memorized location. **Figure 3A** shows discrimination performance as a function of the relative probe distance from the memorized location. Probe was presented either at the memorized location (distance 0°) or at locations 36°, 72° and 108° away, respectively, in a circular arrangement. We see that probe discrimination at the memorized location is better than that at the nonmemorized locations in the Match condition, and worse in the Nonmatch condition, even for the smallest distance of 36° (repeated measures t-test, $t(9)=2.68$, $p<0.03$ for Match condition and $t(9)=-6.11$, $p<0.001$ for Nonmatch condition). However, we did not find an effect of how far away from the memorized locations the probe appeared – probe discrimination was not found to be significantly different when nonmemorized locations (36°, 72° and 108°) were compared with each other.

Oculomotor results. After the delay ended, participants made a saccade either to the memorized location (Match task, mean latency and standard error of the mean were 345 ± 24 ms) or to the new stimulus (Nonmatch task; 383 ± 25 ms). Additionally, in the Nonmatch task, saccadic endpoints at the nonmemorized target locations tended to deviate away from the location at which saccades had to be suppressed (average angular deviation -2.3, 3.9 and 2.7 degrees for targets 36, 72 and 108 degrees away from the forbidden location, all $p<0.05$). Similar effects in the deviation of saccadic trajectories have previously been used as an index of the strength of inhibition of responses to distracting stimuli (Van der Stigchel and Theeuwes, 2006). This is in contrast to the Match task, where average angular deviations away from the memorized locations were very small (~1 degrees).

We also found a strong correlation between suppression in the Nonmatch condition and saccade latencies – the stronger the suppression of attention at the memorized location (that is, the lower the discrimination performance), the faster the correct saccades were to the Nonmatch locations (correlation coefficient - 0.65, $p<0.03$). Stronger suppression thus resulted in faster saccade execution.

Error trials. Subjects showed a tendency towards making more erroneous saccades in the Nonmatch task (20%; saccades to the memorized but forbidden target instead of to the nonmatching target; error bars are not included for graphic clarity) than in the Match task

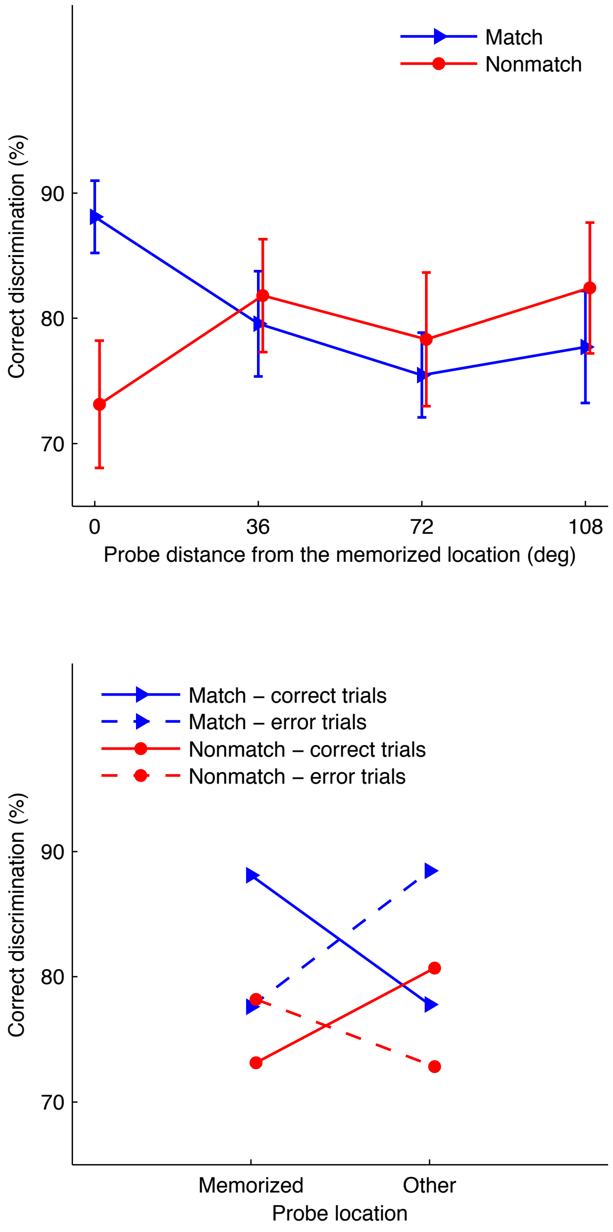


Figure 3. (A) Effects of probe distance from the memorized locations on discrimination performance. Position 0 refers to the memorized locations and the other three positions to nonmemorized locations at relative distances of 36°, 72° and 108° from the position 0, respectively. **(B)** Discrimination performance in the Correct and Error trials in each condition.

(11%; saccades to irrelevant nonmemorized locations instead of to the matching target). Interestingly, our data suggests that these errors were related to where attention was allocated during the preceding delay (**Figure 3B**). In the Match task, if participants failed to allocate more attention to the memorized location during the delay (i.e. discrimination performance was lower than that at other locations), they were then more likely to make an erroneous saccade to one of the nonmemorized location. Conversely, in the Nonmatch task, if participants failed to suppress attention at the memorized but forbidden location during the delay (i.e. discrimination performance was higher than that at other locations), they were more likely to make the incorrect saccade to the forbidden location.

DISCUSSION

In this study, we investigated the role of attentional allocation in planning or suppressing a response to a location. The memorized location in the two cases differed only by the saccadic target it was encoded for – to plan a saccade to it or to avoid making a saccade to it when the target reappeared. Particularly, in the Nonmatch task, the only information available through the delay was the memorized location where the subjects must not look. We found that marking a location as forbidden for saccades led to an attentional cost at that location as compared to the nonmemorized locations that were not forbidden. On the other hand, preselecting a location as a saccade target enhanced attention to that location giving it all the local processing benefits as compared to the nonmemorized locations that were not saccade targets. Previous studies, in our knowledge, that investigated the role of attention in response suppression either involved suppression of object or feature based attention (Ipata et al., 2006; Zanto & Gazzaley, 2009; Snyder and Foxe, 2010) or else relied on indirect measures of suppression like movement trajectories (Van der Stigchel and Theeuwes, 2006). Since no objects or features were present during the delay in our experiments, these results represent a notable example of mediation of response suppression by suppression of spatial attention at a location. We will discuss how these findings help to clarify the strategy used to solve the Nonmatch task, and its implications for current concepts of attention-saccade coupling and working memory function.

Our results show that the target-nontarget distinction in the Nonmatch task is achieved by actively suppressing rather than maintaining spatial attention at the memorized location. A direct corroboration of this strategy comes from Hasegawa et al. (2004), who discovered a counterpart to the saccade planning neurons in the frontal cortex in the form of a distinct neuronal population dedicated to saccade suppression in a spatially selective manner. Using an experimental paradigm similar to ours, they identified a group of neurons (named as ‘don’t look’ neurons) in the frontal eye field and the caudal prefrontal cortex that code selectively for the forbidden stimulus in the Nonmatch task. The delay period activity of these ‘don’t look’ neurons was spatially tuned for the memorized location only in the Nonmatch task while they were not tuned at all for the same location in the

Match task. Neural circuits involved in saccade preparation, in turn, have been shown to play a causal role in directing and modulating covert spatial attention. Subthreshold microstimulation of sites in FEF (Moore and Fallah, 2001, 2004) that are responsible for generating saccades to a particular location led to improved performance in psychophysical visual attention tasks involving stimuli at that location. Similar microstimulation studies have also demonstrated an attention-like enhancement in activity of V4 neurons at retinotopically corresponding locations (Moore and Armstrong, 2003). Collating these results with our data, we believe it to be plausible that the frontal signal demonstrated by Hasegawa et al. (2004) leads to a concomitant suppression of both, saccades and attention.

In a series of human neuroimaging studies using this task, Curtis and colleagues (2004, 2005, 2006) argued for a different strategy to make the correct saccade in the Nonmatch task, namely, encoding the sample location as a retrospective sensory code, sustaining attention to that location throughout the trial right up to the response time and then using the memory information to select the other stimulus as the saccade target. If this strategy were true then in the Nonmatch task perceptual discrimination performance at the memorized location would be expected to be better than that at the nonmemorized location, because of the local processing advantages conferred by sustained spatial attention. Our results clearly show that this is not the case. Attention at the memorized location was not only found unaugmented, but in fact significantly diminished in comparison to both the nonmemorized locations in the same trial and the memorized locations in the Match trials.

These findings have several important implications for current concepts of working memory and its interactions with attention and saccades. Firstly, the primary purpose of the studies by Curtis and colleagues (2004, 2005) was to investigate whether different component nodes of the frontoparietal network that show working memory related persistent neural activity are specialized in maintaining relatively different representations (for example, motor versus spatial code) based on the different task demands in Match and Nonmatch tasks. They found that while the oculomotor areas were more active during the delay period in the Match task, posterior parietal cortex and inferior frontal cortex were more active in the Nonmatch delays. Based on their assumption that the Nonmatch task is solved by keeping sustained attention, and the fact that posterior parietal cortex has been linked to representation of space (Constantinidis and Steinmetz, 1996), they argued that the parietal activity seen in the Nonmatch task represents the maintenance of a retrospective spatial code. However, inferences from our results and those of Hasegawa et al. (2004) suggest that successful execution of the nonmatch task is more nuanced and requires maintenance of a behaviorally relevant location in a manipulatable manner so that saccades and attention to it can be suppressed but it can still be used later in making the right saccade to the novel stimulus. Parietal cortex, in turn, is known to have a role in all of these processes – maintaining working memory representation of a visual stimulus (Constantinidis and Steinmetz, 1996), task dependent manipulation of the maintained information (Assad, 2003; Constantinidis and Steinmetz, 2001), encoding its behavioral relevance (conceptualized as a salience map; Gottlieb et al., 1998) in addition to its role in attentional allocation (Bushnell et al., 1981), saccadic planning, and response suppression (Lindner et al., 2010). Hence, a full interpretation of the parietal activity shown by Curtis et al. (2004, 2005) needs further examination, and, we suggest, is likely to involve not just the maintenance of the sensory code but all the aforementioned parietal functions.

Secondly, several recent studies have argued that an object held in working memory will automatically capture attention on a subsequent presentation (Pashler and Shiu, 1999; Soto et al., 2008). This fact further emphasizes the behavioral necessity for active suppression of the memorized location to solve the Nonmatch task as otherwise when the two targets appear at the response time in the Nonmatch task, attention could be involuntarily captured by the memorized location increasing the likelihood of an erroneous saccadic response to that location. In fact, our error trial analysis (Figure 3B) showed that a failure to suppress a saccade to the forbidden location (error trials in the Nonmatch task) was correlated to a failure in suppressing attention (as shown by undiminished discrimination performance) at that location during the preceding delay. On the other hand, better attentional suppression resulted in faster execution of the correct saccade. This suggests that, although a subsequent presentation of an item that matches the contents of working memory can capture attention, this effect can be overruled by suppressing attention at that location.

Lastly, the modulation of attentional resources has been shown to be coupled to and deployed according to the demands of both saccades and working memory. For instance, Deubel and Schneider (1996) showed that attention remains obligatorily bound to saccade targets until the onset of the saccade and argued for an obligatory and selective coupling between these two mechanisms. Similarly, the attention-based rehearsal hypothesis (Smyth and Scholey, 1994; Awh et al. 2006a) suggests that attention is deployed at the locations held in spatial working memory and that such attention-based rehearsal plays an essential role in maintenance of information in visual working memory. However, both these couplings have mostly been studied in isolation and it is not clear what happens in cases where they overlap and make conflicting demands on attentional resources. The Nonmatch task that we used represents one such unique experimental situation in which saccadic planning and working memory make opposite demands on attentional modulation – the memorized location has to be kept in working memory, but saccades to its location have to be suppressed. We found that in such a scenario attentional resources are preferentially devoted to saccadic goals, despite the conflicting needs of working memory. This confirms and complements the claim, made by Deubel and Schneider (1996), of a selective and obligatory coupling between saccades and attention – saccades at the memorized location could neither be planned nor suppressed without a corresponding effect on attentional performance. However, this does not necessarily mean that working memory representations in this task were maintained without any attentional input. Sustained attentional suppression of a task-relevant location, by definition, requires its spatial coordinates to be maintained through the delay (e.g. by the spatially selective ‘don’t look’ neurons). Hence it seems plausible that an active suppression of attention, much like its enhancement, can contribute to the rehearsal of working memory representations, thereby allowing working memory to interact with attentional resources in a less obligatory and more context-dependent manner.

ACKNOWLEDGEMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (GRK 1091 and De 336/2) and Graduate School of Systemic Neurosciences, Ludwig Maximilians University, Munich.

REFERENCES

Assad J (2003) Neural coding of behavioral relevance in parietal cortex. Curr Opin Neurobiol 13:194-197.

Awh E, Armstrong KM, Moore T (2006a) Visual and oculomotor selection: links, causes and implications for spatial attention. Trends Cogn Sci 10:124-130.

Awh E, Vogel E, Oh S (2006b) Interactions between attention and working memory. Neuroscience 139:201-208.

Bushnell MC, Goldberg ME, Robinson DL (1981) Behavioral enhancement of visual responses in monkey cerebral cortex. I. Modulation in posterior parietal cortex related to selective visual attention. J. Neurophysiol 46:755-772.

Carrasco M, Yeshurun Y (2009) Covert attention effects on spatial resolution. Prog Brain Res 176:65-86.

Constantinidis C, Steinmetz MA (1996) Neuronal activity in posterior parietal area 7a during the delay periods of a spatial memory task. J Neurophysiol 76:1352-1355.

Constantinidis C, Steinmetz MA (2001) Neuronal Responses in Area 7a to Multiple Stimulus Displays: II. Responses Are Suppressed at the Cued Location. Cereb Cortex 11:592-597.

Curtis CE, Rao VY, D'Esposito M (2004) Maintenance of spatial and motor codes during oculomotor delayed response tasks. J Neurosci 24:3944.

Curtis CE, Sun FT, Miller LM, D'Esposito M (2005) Coherence between fMRI time-series distinguishes two spatial working memory networks. NeuroImage 26:177-183.

Curtis CE (2006) Prefrontal and parietal contributions to spatial working memory. Neuroscience 139:173–180.

Deubel H, Schneider WX (1996) Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res 36:1827-1837.

Gottlieb JP, Kusunoki M, Goldberg ME (1998) The representation of visual salience in monkey parietal cortex. Nature 391:481–484.

Hasegawa RP, Peterson BW, Goldberg ME (2004) Prefrontal neurons coding suppression of specific saccades. Neuron 43:415-425.

Ipata AE, Gee AL, Gottlieb J, Bisley JW, Goldberg ME (2006) LIP responses to a popout stimulus are reduced if it is overtly ignored. Nat Neurosci 9:1071-1076.

Lindner A, Iyer A, Kagan I, Andersen RA (2010) Human Posterior Parietal Cortex Plans Where to Reach and What to Avoid. J Neurosci 30:11715-11725.

Moore T, Armstrong KM (2003) Selective gating of visual signals by microstimulation of frontal cortex. Nature 421:370-373.

Moore T, Fallah M (2001) Control of eye movements and spatial attention. Proc Natl Acad Sci U S A 98:1273 -1276.

Moore T, Fallah M (2004) Microstimulation of the frontal eye field and its effects on covert spatial attention. J Neurophysiol 91:152-162.

Pashler H, Shiu LP (1999) Do images involuntarily trigger search? A test of Pillsbury's hypothesis. Psychon Bull Rev 6:445-448.

Smyth MM, Scholey KA (1994) Interference in immediate spatial memory. Mem Cognit 22:1-13.

Snyder AC, Foxe JJ (2010) Anticipatory attentional suppression of visual features indexed by oscillatory alpha-band power increases: a high-density electrical mapping study. J Neurosci 30:4024-4032.

Soto D, Hodsoll J, Rotshtein P, Humphreys GW (2008) Automatic guidance of attention from working memory. Trends Cogn Sci 12:342-348.

Van der Stigchel S, Theeuwes J (2006) Our eyes deviate away from a location where a distractor is expected to appear. Exp Brain Res 169:338-349.

Zanto TP, Gazzaley A (2009) Neural Suppression of Irrelevant Information Underlies Optimal Working Memory Performance. J Neurosci 29:3059-3066.

CHAPTER III

STUDY 2: Independent allocation of attention to eye and hand targets in coordinated eye-hand movements

Psychological science (2011), 22, 339-347.

Independent allocation of attention to eye and hand targets in coordinated eye-hand movements

Donatas Jonikaitis[1] and Heiner Deubel

Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität, München, Germany.

Contribution: The Author of this PhD thesis designed and ran experiments, analysed the results and wrote the manuscript.

ABSTRACT

When reaching for objects, people frequently look where they reach. This raises the question of whether the targets for eye and hand in concurrent eye-hand movements are selected by a unitary attentional system or by independent mechanisms. We used the deployment of visual attention as an index of movement target selection and asked observers to reach and look to separate locations. Results show that during the preparation of coordinated movements, attention is allocated in parallel to saccade and reach targets. Attentional allocation for each of the two movements interacts synergistically when both are directed to a common goal. Delaying the eye movement delays the attentional shift to the saccade target while leaving attentional deployment to the reach goal unaffected. Together, our findings demonstrate that attentional resources are allocated independently to eye and hand movement targets and suggest that the goals for these effectors are selected by separate attentional mechanisms.

---

[1] Correspondence should be addressed to D.J. (djonikaitis@gmail.com).

INTRODUCTION

To interact with objects in their environment, humans often make a combination of eye and reaching movements. The control of these movements is not independent - typically, the eye movement pattern is organized such that it helps to gather the information that is most important for reaching and manipulating the object. In a pick-and-place task for instance humans fixate the item to be picked up, look at possible obstacle locations when lifting it, and then saccade to the end goal of the hand movement before the hand reaches this location (Horstmann & Hoffmann, 2005; Johansson, Westling, Backstrom & Flanagan, 2001; Land, Mennie & Rusted, 1999; Pelz, Hayhoe & Loeber, 2001).

The planning of these coordinated movements requires the selection of the movement targets for eye and hand. Given the commonly observed ‘yoking’ of eye and hand movements, the question arises whether the targets for the eye and for the hand are selected by a common mechanism or rather by independent systems. The first possibility assumes that the planning of coordinated eye-hand movements is based on a shared goal selection, resulting in eye-hand coupling already at early stages of movement planning. Alternatively, goal selection for eye and hand movements may involve separate, largely independent systems, and eye-hand interaction may occur only at later stages of sensorimotor processing.

The view that the selection of eye and hand movement goals involves separate, largely independent systems has gained wide support in a number of neurophysiological studies. Single cell recording studies in monkeys have suggested that separate areas in parietal cortex represent movement goals for saccades and reaches (Calton, Dickinson & Snyder, 2002; Dickinson, Calton & Snyder, 2003; Quiroga, Snyder, Batista, Cui & Andersen, 2006; Scherberger & Andersen, 2007; Snyder, Batista & Andersen, 1997). Functional imaging and magnetoencephalography studies in humans have identified distinct parietal regions showing preparatory activity before eye or hand movements (Astafiev et al, 2003; Tosoni, Galati, Romani & Corbetta, 2008; Van Der Werf, Jensen, Fries & Medendorp, 2010). Saccade goal selection activity has also been demonstrated in prefrontal cortex, both in single cell and neuroimaging studies (e.g. Curtis & Connolly, 2008; Lawrence & Snyder, 2009; Schall & Hanes, 1993). Finally, also psychophysical studies have proposed that early stages of movement planning are separate for eye and hand movements (Prablanc, Echallier, Komilis & Jeannerod, 1979; Sailer, Eggert, Ditterich & Straube, 2000; Thompson & Westwood, 2007).

However, also the alternative view that a single system underlies eye and hand movement goal selection has found support in a number of psychophysical studies (Bekkering, Adam, van den Aarssen, Kingma, & Whiting, 1995; Neggers & Bekkering, 2000; Song & McPeek, 2009). Further evidence for this view came from functional imaging studies that reported an overlap of systems involved in eye and hand movement selection in both, parietal and prefrontal cortex (Beurze, de Lange, Toni & Medendorp, 2009; Levy, Schluppeck, Heeger & Glimcher, 2007; Medendorp, Goltz, Crawford & Vilis, 2005).

It is important to note that the psychophysical studies mentioned above have drawn their conclusions from measures related to the motor output, such as from correlations between saccade and reaching endpoints, movement velocity profiles and movement latencies. Therefore, the results cannot speak directly to the issue of whether coupling of eye and hand occurs at early stages involving movement target selection, or at later processing stages. The current experiments were aimed at studying movement goal selection directly, by using spatial attention as an index of target selection. We made use of the well-established fact that visual attention is allocated to the target of the planned movement before eye saccades (Kowler, Anderson, Dosher & Blaser, 1995; Deubel & Schneider, 1996; Montagnini & Castet, 2007) and before reaching movements (Deubel, Schneider & Paprotta, 1998; Linnell, Humphreys, McIntyre, Laitinen & Wing, 2005). Perceptual measures of attentional allocation are therefore direct indicators of movement goal selection. In our experiments participants were asked to saccade and reach to spatially separate objects while attention allocation was measured by means of a probe discrimination task. The results show that the selection of the saccade target and of the reach goal can occur independently, suggesting that the goals of eye and hand are selected by separate mechanisms. This also implies that eye-hand coupling does not result from a common attentional selection mechanism, but probably follows from interactions at later processing stages.

EXPERIMENT 1

In this experiment we established that attention is allocated to movement goal locations before movement onset. Participants either made a saccade to a centrally cued target ("Saccade-only" task), or they reached towards the cued target without looking at it

("Reach-only" task). We measured covert attentional allocation by briefly presenting a probe at either the movement goal, or at a movement-irrelevant location.

Method

Participants sat in a dimly illuminated room with their right hand on an inclined reaching plane, under a half-translucent mirror. Stimuli were projected from a monitor above onto the mirror. Due to this setup projected visual stimuli appeared on the reaching plane, while participants could not see the reaching hand. Visual feedback about the hand position was provided by LED fixed to the fingertip, which could be switched on and off during the experiment. Reaching movements were recorded at 120 Hz with a Fastrack (Polhemus Inc.)

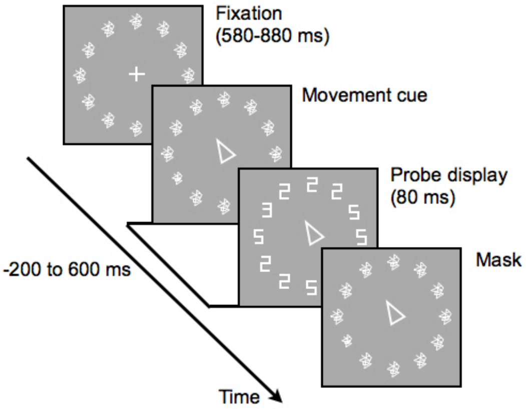


Figure 1 Experimental procedure**.** In Experiment 1, participants quickly looked ("Saccade-only" task) or reached ("Reach-only" task) to the item indicated by the centrally presented movement cue. After the movement they reported the probe identity (the probe was a digital letter "E" or "3" embedded in distractors). The probe display could appear -200 to 600 ms with respect to the movement cue onset. In Experiment 2, the cue was the signal to initiate both the reach to the location indicated by the cue, and to make a saccade to a location that was prespecified within an experimental block.

electromagnetic position sensor attached to the index finger of the right hand. Eye movements were recorded with a video-based eye tracking system (SensoMotoric Instruments, Eyelink-I) at a temporal resolution of 250 Hz.

Figure 1 depicts the stimulus sequence. A central fixation cross and twelve mask elements (size 0.9 x 1.4 deg, composed of randomly generated lines) were presented on a uniform gray background, arranged on an imaginary circle with a radius of 6.5 deg. Participants first directed the index finger and their gaze to the central cross. 580 to 880 ms later, the central cross changed into an arrow which pointed towards any of the 12 the mask stimuli. Participants either made a saccade towards the cued location ("Saccade-only" task), or they reached to the cued location while maintaining central fixation ("Reach-only" task). Visual feedback about reaching accuracy was given 1500 ms later.

While performing the saccade or reaching task, participants had to detect a brief probe stimulus shown at any of the locations occupied by the mask elements. At a random time between 200 ms before movement cue onset and 600 ms after cue onset, 11 of the 12 mask stimuli changed into distractors (digital "2" or "5"), while one mask stimulus changed into the probe letter (digital "E" or "3"). The probe was presented for 80 ms and then was again masked. After finishing the eye or hand movement participants reported whether they had perceived an "E" or "3". Responses were made by non-speeded button press with the left hand. Probe appeared at the movement goal with 50% probability (valid trials). On the other 50% of trials the probe was presented elsewhere (at randomly selected one of all possible movement-irrelevant locations); the probe never appeared directly besides the movement goal.

10 observers took part in the "Saccade-only" task, and 11 in the "Reach-only" task. Each participant performed at least 4 experimental blocks of 192 trials each.

Results

Since the probe was presented at variable times, we were able to analyze the time course of attentional deployment to the probe locations. For each time point (every 30 ms) we calculated the proportion of correct probe discrimination. Probe discrimination rate at both saccade and reach goals increased gradually before the movement (**Figure 2a**). In the "Saccade-only" task, improvement at the saccade target appeared at around 80 ms after movement cue onset (t-test comparison for discrimination at saccade target versus chance level, t(9)=3.30, p<0.01; from that time point probe discrimination was always better than chance, all p<0.05). In the “Reach-only” task, discrimination performance improved at around 140 ms after movement cue onset at the reach goal (t(10)=3.25, p=0.01). Immediately before the onset of the saccade (average latency 250 ± 6 ms standard error of the mean) and the reaching movement (average latency 295 ± 12 ms), probe discrimination levels at saccade and reach goals were comparable (p>0.05). These findings demonstrate that, before the saccade or the reach started, attention shifted to the location of the respective movement goal. In contrast, participants were at chance level to report probe identity at movement irrelevant locations to which no action was directed.

EXPERIMENT 2

In this experiment (“Combined movement” task) participants had to make simultaneous eye and hand movements to two separate locations (with a few trials where both movements were directed to the same location). Again we measured attentional allocation by presenting a brief probe.

Method

In this task saccade location was kept constant (at clock positions of 2, 4, 8, or 10 o’clock) for a block of 190 trials. Stimuli and timing were identical to the Experiment 1. When the movement cue appeared, participants were asked to make two movements simultaneously - a reach to the cued location and a saccade to the remembered location. We used a fixed saccade location because it is known that even when a saccade can be prepared ahead a known location, the attention shift to the target is obligatory (Deubel & Schneider, 2003). We used four different spatial distances between the saccade and the reaching goals: 0 (saccade and reach directed to the same location), 1 (reaching goal besides saccade location), 3, or 5 elements. Probe probability was 33% at the saccade goal, 33% at the reaching location, and 33% at one of the other, movement-irrelevant locations. Ten observers participated in the study. Each participant performed at least 6 experimental blocks.

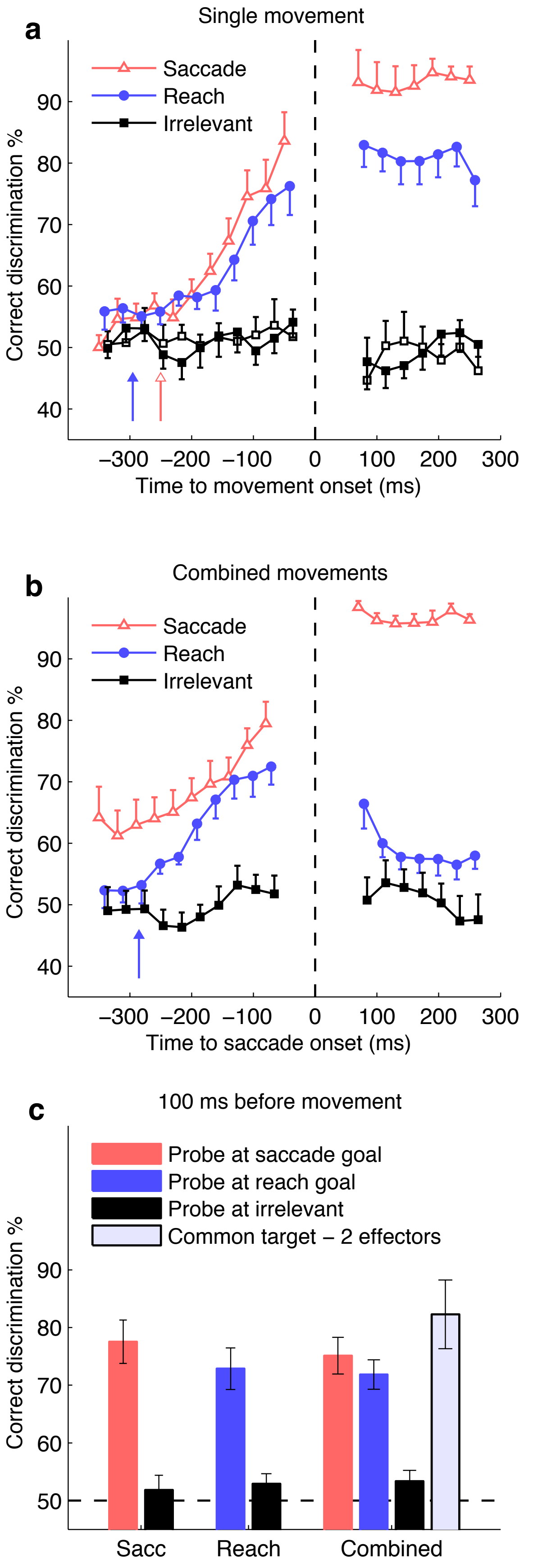


Figure 2 Attention shifts before movement onset. (a) Experiment 1 "Saccade-only" and "Reach-only" tasks. The vertical arrows indicate average time of reach or saccade cue presentation. The vertical dashed line indicates movement onset. Probe discrimination rate increased after movement cue presentation at the saccade target (curve with empty triangles), and at the reaching target (curve with filled circles), respectively. Participants were at chance to discriminate probes at movement-irrelevant locations (black curves for the single movement tasks). (b) Experiment 2 – "Combined movement" task. The vertical dashed line indicates saccade onset. The small vertical arrow indicates the average time of movement cue presentation. Probe discrimination increased in parallel at both saccade and reaching goal locations. (c) Comparison of discrimination rates in single and combined movement experiments. Discrimination rates were determined for probes occurring within 100 ms before movement onset. Performance was comparable between the single and combined movement tasks. Discrimination was best if saccade and reach were directed to the same location.

Results

Average saccade latency in this task was 288 ± 16 ms; average reach latency was 300 ± 20 ms. **Figure 2b** shows discrimination performance for probes appearing at various times before and after saccade onset. Strikingly, probe discrimination performance increased simultaneously at both saccade and reach goals. Thus, before the saccade started, probe discrimination rate was comparable at the saccade and the reach target (repeated measures t-test comparing discrimination at saccade and reach goals, all $p>0.05$), indicating that attention was allocated to both movement goals in parallel.

Having found evidence for the parallel allocation of attention to both movement targets, we next determined whether there was a cost (or benefit) in probe discrimination for the combined movement task in Experiment 2 in comparison to the single movement conditions of Experiment 1 (**Figure 2c**). Discrimination performance at the saccade goal was not different when the participants made only a saccade as compared to making both a reach and a saccade (77% vs. 75%, independent samples t-test, $p>0.05$). The same held for discrimination performance at the reach goal (73% vs. 72%, $p>0.05$). Thus, when simultaneous eye and hand movements were planned, there was no reduction in the attentional resources available for each of these two systems. This is surprising, given that it has been shown previously that planning a saccade leaves only few attentional resources for other, covertly attended locations (Montagnini & Castet, 2007). However, it seems that preparing a second action - with another effector system - is not liable to this fundamental limitation. We also observed that participants were better at discriminating the probes if both eye and hand movements were directed to the same location, as compared to making eye and hand movements to two different locations (**Figure 2c**, rightmost bar; 75% vs. 85%, repeated measures t-test, $t(6)=-2.56$, $p=0.04$ for probes at eye movement goal; 72% vs. 85%, $t(6)=-3.44$, $p=0.01$ for probes at reach goal). This increase in probe discrimination rate shows that the processes selecting eye and hand targets can act synergistically and indicates that separate attentional resources are used in the selection of eye and hand targets.

We next asked to what degree the attentional selection of the saccade target and the reach target are dynamically independent. We split of the data of each participant by median according to whether saccade latencies were short or long. After this split short-latency saccades started on average 112 ± 6 ms earlier than the long-latency saccades,

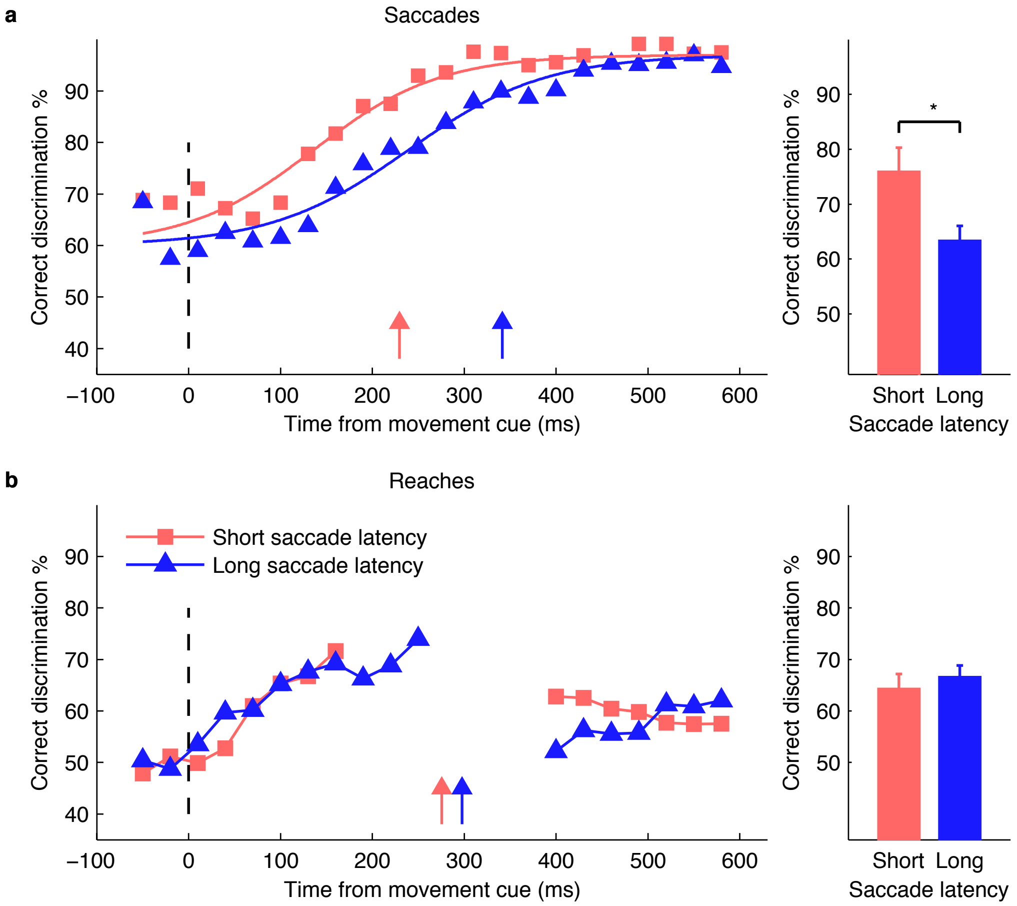


Figure 3 Experiment 2. Independence of attention for eye and hand movements. Performance data for each participant were split into trials with short or long latency saccades by means of a median split. (a) Attention shifted to the saccade location earlier when saccade latencies were short. Accordingly, attention shifted to the saccade location later if saccade latencies were longer. Two vertical arrows denote mean latencies of short or long latency saccades. Right panel - during the interval of 100 to 200 ms after the movement cue presentation participants were better to discriminate the probes presented at the saccade location if saccade latencies were short. (b) Attention deployment at the reaching goal for trials with long and short saccade latencies. Attention did not shift faster to the reaching location if saccade latencies were short and did not shift slower if saccade latencies were long. Thus, regardless of saccade latency, there was no difference in how attention was allocated to the reach targets (right panel).

and this temporal difference was also reflected in the time course of attentional allocation (**Figure 3a**). It took participants 105 ms longer to reach 75% correct probe discrimination if their saccade latencies were longer (determined by fitting probe discrimination for short and long latency saccades with a sigmoidal function). These results demonstrate the close relationship between attentional allocation and saccadic initiation (we found comparable result when we analyzed the “Saccade-only” task; on the other hand, we did not observe this effect for reaching movements in the “Reach-only” task).

In contrast, the time course of attentional allocation at the reach goal was the same for short and long latency saccades, and was thus independent from attentional allocation at the saccade location (**Figure 3b**). In other words, no matter how early or late attention was allocated to the saccade goal, this did not affect attentional allocation at the reach goal. This finding suggests that attentional allocation at both locations is dynamically independent.

It may be objected that the selective processing of saccade and reach goal in this experiment may have resulted from a strategic allocation of attention, since the probe was more likely to appear at saccade and reach goals than at the other, movement-irrelevant positions. To exclude this possibility, we ran an additional control experiment with 7 participants in which the probe was presented with equal probability at any of the 12 stimulus locations. The probes were shown 140-180 ms after the movement cue onset, i.e. at a time which falls within the last 200 ms before saccades and reaches started. We found the same pattern of results as before: If the probe was presented at one of the movement-irrelevant locations, probe discrimination was at chance level (52%). Participants were better if the probe was presented at saccade (68%) or reach (68%) target location, and best if the probe appeared at a location to which both saccade and reach were directed (85%). These results closely mirror the findings of Experiment 1 and Experiment 2, when probe presentation time was matched across the experiments. In conclusion, the results from the control experiment rule out that the previous findings are due to participants strategically attending to locations where the probe was most likely to appear.

EXPERIMENT 3

It could be argued that instead of allocating attention in parallel to both movement goals, participants may have on some trials shifted their attention to the saccade target and on other trials to the reach target. We therefore presented two probes at the same time in a same-different judgment task. The probes were shown for only 80 ms; this time is presumably too short to shift attention from one location to another. Rather, we assume that this task could be solved successfully only if participants allocated their attention in parallel to both, saccade and reach goal.

Method

Stimulus sequence and procedure were the same as in the combined movement experiment except that two probes were shown - one of them was always at one of the movement goals, and the other was either at the second movement goal (50% of trials), or at a movement-irrelevant location. Participants reported whether the two probes were same or different. The same six observers as in Experiment 2 participated in this experiment. Each participant performed 2 blocks of 192 trials.

Results

Participants were better than chance only when the probes were presented at both movement goals simultaneously (63%, $p=0.02$, $t(5)=3.34$). Same/different judgment rates in this experiment could be perfectly from probe discrimination rates observed in Experiment 2. If the probability to identify the probe at the saccade movement goal is p_1 and to identify the probe at the reach goal is p_2, then the probability to correctly identify stimuli appearing at both locations simultaneously as in a same/different task is $(p_1 * p_2)+(1-p_1)*(1-p_2)$. The observed discrimination rate of 63% was indeed not different from the predicted discrimination rate of 62% (repeated measures t-test, $p>0.05$), confirming that participants allocated their attention to both locations in parallel.

EXPERIMENT 4

Experiment 4 was aimed at confirming the dynamical independence of attentional allocation to eye and hand movement targets. In this task, two movement cues were presented centrally, one after the other – a first cue indicating the reach target, and a second cue indicating the saccade target. The cues appeared with a stimulus onset asynchrony (SOA) of 150 or 200 ms. If attention is allocated independently to the two movement goals, we should observe a corresponding delay in attention allocation for the two different SOA conditions.

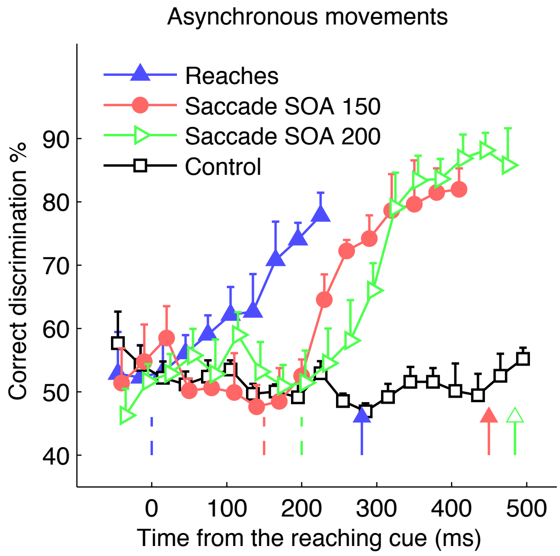


Figure 4 Experiment 4. Attention shifts before delayed eye movements. (a) Dashed lines denote movement cue onsets: at time 0 - reaching cue onset; at time 150 or 200 - saccade cue onsets. Vertical arrows - corresponding reaching and saccade latencies. Attention shifted to the reach goal after the first movement cue, and also shifted to the saccade target after the second movement cue appeared.

Method

Stimuli and procedure were the same as in Experiment 2 except for the following. The reach movement cue was presented for 100 ms and participants had to reach to the instructed location. 50 or 100 ms later a second movement cue appeared for 100 ms, instructing the saccade location. Thus, stimulus onset asynchrony (SOA) between the first and second movement cue was either 150 or 200 ms. The distance between saccade target and the reach goal was either 2 or 4 items. Six observers participated in this experiment. Each participant performed at least 4 blocks of 144 trials.

Results

There was no difference between probe discrimination rates at the reach goal for the two SOA conditions (blue curve combines both SOA conditions in **Figure 4,** repeated measures t-test, all p>0.05). In contrast, probe discrimination performance at the saccade target was modulated by SOA. For the longer SOA condition (SOA = 200 ms), discrimination rate at the saccade target rose above chance level about 80 ms later than for SOA=150 ms.

Note that for the 150 ms asynchrony condition, probe discrimination at the saccade location was far above chance already before the reach movement started (reach latency 272 ± 15 ms). This means that the selection of the saccade goal was not delayed until after reach onset, but rather depended on saccade cue onset. These results demonstrate the temporal independence of attentional allocation to the two movement targets, and rule out the possibility that the parallel allocation of attention observed in Experiment 2 was due to the pre-cueing of the saccade target.

GENERAL DISCUSSION

In a series of experiments we found that when participants made simultaneous eye and hand movements to separate locations, attention was allocated in parallel at both locations, with no cost arising from the need to plan two movements instead of one. Therefore, even though eye and hand systems are linked, this is probably not due to attentional limits when selecting the targets for both movements. Furthermore, we demonstrated that delaying the eye movement led to an according delay of the attention shift to the corresponding target while leaving the attentional deployment to the reach goal unaffected. This indicates that the attentional control mechanisms for eye and hand are dynamically independent. From these results we propose that separate, effector-specific attentional controllers are involved in distributing visual attention to multiple task-relevant locations, instead of a unitary attentional system.

Our experimental findings are perfectly in line with the predictions of the premotor theory of visual attention (Rizzolatti, Riggio & Sheliga, 1994). This theory suggests the existence of multiple spatial pragmatic maps, specific for each effector system. Neurons in these maps become activated when a movement is prepared, and attention results as a consequence of the activity of the pragmatic maps.

The alternative hypothesis is that movement goals for saccades and reaches are selected by a single, shared system representing a unitary map of action-relevant or salient objects (e.g., Itti & Koch, 2000). The existence of such maps has indeed been proposed for both those frontal and parietal areas, frontal eye fields and lateral intraparietal area, which are also implicated in saccade goal selection (Goldberg, Bisley, Powell & Gottlieb, 2006; Gottlieb, Kusunoki & Goldberg, 1998; Moore, Armstrong & Fallah, 2003; Thompson & Bichot, 2005). However, the assumption that these specific areas are representing all salient objects is incompatible with the finding that these regions mainly represent potential saccade, but not reach targets (Quiroga et al, 2006; Snyder et al., 1997). Also, our observation that the selection processes for eye and hand interact synergistically when both effectors are directed to a common target is best explained by assuming that eye and hand movement goal selection occurs in separate systems, rather than in a common, effector-agnostic system. Thus both, our results and current neurophysiological findings seem to indicate that movement goal selection is effector-specific, concerning the objects that are relevant for the particular type of action. Interactions between the selection systems, like the observed synergistic interaction when eye and hand movement goals were shared, may then occur due to backward connections converging onto earlier visual areas (Moore et al., 2003).

While our results have shown that the selection for eye and hand movement targets can be independent, a number of studies reported considerable cross-talk between both systems. For example, saccade amplitudes influence reaching amplitudes (van Donkelaar, 1997), gaze is anchored to the reaching goal location while people are reaching (Neggers & Bekkering, 2000), and people are likely to look where they chose to reach (Horstmann & Hoffmann, 2005). Cross-coupling has also been demonstrated in single cell recording studies showing that eye position signals modulate reach-related activity in parietal cortex (Batista, Buneo, Snyder & Andersen, 1999), and that hand position signals modulate saccade-related activity in frontal cortex (Thura, Hadj-Bouziane, Meunier & Boussaoud, 2008). We interpret these findings as showing that eye and hand movement systems keep track of each other, so that the eye knows where the hand will go and vice versa. These interactions may in principle occur at various possible stages of sensorimotor processing. However, our findings suggest that eye-hand coupling does not result from a common attentional selection mechanism, but probably follows from interactions at later processing stages.

We also demonstrate that attention can be transiently allocated to multiple locations. While classical theories of attention assumed a single focus of selection and this idea has been reinforced recently (Dubois, Hamker & VanRullen, 2009), our data reveal that multiple foci of attention are possible when actions are planned. This is in line with other recent studies showing that when a sequence of eye or hand movements to multiple targets is prepared, attention spreads in parallel to all action-relevant goals, establishing spatially separate attentional foci (Godijn & Theeuwes, 2003; Baldauf & Deubel, 2008, 2010). This is in stark contrast to tasks that involve intentional attention shifts - when making a saccade, people are worse to discriminate visual stimuli presented at locations other than the saccade goal (Tibber, Grant & Morgan, 2009; Wilder, Kowler, Schnitzer, Gersch & Dosher, 2009). Similarly, planning goal-directed pointing or simple button presses reduces performance in tasks requiring attentional shifts to other locations (Brisson & Jolicoeur, 2007; Gherri & Eimer, 2010; Wilder et al, 2009). So, while in these tasks attentional allocation seems to compete with movement planning, attentional resources can be distributed to multiple targets without evidence of resource limitations during the planning of combined eye and hand movements as shown in here, as well as during the preparation of movement sequences. This suggest a dissociation between attention shifts that occur for the purpose of action preparation, and those that are involved in purely perceptual tasks.

In conclusion, we here demonstrate that selective attention is allocated in parallel to the targets of eye and hand movements and propose that the attentional control mechanisms for these two effector systems are largely independent. This highlights the flexibility of the visuomotor system to simultaneously select and process multiple objects relevant for different actions, and suggests the existence of separate sources of signals related to target selection for different effectors.

ACKNOWLEDGEMENTS

This research was supported by the Deutsche Forschungsgemeinschaft (GRK 1091), Graduate School of Systemic Neurosciences, Ludwig Maximilians University, Munich and the 7th Framework Program of the European Community (Project “GRASP”, ICT – 215821).

REFERENCES

Astafiev, S.V., Shulman, G.L., Stanley, C.M., Snyder, A.Z., van Essen, D.C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *The Journal of Neuroscience, 23*, 4689-4699.

Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research, 184*, 411-425.

Baldauf, D., & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research, 50*, 999-1013.

Batista, A.P., Buneo, C.H., Snyder, L.H., & Andersen, R.A. (1999). Reach plans in eye-centered coordinates. *Science, 285*, 257-260.

Bekkering, H., Adam, J.J., van den Aarssen, A., Kingma, H., & Whiting, H.T. (1995). Interference between saccadic eye and goal-directed hand movements. *Experimental Brain Research, 106*, 475-484.

Beurze, S.M., de Lange, F.P., Toni, I. & Medendorp, W.P. (2009). Spatial and effector processing in the human parietofrontal network for reaches and saccades. *Journal of Neurophysiology, 101*, 3053-3062.

Brisson, B., & Jolicoeur, P. (2007). Electrophysiological evidence of central interference in the control of visuospatial attention. *Psychonomic Bulletin & Review, 14*, 126-132.

Calton, J.L., Dickinson, A.R., & Snyder, L.H. (2002). Non-spatial, motor-specific activation in posterior parietal cortex. *Nature Neuroscience, 5*, 580-588.

Curtis, C.E., & Connolly, J.D. (2008). Saccade preparation signals in the human frontal and parietal cortices. *Journal of Neurophysiology, 99*, 133-145.

Deubel, H. & Schneider, W.X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals New York Academy of Sciences, 1004*, 289-296.

Deubel, H., & Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research, 36*, 1827-1837.

Deubel, H., Schneider, W.X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81-107.

Dickinson, A.R., Calton, J.L., & Snyder, L.H. (2003). Nonspatial saccade-specific activation in area LIP of monkey parietal cortex. *Journal of Neurophysiology, 90*, 2460-2464.

Dubois, J., Hamker, F.H., & Van Rullen, R. (2009). Attentional selection of noncontiguous locations: the spotlight is only transiently "split". *Journal of Vision, 9*, 3:1-11.

Horstmann, A., & Hoffmann, K.P. (2005). Target selection in eye-hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research, 167*, 187-195.

Gherri, E., & Eimer, M. (2010). Manual response preparation disrupts spatial attention: an electrophysiological investigation of links between action and attention. *Neuropsychology, 48*, 961-969.

Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 882-896.

Goldberg, M.E., Bisley, J.W., Powell, K.D., & Gottlieb, J. (2006). Saccades, salience and attention: the role of the lateral intraparietal area in visual behavior. *Progress in Brain Research, 155*, 157-175.

Gottlieb, J.P., Kusunoki, M., & Goldberg, M.E. (1998). The representation of visual salience in monkey parietal cortex. *Nature, 391*, 481-484.

Itti, L., & Koch, C. (2000). A saliency-based search mechanism for overt and covert shifts of visual attention. *Vision Research, 40*, 1489-1506.

Johansson, R.S., Westling, G., Backstrom, A., & Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience, 21*, 6917-6932.

Lawrence, B.M., & Snyder, L.H. (2009). The responses of visual neurons in the frontal eye field are biased for saccades. *Journal of Neuroscience, 29*, 13815-13822.

Kowler, E., Anderson, E., Dosher, B., & Blaser, E. (1995). The role of attention in the programming of saccades. *Vision Research, 35*, 1897-1916.

Land, M.F., Mennie, N., and Rusted, J. (1999) The roles of vision and eye movements in the control of activities of daily living. *Perception, 28,* 1311-1328.

Levy, I., Schluppeck, D., Heeger, D.J., & Glimcher, P.W. (2007). Specificity of human cortical areas for reaches and saccades. *The Journal of Neuroscience, 27*, 4687-4696.

Linnell, K.J., Humphreys, G.W., McIntyre, D.B., Laitinen, S., & Wing, A.M. (2005). Action modulates object-based selection. *Vision Research, 45*, 2268-2286.

Medendorp, W.P., Goltz, H.C., Crawford, J.D., & Vilis, T. (2005). Integration of target and effector information in human posterior parietal cortex for the planning of action. *Journal of Neurophysiology, 93*, 954-962.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*, 8:1-16.

Moore, T., Armstrong, K.M. & Fallah, M. (2003). Visuomotor origins of covert spatial attention. *Neuron, 40*, 671 - 683.

Neggers, S.W.F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*, 639-651.

Pelz, J., Hayhoe, M.M., & Loeber, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research, 139*, 266-277.

Prablanc, C., Echallier, J.F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at visual target. *Biological Cybernetics, 35*, 113-124.

Quiroga, R.Q., Snyder, L.H., Batista, A.P., Cui, H., & Andersen, R.A. (2006). Movement intention is better predicted than attention in the posterior parietal cortex. *The Journal of Neuroscience, 26*, 3615-3620.

Rizzolatti, G., Riggio, L., & Sheliga, B.M. (1994). Space and selective attention. In C. Umilta & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 231–265). Cambridge, MA: MIT Press.

Sailer, U., Eggert, T., Ditterich, J., & Straube, A. (2000). Spatial and temporal aspects of eye-hand coordination across different tasks. *Experimental Brain Research, 134*, 163-173.

Schall, J.D., & Hanes, D.P. (1993). Neural basis of saccade target selection in frontal eye field during visual search. *Nature, 366*, 467-469.

Scherberger, H., & Andersen, R.A. (2007). Target selection signals for arm reaching in the posterior parietal cortex. *The Journal of Neuroscience, 27*, 2001-2012.

Snyder, L.H., Batista, A.P., & Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167-170.

Song, J.-H., & McPeek, R. M. (2009). Eye-hand coordination during target selection in a pop-out visual search. *Journal of Neurophysiology, 102*, 2681-2692.

Thompson, K.G., & Bichot, N.P. (2005). A visual salience map in the primate frontal eye field. *Progress in Brain Research, 147*, 251-262.

Thompson, A.A., & Westwood, D.A. (2007). The hand knows something that the eye does not: reaching movements resist the Müller-Lyer illusion whether or not the target is foveated. *Neuroscience Letters, 426*, 111-116.

Thura, D., Hadj-Bouziane, F., Meunier, M., & Boussaoud, D. (2008). Hand position modulates saccadic activity in the frontal eye field. *Behavioural Brain Research, 186*, 148-53.

Tibber, M.S., Grant, S., & Morgan, M.J. (2009). Oculomotor responses and visuospatial perceptual judgments compete for common limited resources. *Journal of Vision, 9*, 12:11-13.

Tosoni, A., Galati, G., Romani, G.L., & Corbetta, M. (2008). Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions. *Nature Neuroscience, 11*, 1446-1453.

Van Der Werf, J., Jensen, J., Fries, P., & Medendorp, W.P. (2010). Neuronal synchronization in human posterior parietal cortex during reach planning. *Journal of Neuroscience, 30*, 1401-1412.

Wilder, J.D., Kowler, E., Schnitzer, B.S., Gersch, T.M., & Dosher, B.A. (2009). Attention during active visual tasks: counting, pointing, or simply looking. *Vision Research, 49*, 1017-1031.

van Donkelaar, P. (1997) Eye–hand interactions during goal-directed pointing movements. *Neuroreport, 8*, 2139-2142.

CHAPTER IV

STUDY 3: Preparing coordinated eye and hand movements: Dual task costs are not attentional

Journal of Vision (2011), 10, Article 23.

Preparing coordinated eye and hand movements: Dual task costs are not attentional

Donatas Jonikaitis[1], Torsten Schubert and Heiner Deubel

Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität, München, Germany.

Contribution: The author of this PhD thesis designed and ran experiments, analysed the results and wrote the manuscript.

ABSTRACT

Dual task costs are observed when people perform two tasks at the same time. It has been suggested that these costs arise from limitations of movement goal selection when multiple goal-directed movements are made simultaneously. To investigate this, we asked participants to reach and look at different locations while we varied the time between the cues to start the eye and the hand movement between 150 ms and 900 ms. In Experiment 1, participants executed the reach first, and the saccade second, in Experiment 2 the order of the movements was reversed. We observed dual task costs - participants were slower to start the eye or hand movement if they were planning another movement at that time. In Experiment 3 we investigated whether these dual task costs were due to limited attentional resources needed to select saccade and reach goal locations. We found that the discrimination of a probe improved at both, saccade and reach locations, indicating that attention shifted to both movement goals. Importantly, while we again observed the expected dual task costs as reflected in movement latencies, there was no apparent delay of the associated attention shifts. Our results rule out attentional goal selection as the causal factor leading to the dual-task costs occurring in eye-hand movements.

INTRODUCTION

---

[1] Correspondence should be addressed to D.J. (djonikaitis@gmail.com).

In everyday situations we frequently reach for objects - be it a simple task like picking up a cup of coffee or a complex task like clearing an office table. However since we usually look at the object we reach for, most reaching movements actually require doing two things at the same time, that is, planning and executing an eye and a hand movement simultaneously. (Horstmann & Hoffmann, 2005; Johansson, Westling, Backstrom & Flanagan, 2001; Land & Hayhoe, 2001; Pelz, Hayhoe & Loeber, 2001). It might seem trivial to plan both eye and hand movements together but it constitutes an instance of cognitive multitasking.

It is known that doing two tasks simultaneously bring costs, since both error rates and reaction times typically increase as compared to doing only one task at a time. These are typically referred to as dual task costs (Pashler, 1994; Schubert, 2008), which arise when two different tasks compete for limited cognitive resources. In such a scenario the limited resources could either be shared between the two tasks, leading to a slowing of both (Kahneman, 1973), or else execution of one of the tasks could be postponed until critical processing in the other is finished (Pashler, 1994; Schubert, 1999). While much is known about dual task costs and the situations in which they arise, it remains debated whether these do occur in the case of simultaneous eye and hand movements, and if so, which particular processing stage(s) between early stimulus processing and final execution of the movement might be specifically involved in the processing bottleneck.

A number of studies have shown that whether there is interference between eye and hand movements depends on a variety of factors, such as on how the saccade is elicited and on what type of manual response is required. Pashler and colleagues have demonstrated that there are almost no dual-task costs when simple button presses and eye movements to an abrupt onset are prepared together (Pashler, Carrier & Hoffman, 1991), suggesting that reflexive saccades directed towards an onset stimulus can be possibly executed without interference. Similarly, no dual task costs have been reported when people made reflexive saccades to a peripheral location and simultaneously performed a rhythmic manual tapping task (Sharikadze, Cong, Staude, Deubel & Wolf, 2008). In contrast, dual-task interference was found to occur even with simple button presses when non-reflexive saccades had to be performed to a location indicated by a central cue (Pashler et al., 1991); obviously, the planning of these saccades required an intentional selection of the movement goal.

Dual task interference becomes more prominent when, instead of a simple button press, a manual reaching movement is required. It has been observed that latencies of saccades directed to peripheral onsets are longer if, simultaneous to saccade preparation, a reaching movement has to be planned to the same target (Bekkering, Adam, Kingma, Huson & Whiting, 1994; Bekkering, Adam, van den Aarssen, Kingma & Whiting, 1995). This suggests that dual task costs for saccades arise when a reach must be directed to a spatial target, but not when the movement involves just a simple (non-spatial) button press. In other words, it seems that dual task costs do arise when both eye and hand movements rely on the selection of a spatial movement goal. They also arise when saccades and button press responses have the same or a different directional component (e.g., to make a saccade to the right and press the left button; Huestegge & Koch, 2009). These findings make it likely that the mutual interference between the two tasks occurs in the movement planning phase, for instance, during the selection of the movement target (Bekkering et al, 1995), rather than in movement execution. Movement goal selection ("I will reach for this apple") occurs at an early stage of movement planning during which object parameters such as target location in space and object size are specified (Milner & Goodale, 1995; Andersen & Buneo, 2002).

While at least some of the dual task costs can be explained by assuming that the two effectors compete for resources to select the movement goal, not all findings suit this pattern. Some studies reported even shorter saccade or reach latencies if participants made simultaneous eye and hand movement to the same object as compared to making single eye or hand movements (Niechwiej-Szwedo, McIlroy, Green, & Verrier, 2005; Lünenburger, Kutz & Hoffmann, 2000). However, these observations do not necessarily contradict the hypothesis that movement goal selection leads to dual task costs, since in all of the above-mentioned studies movement goal selection was limited by the fact that participants were asked to make eye, hand, or both movements to only one common target present on the screen (or to one of two targets present in separate visual hemifields). This raises the question as to which degree saccade or hand movement goal selection was activated, since in some cases movements might have been purely reflexive, towards a single target present within one visual hemifield.

It is important to note that none of these studies analysed movement goal selection directly but instead relied on indirect measures such as reaction times or movement endpoint errors. Thus, it is possible that while movement execution was delayed in a dual-task situation, movement goal selection was not affected by the need to perform a second task.

It is now well established that the selection of a stimulus as the goal of a movement is related to attention shift to the movement target. A number of studies have shown that these attention shifts precede the initiation of goal-directed saccades, reaching movements and grasping (Deubel & Schneider, 1996; Montagnini & Castet, 2007; Schiegg, Deubel & Schneider, 2003; Deubel, Schneider & Paprotta, 1998; Baldauf & Deubel, 2010). Hence, spatial attention can be used as an index of movement goal selection before movement onset.

By measuring both, movement latencies and spatial attention we investigated whether movement goal selection is the causal factor that leads to the costs observed in these dual task situations. Participants performed conjoint saccades and manual reaching movements while we manipulated the temporal overlap between the planning of these movements. In three experiments two central movement cues were presented sequentially, with a variable stimulus-onset asynchrony (SOA) between the presentations. The movement cues could indicate either the same spatial location or spatially separate locations. The range of SOAs was selected such that in the short SOA conditions planning of saccade and reaches would overlap, whereas in the long SOA conditions those tasks would not overlap. If dual-task costs would occur, they should be largest at the shortest SOAs and smallest at the longest SOAs. In Experiment 1 the first cue specified the reach goal, and the second cue indicated the saccade goal. In Experiment 2 we measured whether dual task costs are observed also when the movement order was reversed – the first movement cue indicated the saccade and the second cue specified the reach. Finally, in Experiment 3 we measured movement goal selection by using spatial attention as its index. Participants had to reach and look to two different locations while we presented a perceptual probe (a letter) at randomly chosen times during movement planning. This probe could be presented at cued saccade or reach locations, or at locations that were not relevant for the action. It is established that probe discrimination at exogenously or endogenously (as is the case with movement planning) cued locations can index attention at that location (for a review see Carrasco, 2006). Thus we could measure whether attention shifted to saccade or reach locations, and whether this shift was delayed when saccade and reach planning overlapped. Combined, the three experiments should reveal (1) whether there are dual task costs for combined eye and hand movements as reflected in movement latencies, and (2) whether these costs would arise due to movement goal selection as measured in probe discrimination at the saccade and reach goals.

EXPERIMENT 1

In Experiment 1 we determined the dual task costs arising in a situation in which participants first made a reach, and then a saccade. We varied the time interval (SOA) between two arrow cues instructing to start each movement. If dual-task costs occur the costs should be largest at the shortest SOAs and smallest at the longest SOAs (Schubert, 1999), since under the first conditions saccade and reach planning are temporally more overlapping than under the latter in which saccade planning starts long after the reaching onset. Additionally, we manipulated whether eye and hand movement goals were shared or not: on half of the trials participants made saccades and reaches to the same location, and on the other half of trials to two different locations. If eye and hand movement planning shares a common goal selection process, then for the short SOAs there should be a crosstalk between these two systems, resulting in faster saccades and reaches when the two movements were directed to the same goal. On the other hand, if the goals for eye and hand movements are selected independently, there should be no benefit to plan saccades and reaches to the same location.

Methods

Participants. 22 participants (mean age 23 years, 10 females) participated in this study. All participants had normal or corrected-to-normal vision. Informed consent was obtained from all participants.

Apparatus. Participants sat in a dimly illuminated room. They placed their right hand on a slightly inclined pointing plane, under a one-way mirror. Stimuli for pointing and saccades were projected from a monitor above onto the mirror. This setup allowed the visual stimuli to appear on the pointing plane, while the participants could not see their hand. In order to provide visual feedback about the hand position a LED fixed to the tip of the right index finger could be illuminated during the experiment. LED was lit up in the beginning of the trial for participants to arrange their finger with visual stimulus, and was illuminated at the end of the trials to provide feedback about reaching accuracy. Stimuli were presented on a 21 inch Conrac 7550 C21 display with frame frequency of 100 Hz, at a display resolution of 1024*768 pixels. Visual stimuli were shown on a gray background with a mean luminance of 5.1 cd/m2.

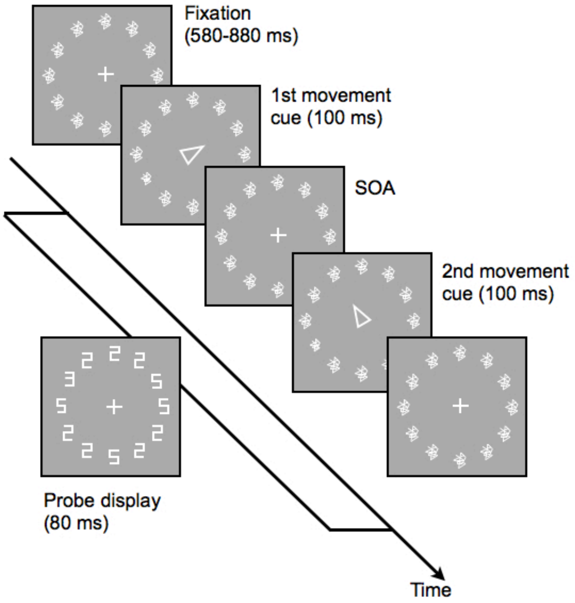


Figure 1. Experimental procedure. In Experiment 1, participants were asked to quickly reach to the location indicated by the first arrow and then quickly saccade to the location indicated by the second arrow. The time interval between the arrow onsets (SOA) was varied. In Experiment 2, the arrow appearing first instructed the saccade, while the second appearing arrow instructed the reaching. In Experiment 3, participants again reached and looked to two objects indicated by the two subsequent cues. Additionally, a probe display appeared at -50 to 650 ms with respect to the first movement cue onset. The probe was a digital letter “E” or “3”, embedded in a circular array of distractors. Participants reported the probe identity after completing the movement task.

Reaching movements were recorded with a Fastrack electromagnetic position and orientation measuring system (Polhemus Inc., 1993), consisting of a central transmitter unit and a small receiver, mounted on the tip of the index finger of the participant’s right hand. The sender unit was placed 60 cm in front of the participant. The device allows for a maximal translation range of 10 ft, with an accuracy of 0.03 in RMS. The frequency bandwidth of the system is 120 Hz; the time delay is 4 ms. Eye movements were recorded with a video-based eye tracking system (SensoMotoric Instruments, Eyelink-I), which provides an accuracy better than 0.1 degrees, at a recording frequency of 240 Hz. Head movements were minimized by means of an adjustable chin rest.

Procedure and stimuli. **Figure 1** depicts the stimulus sequence. During each trial a central fixation cross and twelve mask elements (size 0.9 x 1.4 deg, composed of randomly generated lines) were presented on the uniform background, arranged on an imaginary circle with a radius of 6.5 deg. Participants first directed the index finger of the right hand and their gaze to the central cross. 580 to 880 ms later the first movement cue - an arrow which pointed towards one of the mask stimuli - was presented at the central fixation. The mask elements were arranged on the circle as if forming a clock face, and the arrow could point towards 2, 4, 8 or 10 o'clock. The arrow was presented for 100 ms, and participants were instructed to reach with the right index finger to the object indicated by this cue. After a variable time (SOA) from the first cue onset, a second movement cue was presented, again for 100 ms. Participants were instructed to saccade to the location indicated by the second arrow. On 50% of the trials the second cue indicated the same target as the first cue (thus participants had to reach and look to the same location); on the other 50% the second movement cue indicated a different target than the first cue. In those trials where the cues indicated different targets, the distance between the first and the second movement target was either three items in the clockwise direction or three items in the anti-clockwise direction (for example, if the first cue indicated a reach target at 2 o'clock, then the second cue would indicate (with equal probability) a saccade target at 5 or 11 o'clock,which amounts to an angular distance of 90 degrees from the first cued location). The SOA between the two movement cue onsets was 150, 200, 300, 350, 400, 450, 500, 600, 700, 800 or 900 ms. We chose this wide interval of SOAs in order to precisely measure at which cue delay dual task costs would appear for saccades and reaches. Since the reaching latencies were typically 200-300 ms, the interval covered the time when reaches were still planned, when the hand was in motion and when the finger was already at the object.

Participants were instructed to reach and look as quickly as possible when the respective movement cues appeared, without delaying their movements or trying to group them. Each participant performed 4 experimental blocks of 144 trials each. All participants had a practice block before starting the experimental task. Six of the participants performed 12 experimental blocks in order to investigate possible practice effects.

Movement data analysis. Saccade and reach movement data were stored for offline analysis and saccades and reaches were detected using custom software. Reach onsets were defined as points in time when the vectorial velocity reached a threshold of 1°/s. Saccades onsets were defined as points in time when eye velocity threshold exceeded 150°/s. We further defined a 2° radius circle around central fixation as a maximum window within which saccade and reach movement starting position could vary. We removed all trials in which saccades smaller than 2° in size appeared before saccade cue onset. We accepted reach or saccade endpoint as correct if it fell closer to the reach/saccade goal than to any other irrelevant location besides the goal, and if the movement had a minimum latency of 100 ms after the movement cue appeared. Additionally, all trials with saccade or reach latencies longer or shorter than 3 standard deviations from the mean of each subject were rejected.

Results

We analysed whether there were dual task costs when participants made combined eye and hand movements. If there were no dual task costs, then neither the reaction time of the first task (the reaching) nor the reaction times of the second task (the saccade) should be influenced by the SOA manipulation. Typical dual task costs would be reflected in an effect of SOA on the reaction times of the second task (the saccade) - these should be longer for the short SOA conditions than for the long SOA conditions. For the reaction time of the first task, there should be either no effect of SOA, or an effect which should also depend on SOA.

The data indeed revealed that the SOA manipulation did not affect the reaction times of the first task - reaching latencies for the shortest SOA of 150 ms were 336 ± 14 ms (mean and standard error of the mean) and were 337 ± 15 ms for the longest SOA of 900 ms (repeated measures ANOVA, $F(10, 210)=0.79$, $p>0.6$)). This means that participants started the reach movement immediately after the first movement cue appeared, and did not try to postpone their response until the second movement cue was shown.

The SOA manipulation had a markedly different effect on the saccade latencies. Saccade latencies decreased with increasing SOA (repeated measures ANOVA, $F(10, 210)=53.03$, $p<0.01$), indicating that in the short SOA condition participants were not able to initiate their saccade immediately after the saccade cue appeared. The observed dual task costs were about 100 ms - saccade latency decreased from 384 ± 14 ms for the 150 ms SOA condition to 280 ± 9 ms for the 900 ms SOA condition. Thus, typical dual task costs did occur under these conditions, with participants being unable to perform the eye movement before they finished preparing the reaching movement.

We next analysed whether there were any costs or benefits when saccades and reaches were directed to the same location or to different locations. First we analysed reaching movements, as it has been shown that in dual-task situation the task that is performed first (here, the reach) is completed faster if the second task shares a common response code (here, the saccade made to same location as the reach), compared to a situation with different responses in the two tasks (Hommel, 1998; Lien & Proctor, 2002). Unexpectedly, we did not observe this effect - reaching latencies were not shorter when saccades and reaches were directed to the same location (**Figure 2A**; none of the planned one-tailed repeated measures t-tests comparing each time bin was significant, all ps>0.5). This indicates that planning saccade and reach to same location did not facilitate the preparation of the reach. One possibility of explaining this discrepancy is that we used a larger number of potential target locations (targets could appear at 8 different locations), unlike other studies (e.g. Hommel, 1998; Lien & Proctor, 2002) which used mostly two opposing response categories (e.g. left vs. right motor response). Furthermore, our task required precise spatial location coding - to reach to one of the multiple locations on the screen while making a saccade to a different location - instead of button presses. Note that

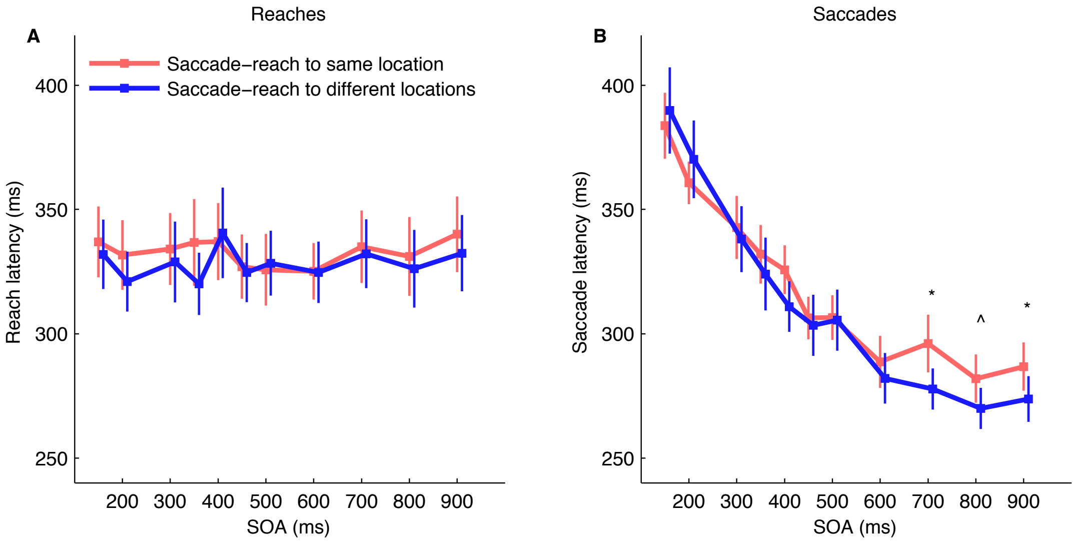


Figure 2. Dual task interference in Experiment 1. (A): Latencies of the reaching movements as a function of SOA. (B): Saccade latencies as a function of SOA. Data are shown separately for trials when saccades and reaches were directed to the same location (red curves), or to different locations (blue curves). Symbols in panel B: * - $p<0.05$, ^ - $p=0.08$. Vertical bars indicate +-SE. Data are slightly translated horizontally to increase the visibility of different conditions.

the need to plan spatially directed movements and the number of potential reach locations could also interact, as reaches to displays with multiple objects are executed faster than reaches to displays with fewer objects (Song & Nakayama, 2006).

Next we analysed whether there were benefits when the saccade was directed to the same location as the reach. It has been demonstrated that movement planning leads to a shift of attention to the movement goal location (Deubel & Schneider, 1996; Linnell, Humphreys, McIntyre, Laitinen & Wing, 2005); thus, planning a movement to one location is likely to be helpful as a cue in planning a subsequent movement to the same location. This leads to the prediction that latencies of saccades when they are directed to the same location as the reaching should be shorter than latencies of saccades directed to different locations than reaches. A two-way ANOVA with the first factor SOA and the second factor specifying saccade/reach location agreement did not show significant effect of the second factor (F (10,210)=1.51; p=0.2). However, interaction between the second and SOA and saccade/reach location agreement was significant (F(10,210)=2.42; p<0.01). We looked in more detail at short and long SOA conditions by performing separate t-tests. Our planned comparisons also showed that for SOA's less than or equal to 600 ms saccade latencies were not shorter if the saccades were directed to the same location as reaching, not even for the shortest 150 ms SOA condition (**Figure 2B**; at this time bin, mean latency of the saccades directed to the same direction as reaching was 384 ± 13 ms, mean latency of the saccades made to a different location than reaching was 390 ± 17 ms, repeated measures t-test p=0.60).

For the long SOA conditions starting at 700 ms, saccade latencies were found to be even longer if saccades were directed to the same as compared to a different location than the reaching movement (**Figure 2B,** last three SOA conditions). An two-way ANOVA over these 3 last SOA conditions with second factor specifying saccade/reach location agreement was significant for the second factor (F(1,21)=13.21, p<0.01). This effect seemed to persist over all three SOA conditions (SOA 700, 800 and 900 ms; individual repeated measures t-tests), and individual subject data showed that majority of the subjects demonstrated this effect. This effect can possibly be attributed to Inhibition of Return (Klein, 2000), which we will discuss in more detail later.

Our findings demonstrate that the second (saccade) task was delayed while the first (reach) task was processed. In order to provide further evidence that reach planning indeed delayed saccades, we analyzed whether on trials with longer reach latencies the

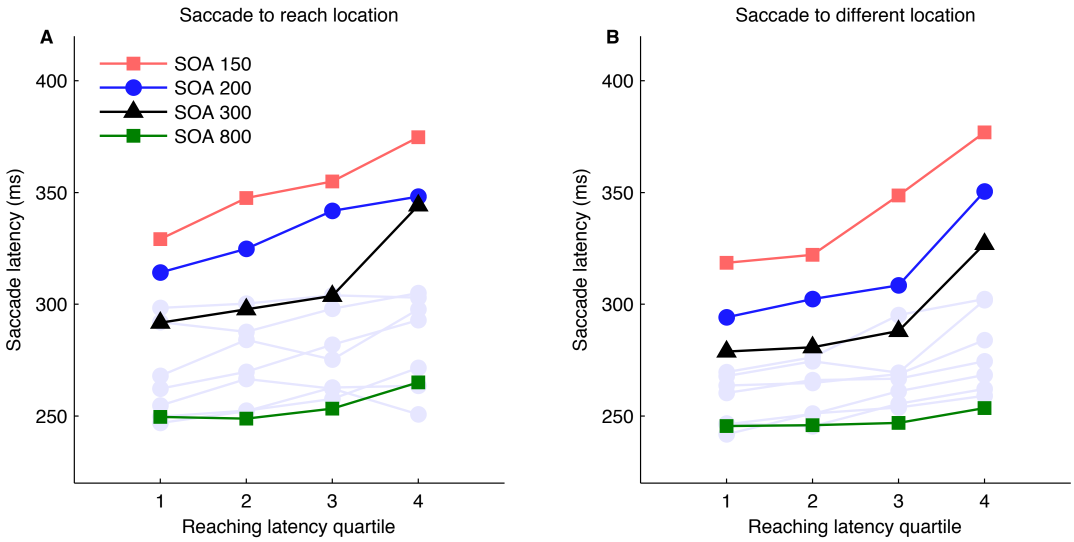


Figure 3. Reaching movements delay saccades. Data are shown for trials where the saccade was directed to the same location as the reaching (A), or to a different location (B). Reaching latencies were divided into quartiles; the higher the quartile number, the longer the reaching latency. Four example SOA conditions are shown (see figure legend). Other SOA conditions are plotted as light blue lines.

saccades also exhibited longer delays. For this purpose, reach latency in each trial was assigned to one of four quartiles (movement latencies increased from 260 ms in the first quartile to 380 ms in last quartile). Then saccade latencies were separated into trials where the reaching latencies belonged to the 1st, 2nd, 3rd and 4th quartile. If reaching movements were delayed, then saccade latencies should be delayed as well. Thus, for short SOAs saccade latencies should be shorter if reaching latencies were shorter, and longer if reaching latencies were longer. For long SOA conditions this effect should disappear, as reaches would have already started or even finished. For this analysis we again split the data according to reach/saccade location agreement. **Figure 3** shows the result of this analysis, depicting saccade latencies for all SOA conditions. **Figure 3A** depicts the results for trials where reaches and saccades were directed to the same location, and **Figure 3B** those for trials where the movements were aimed to different locations. The data show that longer reaching latencies indeed resulted in longer saccade latencies. This effect was most pronounced for the shortest SOA conditions. For SOA 150 ms the saccades were about 50 ms slower for the longest as compared to the shortest reaching latency quartile, whereas in the SOA 800 ms condition this difference was only 20 ms.

We computed repeated measures two-way ANOVAs with quartile and SOA as main factors. We split this analysis for trials with saccades and reaches to the same location, and trials with saccades and reaches to different locations. When reaches and saccades were directed the same location, the main effect of SOA was significant, indicating that saccade latencies decreased with increasing SOA, F(10, 150)=7.93, $p<0.01$. The main effect of quartile was also significant, showing that longer reaching latencies lead to longer saccade latencies (F(3, 150)=18.12, $p<0.01$). The interaction between these two factors was also significant, F(30, 150)=1.61, $p<0.05$.

An equivalent analysis performed for trials when the saccade and reaches were directed to different locations revealed similar results. Again, saccade latencies decreased with increasing SOA (main effect of SOA was significant, F(10, 150)=8.88, $p<0.01$), and longer reaching latencies led to longer saccade latencies (main effect of quartile, (F(3, 150)=27.65, $p<0.01$). The interaction between SOA and quartile was also significant (F(30, 150)=1.60 $p<0.05$), again meaning that longer reaching latencies delayed saccades most in the shortest SOA conditions.

We also analyzed whether longer reach latencies delayed saccades more or less, if saccades were directed to same or different location as reaches. We found no significant differences between those conditions (paired samples t-test comparisons for saccades directed to same versus saccades directed to different location than reaching for each reaching latency quartile were not significant, $p>0.05$).

Last, we analyzed movement end-point errors. When making saccades and reaches to two different locations, participants sometimes made movement errors by either looking at the reach goal (15% of trials in this condition), or by reaching to the saccade goal (14% of trials), implying a crosstalk between the movement planning for the hand and for the eye. We propose that these errors may result from the difficulty of our task in which two types of trials were interleaved - eye and hand movements directed to same location or to different locations. Participants may have sometimes failed to switch to the less preferred type of task (eye and hand movements directed to different locations), and instead looked and reached to the same target.

EXPERIMENT 2

In the second experiment we asked whether similar dual task costs could be observed

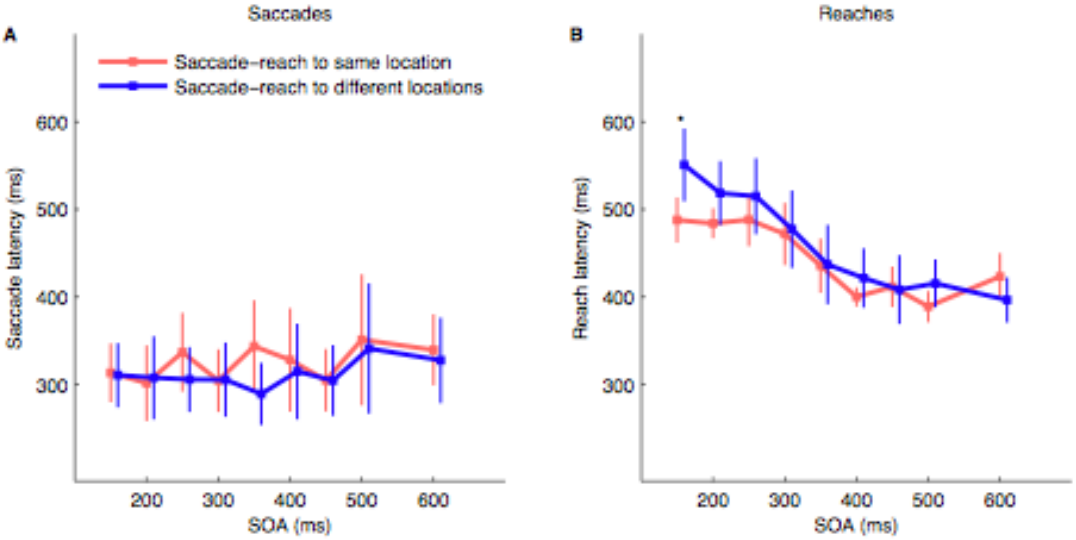


Figure 4. Dual task interference in Experiment 2. The first movement cue directed the saccade target, the second movement cue instructed the reach target. Data is shown for trials when saccades and reaches were directed to the same location (red line), or to different locations (blue line). Symbol in (B) * - $p<0.05$. Vertical bars indicate +-SE. Data is slightly translated horizontally to increase the visibility of different conditions.

when the participants first made a saccade, and then a reach.

Methods

Seven participants (mean age 25 years, 3 females) participated in the study. All participants had normal or corrected-to-normal vision. Informed consent was obtained from all participants.

The procedure was the same as in Experiment 1, with the following exceptions. The first movement cue now directed the saccade, while the second movement cue directed the reaching movement. SOA between the cues varied between 150 and 600 ms (150, 200, 250, 300, 350, 400, 450, 500 and 600 ms). Each participant completed 3 blocks of 144 trials.

Results

After the first movement cue appeared, a saccade was initiated with a similar latency for all SOA conditions (repeated measures ANOVA, main effect of SOA not significant, $F(8, 48)=0.37$, $p > 0.9$). Thus for the SOA 150 ms condition, i.e. the shortest SOA, mean saccade latencies were 314 ± 33 ms, which was not different from the longest SOA, the SOA

600 ms condition, in which saccade latencies were 334 ± 46 ms. In contrast, reaching latencies showed pronounced dual task costs - as SOA increased, reaching latencies decreased (F(8,48=8.05, $p<0.01$)). For the SOA 150 ms condition mean reaching latency was 499 ± 27 ms, which was longer than for the SOA 600 ms condition in which mean reaching latency was 417 ± 25 ms ($t(6)=6.06$, $p<0.01$). Thus, in the present task the reach latencies revealed dual task costs of around 80 ms (mean RT at SOA 150 ms – mean RT at SOA 600 ms). **Figure 4** shows saccade and reach latencies as a function of SOA for trials when saccades and reaches were directed to the same location, or to different locations. Again, saccade latencies were not shorter when saccades and reaches were directed to the same location (repeated measures t-test, all $p>0.05$). On the other hand, reach latencies were affected by saccade target location. When a two-way ANOVA was performed, with SOA and saccade/reach location agreement as factors, the main effect of saccade/reach location agreement was not significant ($F(8,48)=1.09$, $p>0.30$), but interaction between the two factors was ($F(8,48)=2.44$; $p<0.05$). For the SOA 150 ms condition reaches directed to the saccade location started after 488 ms ± 26 ms; these latencies were 63 ms shorter than when the reaches were directed to a different location (551 ms ± 42 ms; repeated measures t-test, $t(6)=-2.46$, $p<0.05$); none of the other SOA conditions showed significant differences. The benefit observed at the SOA 150 ms condition could be explained by previous observations that people are faster to reach to the objects they are allowed to look at (Prablanc, Echallier, Komilis & Jeannerod, 1979).

Finally, we analyzed movement errors. On trials when saccades and reaches where directed to different locations, participants made 23% of errors by looking to the location they were supposed to reach, and on 4% of trials they reached to the location they were supposed to look to. The proportion of errors did not vary as a function of SOA (ANOVA for saccade errors, with SOA as the main factor - $F(8,48)=0.38$, $p>0.9$; $F(8,48)=0.99$, $p>0.4$ for reach errors). This demonstrates that there is some cross-talk when saccade and reach targets have to be selected. It is not clear, though, whether these saccade and reach errors are due to participants being used to look and reach to the same locations in every day situations.

In sum, these results show that dual-task costs arise for reaches when the saccade was executed first.

EXPERIMENT 3

In two parts of the Experiment 3, we tested directly whether movement goal selection (in contrast to movement execution) is affected by the need to do two tasks simultaneously. As is has been shown that attention may shift to saccade and reach locations early during movement planning (Deubel & Schneider, 1996; Rizzolatti, Riggio & Sheliga, 1994), we measured attention at saccade and reach locations by presenting an attentional probe - a briefly shown letter which participants had to report at the end of the trial. During this task the first cue indicated a reach target and a subsequent cue indicated the saccade target (like in Experiment 1), and a probe could appear sometime during saccade or reach planning at different locations on the screen. If participants shifted their attention to saccade or reach location, probe discrimination should be better at those locations than at other locations, to which no movement was planned. During the experiment we also varied probe presentation time, which allowed us to determine at which point in time attention shifted to saccade or (and) reach locations. For example, it could be that attention deployment associated with saccade planning is delayed as long as the reaching does not start, leading to the prolongation of the saccade latencies as demonstrated in Experiment 1. Alternatively, it is possible that there are no dual task costs to select a saccade goal even when the selection occurs during reach planning - this should be reflected in a parallel attention allocation to both saccade and reach targets before reaching onset.

Methods

Participants. Eight participants (mean age 23 years, 3 females) participated in Experiment 3. Ten participants took part in the “Saccade-only” control task (mean age 25, 4 females). They had normal or corrected-to-normal vision. Informed consent was obtained from each participant.

Apparatus and procedure. The apparatus and procedure of the experiment were same as in Experiment 1, with the following exceptions. After the first movement cue appeared, participants had to reach to the object indicated by the cue. There were only 4 possible reaching locations (at 2, 5, 7 and 10 o’clock). With a SOA of 150 or 400 ms after the first cue, a second arrow cue was shown indicating the saccade goal (see Figure 1). The saccade goal could be located 3 or 5 items clockwise or anti-clockwise from the reaching location. Saccade and reaching movement goal selection was measured by presenting a probe stimulus. For this purpose, the display containing the mask elements changed into a display containing 11 distractor digits (digital “2” and “5”) and one target character (digital letter “E” or digital “3”). This probe display was presented for 80 ms and was then masked. Given the short presentation time of the probe display, the probes could be detected only if participants attended to the probe location at the time when the probe was presented. The probe display could appear randomly in a time interval ranging from 50 ms before to 650 ms after the onset of the first movement cue. In other words, the mask elements could change into probe and distractors at any point of time, before the appearance of the first movement cue, up to a point in time when both movements were already finished. The probe was presented with either at the saccade goal (33% of trials), at the reach goal (33% of trials), or at one of the other, movement-irrelevant locations (33% of trials). Participants were asked to indicate the probe identity (‘E’ or ‘3’) at the end of each trial. We analysed only trials where the probe appeared before eye movement onset.

Each block consisted of 144 trials. Participants completed at least 6 blocks of the task.

“Saccade-only” control experiment. In order to provide a baseline on how attention shifted to saccade goals when no simultaneous reach were to be made, we additionally performed a control experiment in which participants only looked at the object, without executing any reach movement (Saccade-only task). The design of this experiment was identical to Experiment 3, except that only one movement cue was presented. Participants had to saccade to the location indicated by the cue. The probe could be presented at the saccade target (50% of trials) or at a randomly selected, movement-irrelevant location (50% of trials). Each participant performed at least 4 experimental blocks of 192 trials each.

Results

Next we analysed whether participants were able to select movement goals during the preparation of the movements. For this purpose, we used probe discrimination rate as a measure of movement goal selection. Since the probe was presented at variable times, we were able to analyse the time course of attentional deployment to the probe locations. For each time point (every 50 ms) we calculated the proportion of trials in which participants correctly discriminated the probe. As we were interested in the shift of attention to saccade and reach goals before the movement onset, we excluded all trials in which probes were presented either after saccade or reach onset. The results are depicted in

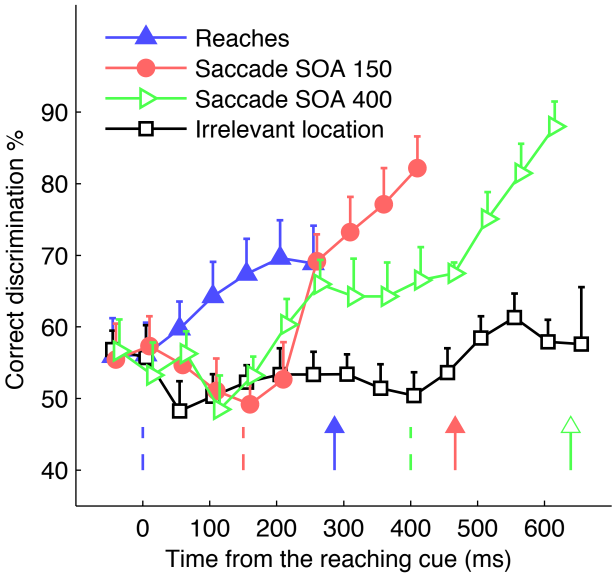


Figure 5. Probe discrimination rate at saccade and reach goals in the dual task of Experiment 3 (results do not include data from the Saccade-only task), as a function of time after reach cue presentation. Vertical dashed lines indicate the onsets of the cues for respective movements (e.g., blue dashed line - reaching cue presentation). Vertical arrows indicate the average movement latencies (e.g., blue arrow - reaching onset). Vertical error bars indicate +-SE. Data are slightly translated horizontally to increase the visibility of different conditions.

Figure 5. It can be seen that after the reach cue appeared, participants were at chance to discriminate the probes if they were presented at movement-irrelevant locations (probe discrimination was not different from chance level, $p>0.05$). In contrast, probe discrimination at the reach goal increased gradually following the presentation of the respective cue. Further data analysis revealed that 50 ms after presentation of the reaching cue, participants became better than chance to discriminate probes presented at the reaching location (t-test comparing discrimination at reaching location versus 50% chance level, $t(7)=2.56$, $p<0.05$). This demonstrates that participants shifted their attention to the reach goal before the start of the reaching movement.

For the SOA 150 ms condition, and about 100 ms after the saccade cue appeared, probe discrimination became significantly better than chance also at the saccade goal ($t(7)=5.13$, $p<0.01$). After this point in time, i.e., already relatively long before saccade onset and also before the onset of the reach movement participants were consistently better than chance to discriminate probes presented at the location of the saccade goal (all $p<0.05$). This shows that the attentional shift to the saccade goal started well before sac-

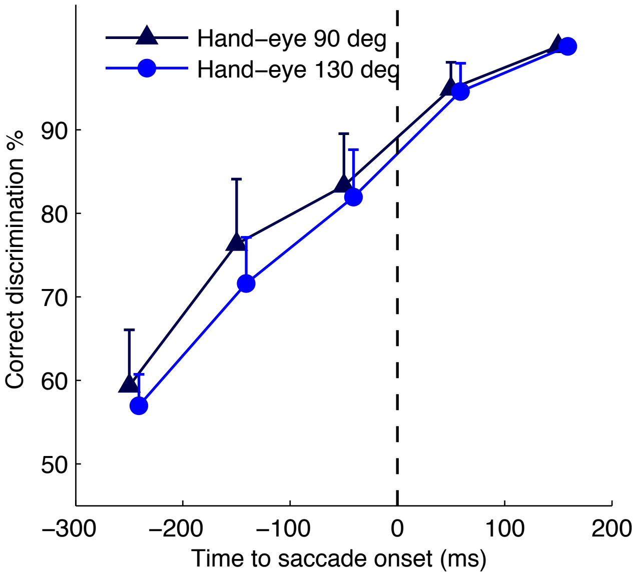


Figure 6. Probe discrimination at saccade goal in Experiment 3 as a function of the distance between eye and hand movement goal locations. Dashed gray line indicates saccade onset. Vertical error bars indicate +-SE. Data are slightly translated horizontally to increase the visibility of different conditions.

cade onset. These results are in line with previous demonstrations showing increased probe discrimination at the saccade locations (Deubel & Schneider, 1996; Baldauf & Deubel, 2008; Godijn & Theeuwes, 2003).

Two important conclusions can be drawn from these results. First, improvement of probe discrimination at the saccade target was better than chance already before the reaching movement started. So, even though these saccades were markedly delayed due to the dual task conditions, participants did not delay the *selection* of the saccade goal until after they started their reaching – the saccade goal was obviously selected before the start of the reaching movement. Second, the data demonstrate that attention was allocated to the two target locations simultaneously, as participants were better than chance to discriminate probes presented at both, the saccade and the reaching goal before the reach started.

Somewhat unexpectedly, we found that for the SOA 400 ms condition, discrimination rate at the saccade goal increased already 150 ms before the saccade cue appeared ($t(7)=2.88$, $p<0.05$); from that time onwards participants were better than chance to discriminate probes presented at the saccade location. Note that after this initial increase in accuracy, discrimination rate at the saccade goal did not change over time until the appearance of the saccade cue. Only then, discrimination performance improved further. The predictive increase in probe discrimination accuracy suggests that participants tried to anticipate where they would have to make a saccade. If we assume that participants split their attention evenly between 4 possible saccade target locations, and given that probability to guess the probe identity correctly was 0.5 in our two-alternative forced choice task, then probe discrimination at possible saccade target should be 63% (1/4+(1-1/4)*0.5), which was similar to what we observed.

It should be noted here that, given the similarity of the initial increase of discrimination performance for both SOA conditions (red and green curves in **Figure 5**), we cannot exclude that anticipatory effects may also be involved in the SOA 150 ms condition. However, the assumption that the early attention shifts to the saccade target in the SOA 150 ms condition are elicited by the presentation of the saccade cue seems to be more parsimonious.

Further converging evidence for this assumption comes from the results of a parallel study in which we used a different combination of SOAs (SOA 150 ms and SOA 200 ms). In this study we also observed that probe discrimination increased at the saccade location before the reach onset for the SOA 150 ms condition, while attention shifts were accordingly delayed for the SOA 200 ms condition (Jonikaitis & Deubel, in press, cf. Figure 4). Importantly, there were no anticipatory attentional shifts apparent for the SOA 200 ms condition in this study, which further confirms that saccade targets can indeed be selected during reach planning.

Thus combined we found that 250 ms after the reach cue appeared (time when green and red curves start rising in **Figure 5**) - and still before the reach onset - probe discrimination was already better than chance at either the already specified saccade goal (SOA 150 ms condition), or at the yet to be specified saccade goal (SOA 400 ms condition). These two observations strongly argue that reach movement planning did not prevent the attentional shift to specified or potential saccade locations; thus, attentional selection of saccade locations was not delayed in time.

Even though participants shifted their attention to saccade locations during reach planning, it could be that this was an effect observed by mixing two different groups of trials in our design - on some trials saccade and reach locations were close by, and on other

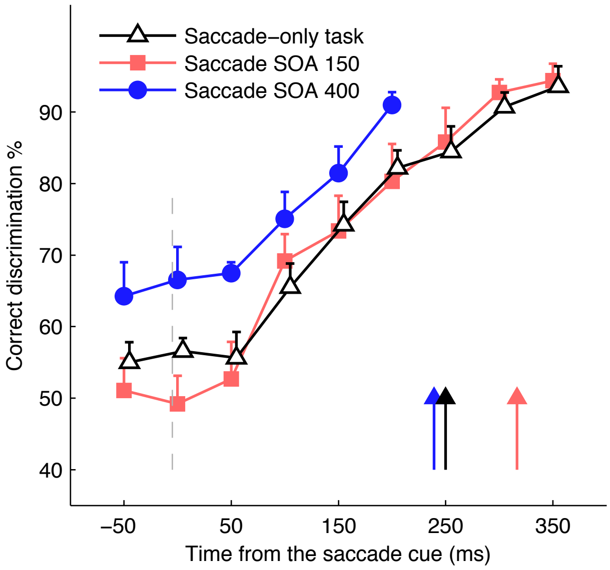


Figure 7. Probe discrimination at saccade goal during the dual task of Experiment 3 and the Saccade-only task. Dashed gray line indicates saccade cue presentation. Vertical arrows indicate average saccade latencies (i.e., saccade onset times) in the different conditions. Note that for both, dual and single task conditions attention allocation to the saccade goal follows the same pattern, even after the onset of the saccade in the control Saccade-only task. Vertical error bars indicate +-SE. Data are slightly translated horizontally to increase the visibility of different conditions.

trials, those locations were further away. Participants could have shifted their attention only to saccade locations further away, or to saccade locations in the different visual hemifield than the reaches (for example, Alvarez & Cavanagh, 2005). To assess this possibility, we split the data by trials with saccades made to the opposite hemifield than the reaches and trials with saccades made to the same hemifield. We observed no effect on probe discrimination due to this data split (all p>0.7). We also split trials by whether saccade location was close or far from the reach location (3 or 5 items away from the reach object on the display). Again, we observed no discernible differences (all p>0.5; **Figure 6**).

Even though participants were able to select the saccade target before reaching onset, it is still possible that participants would have selected the target faster if there were no need to perform simultaneous reaching. In other words, the observed dual task costs may have partly arisen because saccade target selection was somewhat delayed (even though it started before the reaching onset). To investigate this possibility, we compared the discrimination performance from the dual task conditions with performance in the "Saccade-only" task, which did not include a reaching movement. **Figure 7** shows discrimination performance, aligned to the time of saccade cue presentation, for the dual task

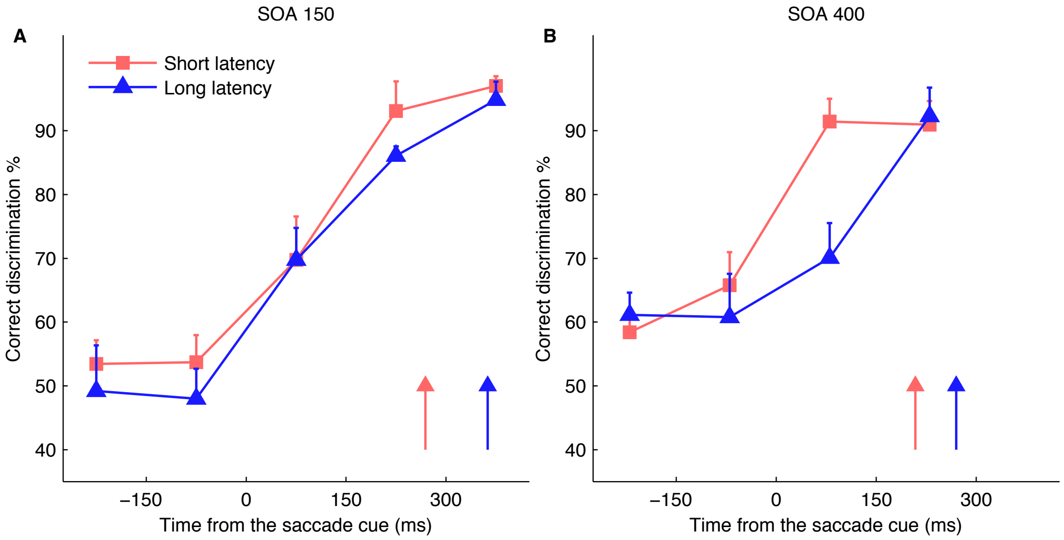


Figure 8. Probe discrimination before short and long latency saccades. Saccade cue appeared at time 0. Vertical arrows - average short and long saccade latencies. Color curves - probe discrimination rate at saccade target when saccades latencies were short (red line) or long (blue line). Vertical error bars indicate +-SE.

conditions and for the Saccade-only task. It can be seen that probe discrimination increased at about the same time after saccade cue onset in both, the dual task and the Saccade-only task. We calculated at which time probe discrimination after the saccade cue onset was better than performance 50 ms before the saccade cue onset (in order to equate for baseline differences in discrimination before cue onset in the SOA 400 ms task). This analysis shows that 100 ms after saccade cue onset in the Saccade-only task probe discrimination was better than baseline (t(9)=3.21, $p<0.05$); the same time value was found for the SOA 150 ms task (t(7)=4.86, $p<0.01$), and for the SOA 400 ms task (t(7)=2.85, $p<0.01$). **Figure 7** includes also the data where the probe appeared after saccade onset. Note that in the Saccade-only task probe discrimination reached a certain level before the saccade, and improved after saccade onset, as participants were then looking at the target directly. Interestingly, in the SOA 150 ms condition, probe discrimination at the saccade goal kept improving as long as the saccade did not start. The similarity of the temporal dynamics between the two conditions (SOA 150 ms and Saccade-only task) is striking, even though the saccade started in one condition considerably earlier than in the other. So, although saccade execution was considerably delayed in the SOA 150 ms condition, the attention shifts to the saccade target were not delayed. In other words, reach planning and execution did not delay saccade goal selection in the dual task condition, as probe discrimination was not different from that in the “Saccade-only” task.

Further evidence that the delay of the saccades in the SOA 150 ms task was not related to the timing of the presaccadic attention shifts was provided by an analysis of the temporal relation between presaccadic attention shift and saccade onset. In a different study we observed that saccades with shorter latencies are normally preceded by an earlier attention shift to the saccade target (Jonikaitis & Deubel, in press) - the faster the participants shifted their attention to the saccade goal, the shorter were the saccade latencies. For the dual task conditions of the present experiment we expected to find this tight temporal coupling between attention shift and saccade onset for the SOA 400 ms condition, where reaching movement and saccade processing no longer interfered. For the SOA 150 ms condition, however, the coupling should disappear, given that the dual task costs as reflected in the saccade delay were unrelated to the presaccadic attention shift. In order to test this prediction we split, for each SOA condition and each participant, saccade latencies by median into short latency saccades and long latency saccades.

As we had expected, saccadic reaction times were not related to speed of attention deployment in the SOA 150 ms condition. While the median split in this condition leads to a mean latency of 270 ± 16 ms for the faster saccades and 363 ± 29 ms for the slower saccades, this difference is not reflected in the attentional allocation for longer or shorter latency saccades (**Figure 8**, left panel, all repeated measures comparisons not significant).

In the SOA 400 ms condition the trials with faster saccades had an average saccade latency of 209 ± 16 ms; the trials with slower saccades had an average latency of 270 ± 17 ms. As can be seen from the right graph of **Figure 8**, probe discrimination at the saccade goal increased earlier for the trials when saccades had shorter latencies than on trials with longer latency saccades. At 150 ms after the saccade cue, discrimination was better at the saccade target if the saccade latencies were shorter ($t(7)=2.56$, $p<0.05$), while attention deployment occurred considerably later for the slower saccades. Thus, at the time when there were no dual task costs observed, earlier attention shifts were associated with shorter saccade latencies. This finding suggests that the dual task costs in the SOA 150 ms condition arise at a processing stage different from - and probably later than - the attentional selection of the saccade goal.

Together the findings show that the participants were able to shift their attention to saccade and reaching goals before reaching onset, and that there was no delay in saccade goal selection while the reaching was planned. Thus, while the saccade onset became markedly delayed due to the dual-task condition, this delay was not reflected in the time course of attentional allocation before the saccade.

DISCUSSION

Our experiments investigated whether dual task costs in the simultaneous planning of eye and hand movements result from a competition for attentional resources. Movement latencies showed large dual task costs when saccades had to be planned during reaching preparation. However, these costs did not arise from the attentional selection of the movement goals. The results show that participants can shift their attention to a saccade target even while the reaching movement is being planned and has not yet started.

Dual task costs in the planning of saccades and reaches. We found that there are large dual task costs when the planning of goal directed saccades and reaches overlapped in time. Our results are comparable to findings reported by Pashler et al. (1991). In their study participants were not able to elicit a saccade if the central cue instructing the saccade appeared while the participants performed a tone discrimination task requiring a manual button press. The magnitude of the effects found in our study (about 100 ms dual task cost for saccades made in the SOA 150 ms condition) was equal to the effect observed in the Pashler *et al.* study (also 100 ms cost for SOA 150). The main difference between these two studies is that in our experiments participants had to plan two movements directed to different locations, whereas in the study of Pashler *et al.* the first task was a button press and the second task was a goal-directed saccade.

The dual task interference observed in our experiments could result from various stages of movement planning. In our task participants had to interpret each cue, select an appropriate response (to make an eye or a hand movement), and to plan the movement itself. Movement planning consists of selecting an appropriate target for the movement and specifying all movement parameters. Additionally, factors such as uncertainty about when the second cue appears (Gottsdanker, 1980), impaired timing judgments during dual tasks (Brown, 1997), and confusability regarding the direction of motion of the effector (Huestegge & Koch, 2009) may also play a role. Our results suggest that one of the most important processes involved in the task, namely the selection of the movement goals, did not cause the dual task interference. It remains to be investigated at which stage during movement planning the interference actually occurs.

It is difficult to directly compare our results to some of the other studies that investigated saccade-reaching dual task costs, since these did not systematically manipulate the overlap between saccade and reach planning (Bekkering et al., 1994, 1995; Lünenburger, Kutz & Hoffmann, 2000). Although it has been reported that saccade latencies are shorter if concurrent reaches to the same object are planned (Lünenburger, Kutz & Hoffmann, 2000), the opposite pattern of results was found in a different set of studies (Bekkering et al., 1994, 1995). It is possible that the requirement to make two movements to the same object simultaneously might evoke a pattern of eye-hand coordination that is “hard-wired”. For example, both Lünenburger et al. and Bekkering et al. have suggested that the superior colliculus might mediate the observed coupling between the eye and hand, as some of the neurons in intermediate and deep layers of superior colliculus are known to fire before arm movements (Werner, Dannenberg & Hoffmann, 1997). The assumption that simultaneous eye and hand movements might be coordinated in a special way is also supported by the finding that saccade durations decrease if saccades are made simultaneously with hand movements (Snyder, Calton, Dickinson & Lawrence, 2002).

Movement goal selection for eye and hand. Another matter of debate in eye-hand movement studies has been whether the target representation for movement planning is shared between both systems or is separate. We did not find a saccadic latency benefit when the saccade was planned to the same location as the reach. Thus, even though participants selected a target for the reach, they were not faster to saccade to that same target than to saccade to a different target. This indicates that movement goal selection for the eye and the hand movements is relatively independent. In other words, when the reach is planned, the saccade does not have to be planned to the same target (for a similar observation see also Stritzke & Trommershäuser, 2007)

Our results argue against some findings that were interpreted as showing that eye and hand movement goal selection is shared. Neggers and Bekkering (2000, 2001) for example reported that if participants are making a saccade and a reach to the same object, they are unable to move their eyes to a different location while the hand is still moving. Also it has been observed that saccade latencies are longer if a simultaneous hand movement is planned to the same location (Bekkering et al., 1994, 1995).

We think that those studies could be interpreted in a different way - it might be advantageous to keep the eyes stable while the hand movement is planned or executed. A number of studies, behavioural and neurophysiological, show that eye position influences the planning for reaching and pointing (Medendorp, Goltz, Vilis & Crawford, 2003; Medendorp & Crawford, 2002; Batista, Buneo, Snyder & Andersen, 1999). This indicates that the visual system keeps track of where the hand and the reach goals are relative to the eye, and suggests that every eye movement requires the recalculation of the hand movement goal position with respect to the new eye position. Thus, keeping the eyes stable might be advantageous for fast hand movement planning, but this coupling does not necessarily mean that movement goal selection is shared for eye and hand movements. Further research needs to be carried out to clarify whether targets for eye and hand are selected independently.

In Experiment 3 we demonstrated that two targets, one for the saccade and one for the reach, can be selected in parallel, before reaching movement onset. In other words, before reaches started, participants were attending simultaneously to both, saccade and reach locations. Also, attention was allocated to the saccade goal immediately after the saccade cue onset - regardless of SOA. Thus, it did not matter whether the hand movement was planned at that time or not - participants selected the saccade target immediately after saccade cue onset. This demonstrates that saccade goal selection was independent of whether the reach goal was selected at that time or not. The finding further supports the conjecture that the mechanisms selecting the goals for eye and hand movements are dynamically independent (Jonikaitis & Deubel, in press).

Split attention. We also demonstrate that attention can be split to multiple locations, as illustrated by our finding that probe discrimination was better than chance at saccade and reach goal locations before reach onset. That attention can be split has been proposed in a number of studies (e.g., Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Bichot, Cave & Pashler, 1999; Adamo, Pun, Pratt, and Ferber, 2008), however, this view has also been vigorously objected (e.g., Dubois, Hamker & VaRullen, 2009; Jans, Peters & Weerd, 2010). Our data clearly support the view that attention can be split to parallel locations in a task involving the preparation of eye and hand movements, in line with further recent evidence (Jonikaitis & Deubel, in press). One interesting question concerns how this split is achieved. Our task, contrary to typical tasks investigating parallel attention foci, did not explicitly instruct attention to shift to any location. The main task was the movement task, and we observed that probe discrimination increased at the movement goal locations. The shift of attention to the movement goals seems to be involuntary to some degree, as probe discrimination at movement goal locations increases even when participants are explicitly informed that probe is more likely to appear at other locations (Deubel & Schneider, 1996; Jonikaitis & Deubel, in press; Tibber, Grant & Morgan, 2009; Wilder, Kowler, Schnitzer, Gersch & Dosher, 2009). This seems to be true also in cases where no discrimination task is present, but attention is measured using ERPs (Baldauf & Deubel, 2009). Moreover, attention was found to shift to multiple locations when a sequence of eye or hand movements to multiple targets is prepared (Godijn & Theeuwes, 2003; Baldauf, Wolf & Deubel, 2006; Baldauf & Deubel 2008, 2010). All this evidence suggests that attentional resources can be distributed to multiple targets during the planning of combined eye and hand movements as shown in here, as well as during the preparation of movement sequences.

The question still remains as to the relationship between automatic attention allocation to movement goals as studied here and the intentional, simultaneous attention allocation to multiple stimuli. It could be that different attentional resources exist for the shifting attention before movement onset and the intentional attending to other locations (Montagnini & Castet, 2007). While this question remains to be investigated, our data support the view that attention can be transiently split.

Inhibition of return. We also observed that saccades were delayed when participants already reached to that location. This effect occurred late, at a SOA of around 700-900 ms and thus was within the time frame when “inhibition of return” (IOR) is known to occur (Klein, 1988, 2000). IOR is regarded as a mechanism that discourages attentional (or saccadic) revisiting of previously attended locations. Our results show that targets selected for hand movements can inhibit saccadic orienting to those targets. In other words, within the IOR time frame, participants tended not to direct saccades to the locations they already reached at.

It has been suggested that IOR originates from either attentional or saccadic systems. A possible attentional explanation of our findings is that participants shifted their attention to the hand movement target when they planned the hand movement. Later, when the saccade had to be planned to that same target, the shift of attention to this location was delayed, resulting in the observed IOR effect.

Another possible explanation is that the observed IOR is a saccadic effect (Theeuwes & Godijn, 2002). It could be argued that participants planned a saccade to every reach target - without executing the saccade, which resulted in an IOR effect. However, if this were the case then at short SOAs saccades directed to the reaching goal should have been faster than saccades directed elsewhere, a result that we did not observe. Our findings Thus argue for an attentional origin of IOR.

Reaction time is not attention. A striking observation of this study is that while saccades showed large dual task costs as measured in saccadic latencies, there were no attentional target selection costs, i.e., the attention shift preceding the saccade showed no delay. This is surprising given the common assumption that attention and saccades are closely coupled when people are asked to make speeded responses while eye or hand movements are planned. The clear dissociation between saccadic reaction time and attentional selection indicates that caution should be taken in using saccade or hand movement latencies as a measure of target selection or attentional allocation. Instead of attentional processing, the latencies may merely reflect dual task constraints occurring at later stages of sensorimotor processing.

ACKNOWLEDGMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (GRK 1091) and by the 7th Framework Program of the European Community (Project “GRASP”, ICT – 215821)

REFERENCES

Adamo, M., Pun, C., Pratt, J., & Ferber, S. (2008). Your divided attention, please! The maintenance of multiple attentional control sets over distinct regions in space. *Cognition, 107*, 295–303.

Alvarez, G.A. & Cavanagh, P. (2005). Independent resources for attentional tracking in the left and right visual hemifields. *Psychological Science, 16*, 637-643.

Andersen, R.A., & Buneo, C.A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience, 25*, 189-220.

Awh, E., & Pashler, H. (2000). Evidence for split attentional foci. *Journal of Experimental Psychology: Human Perception and Performance, 26,* 834-846.

Baldauf, D., Wolf, M., & Deubel, H. (2006). Deployment of visual attention before sequences of goal-directed hand movements. *Vision Research, 46*, 4355-4374.

Baldauf, D., & Deubel, H. (2008). Properties of attentional selection during the preparation of sequential saccades. *Experimental Brain Research, 184*, 411-425.

Baldauf, D., & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: an event-related potential study. *Journal of Cognitive Neuroscience, 21*, 18-29.

Baldauf, D. & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research*, *50*, 999-1013.

Batista, A.P., Buneo, C.H., Snyder, L.H., & Andersen R.A. (1999). Reach plans in eye-centered coordinates. *Science, 285*, 257-260.

Bichot, N.P., Cave, K.R., Pashler, H. (1999). Visual selection mediated by location: feature based selection of noncontiguous locations. *Perception and Psychophysics, 61*, 403-423.

Bekkering H., Adam, J.J., Kingma, H., Huson, A., & Whiting H.T. (1994). Reaction time latencies of eye and hand movements in single- and dual-task conditions. *Experimental Brain Research, 97*, 471-476.

Bekkering, H., Adam, J.J., van den Aarssen, A., Kingma, H., & Whiting H.T. (1995). Interference between saccadic eye and goal-directed hand movements. *Experimental Brain Research, 106*, 475-484.

Brown, S. W. (1997). Attentional resources in timing: Interference effects in concurrent temporal and nontemporal working memory tasks. *Perception and Psychophysics, 59*, 1118–1140.

Carrasco, M. (2006). Covert attention increases contrast sensitivity: Psychophysical, neurophysiological and neuroimaging studies. *Progress in Brain Research, 154*, 33-70.

Deubel, H., & Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. *Vision Research, 36*, 1827-1837.

Deubel, H., Schneider, W.X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81-107.

Dubois, J., Hamker, F.H., & VanRullen, R. (2009). Attentional selection of noncontiguous locations: the spotlight is only transiently "split". *Journal of Vision, 9*, 3:1-11.

Hommel, B. (1998). Automatic stimulus-response translation in dual-task performance. *Journal of Experimental Psychology: Human Perception and Performance*, *24*, 1368-1384

Horstmann, A., & Hoffmann, K.P. (2005). Target selection in eye-hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research, 167*, 187-195.

Huestegge, L., & Koch, I. (2009). Dual-task crosstalk between saccades and manual responses. *Journal of Experimental Psychology: Human Perception and Performance, 35*, 352-362.

Jonikaitis, D. & Deubel, H. (in press). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological Science*.

Godijn, R., & Theeuwes, J. (2003). Parallel allocation of attention prior to the execution of saccade sequences. *Journal of Experimental Psychology: Human Perception and Performance, 29*, 882-896.

Gottsdanker, R. (1980). The ubiquitous role of preparation. In G. E. Stelmach and J. Requin (Eds.), *Tutorials in Motor Behavior* (pp. 315–371). Amsterdam: North-Holland.

Jans, B., Peters, J.C., & De Weerd, P. (2010). Visual spatial attention to multiple locations at once: the jury is still out. *Psychological Review, 11*, 637-684.

Johansson, R.S., Westling, G., Backstrom, A., & Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience, 21*, 6917-6932.

Kahneman, D. (1973). *Attention and effort*. Englewood Cliffs, NJ: Prentice Hall.

Klein, R. (1988). Inhibitory tagging system facilitates visual search. *Nature, 334*, 430-431.

Klein, R. (2000). Inhibition of Return. *Trends in Cognitive Sciences, 4*, 138-147.

Land, M.F., & Hayhoe, M.M. (2001) In what ways do eye movements contribute to everyday activities? *Vision Research, 41*, 3559-65.

Lien, M-C., & Proctor, R.W. (2002). Stimulus-response compatibility and psychological refractory period effects: implications for response selection. *Psychonomic Bulletin & Review, 9,* 212-238.

Linnell, K.J., Humphreys, G.W., McIntyre, D.B., Laitinen, S., & Wing, A.M. (2005). Action modulates object-based selection. *Vision Research, 45*, 2268-2286.

Lünenburger, L., Kutz, D.F., & Hoffmann, K.P. (2000). Influence of arm movements on saccades in humans. *European Journal of Neuroscience, 12*, 4107-4116.

Medendorp, W.P., Goltz, H.C., Vilis, T., & Crawford, J.D. (2003). Gaze-centered updating of visual space in human parietal cortex. *Journal of Neuroscience, 23*, 6209-6214.

Medendorp, W.P., & Crawford J.D. (2002). Visuospatial updating of reaching targets in near and far space. *NeuroReport, 13*, 633-636.

Milner, A.D. & Goodale, M.A. (1995). *The Visual Brain in Action*. Oxford University Press.

Montagnini, A., & Castet, E. (2007). Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *Journal of Vision, 7*, 8:1-16

Neggers, S.W.F., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*, 639-651.

Neggers, S.W.F., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal of Neurophysiology, 86*, 961-970.

Niechwiej-Szwedo, N., McIlroy, W.E., Green, R., & Verrier M.C. (2005). The effect of directional compatibility on the response latencies of ocular and manual movements. *Experimental Brain Research, 162*, 220-229.

Pashler, H.E. (1994). Dual-task interference in simple tasks: data and theory. *Psychological Bulletin, 116*, 220-244.

Pashler, H.E., Carrier, M., & Hoffman, J. (1991). Saccadic eye movements and dual-task interference. *The Quarterly Journal of Experimental Psychology, 46*, 51-82.

Prablanc, C., Echallier, J.F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at visual target. *Biological Cybernetics, 35*, 113-124.

Pelz, J., Hayhoe, M.M, & Loeber, R. (2001). The coordination of eye, head, and hand movements in a natural task. *Experimental Brain Research, 139*, 266-277.

Rizzolatti, G., Riggio, L., & Sheliga, B.M. (1994). Space and selective attention. In C. Umilta & M. Moscovitch (Eds.), *Attention and performance XV: Conscious and nonconscious information processing* (pp. 231–265). Cambridge, MA: MIT Press.

Schubert, T. (1999). Processing differences between simple and choice reactions affect bottleneck localization in overlapping tasks. *Journal of Experimental Psychology: Human, Perception, & Performance, 25*, 1-18.

Schubert, T. (2008). The central attentional limitation and executive control. *Frontiers in Bioscience, 13*, 3569-3580.

Schiegg, A., Deubel, H., & Schneider, W.X. (2003). Attentional selection during preparation of prehension movements. *Visual Cognition, 10*, 409-431.

Sharikadze, M., Cong, D.K., Staude, G., Deubel, H., & Wolf, W. (2008). Dual-tasking: Is manual tapping independent of concurrently executed saccades? *Brain Research, 1283,* 41-49.

Snyder, L.H., Calton, J.L., Dickinson, A.R., & Lawrence, B.M. (2002). Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology, 87*, 2279-2286.

Song, J-H., & Nakayama, K. (2006). Role of focal attention on latencies and trajectories of visually guided manual pointing. *Journal of Vision, 6*, 982-995.

Stritzke, M., & Trommershäuser, J. (2007). Eye movements during rapid pointing under risk. *Vision Research, 47*, 2000-2009.

Theeuwes, J., & Godijn, R. (2002). Oculomotor capture and Inhibition of Return: evidence for an oculomotor suppression account of IOR. *Psychological Research, 66*, 234-246.

Tibber, M.S., Grant, S., & Morgan, M.J. (2009). Oculomotor responses and visuospatial perceptual judgments compete for common limited resources. *Journal of Vision, 9*, 12:11-13.

Werner, W., Dannenberg, S., & Hoffmann, K.P. (1997). Arm-movement-related neurons in the primate superior colliculus and underlying reticular formation: Comparison of neuronal activity with EMGs of muscles of the shoulder, arm and trunk during reaching. *Experimental Brain Research, 115*, 191-205.

Wilder, J.D., Kowler, E., Schnitzer, B.S., Gersch, T.M., & Dosher, B.A. (2009). Attention during active visual tasks: counting, pointing, or simply looking. *Vision Research, 49*, 1017-1031.

CHAPTER V

STUDY 4: Reach decisions are affected by saccade preparation

Manuscript for submission

Reach decisions are affected by saccade preparation

Donatas Jonikaitis[1] **and Michael Hegenloh**

Allgemeine und Experimentelle Psychologie, Ludwig-Maximilians-Universität, München, Germany.

Contribution: The author of this PhD thesis designed and ran experiments, analysed the results and wrote the manuscript (introduction, methods and results sections)

ABSTRACT

Most routine hand movements are preceded by a shift of gaze towards the reach target. However, reach planning must take into account that eyes move very frequently (on an average of 2-3 times a second). The evidence that at least some stages of reach planning are carried out in a gaze centered reference frame further compounds the problem as any eye movement during reach planning could potentially disrupt visual representation of the reach target. While it has been shown that reach target representations are updated after saccade movements, it is still not clear how the saccade plan itself is taken into account. More specifically, are visual representations for reaches updated before, during or after saccade onset? In this study, we measured reaching target selection while participants planned eye movements. We found that participants were more likely to select reach objects in the direction they planned their saccade to. Importantly, reaching goal selection was influenced by eye position approximately 100 ms before saccade started. These findings suggest that reach planning is influenced not just by the current gaze position but also by eye movement preparation.

---

[1] Correspondence should be addressed to D.J. (djonikaitis@gmail.com).

INTRODUCTION

To interact with objects in their environment, humans often make a combination of eye and reaching movements. Most often we look at or fixate the object before we reach for it (Hayhoe, 2000; Johansson, Westling, Backstrom & Flanagan, 2001; Land, Mennie & Rusted, 1999). Such coupling of saccades and reaches serves a function – reaches are more accurate if gaze is directed to the reach goal (Prablanc, Echallier, Komilis, & Jeannerod, 1979), as our eyes collect information necessary for planning hand movements (Horstmann & Hoffmann, 2005).

A number of studies have demonstrated that such yoking of reach and saccade planning might be obligatory. Neggers & Bekkering (2000, 2001) showed that eye position is "anchored" to the reach goal. In that task participants are unable to start a saccade to a newly appeared object as long as the reach towards currently foveated object is being carried out. This holds true even when the hand is not visible and only proprioreceptive feedback about ongoing reach is available. Concurrent reaches, if directed to same location as saccades, also affect saccade latency and speed (Bekkering, Adam, van den Aarssen, Kingma, & Whiting, 1995; Snyder, Calton, Dickinson, Lawrence, 2002). Additionally, eye position seems to affect which targets for reaches are selected (Scherberger & Andersen, 2007).

Physiological studies have also asserted that the there is a significant cross-talk between saccade and reach planning. Patients with brain lesions in parietal cortex seem to be unable to reach to the locations they are not looking at (Carey, Coleman, & Della Sala, 1997). When initiating movements, these patients show very long movement latencies, and it seems that they are impaired in updating visual information after saccades (Gaveau et al, 2008), a finding which has been replicated using trans-cranial magnetic stimulation in healthy participants (Desmurget et al, 1999). Additionally, parietal cortex has been suggested to be involved in early stages of reach planning (Snyder, Batista & Andersen, 1997), and neurons in those reach related areas are modulated by gaze position (Batista, Buneo, Snyder, & Andersen, 1999). This last finding demonstrates that early stages of reach planning might be carried out in gaze centered reference frame (Cohen & Andersen, 2002; Beurze, Van Pelt, & Medendorp, 2006).

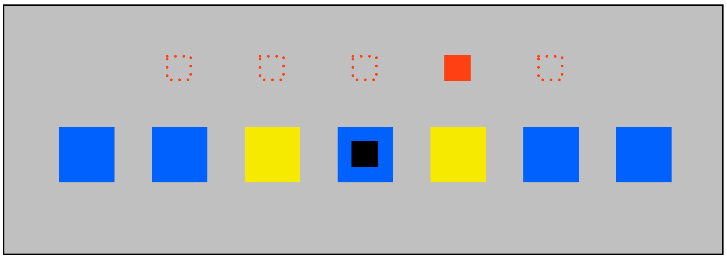


Figure 1. Experimental setup in Experiments 1 and 2. Participants looked at the red eye fixation square through the trial, and while pointing at the central blue square marked with black square inside of it. When two reach targets appeared - blue boxes were highlighted in yellow - participants chose a target to reach to.

However, while saccades and reaches are coordinated to the task demands, reach planning has to take into account that eyes move frequently, and reaches are preceded by saccades. As at least during some of the movement planning stages reach targets are represented in gaze centered coordinates, any eye movement during reach planning could potentially disrupt visual representation of the reach target. While it has been demonstrated that reach target representations are updated after saccade movements (Medendorp & Crawford, 2002; Beurze et al, 2006), it is not clear how saccade plan itself is taken into account. In other words, are visual representations for reaches updated before saccade onset, or only after?

In order to investigate whether saccade planning affects reach movement goal selection, we used a reach preference task. In this task, gaze position is fixed through the trial and two targets for reaches are presented. Participants are free to choose whichever target they want to point to (Scherberger, Goodale & Andersen, 2003). It has been observed before that gaze direction affects reach preferences. In this study we asked participants to make a saccade to the centrally cued location while two reach objects were briefly flashed during saccade planning. After finishing the saccade task participants were required to reach for one of these objects.

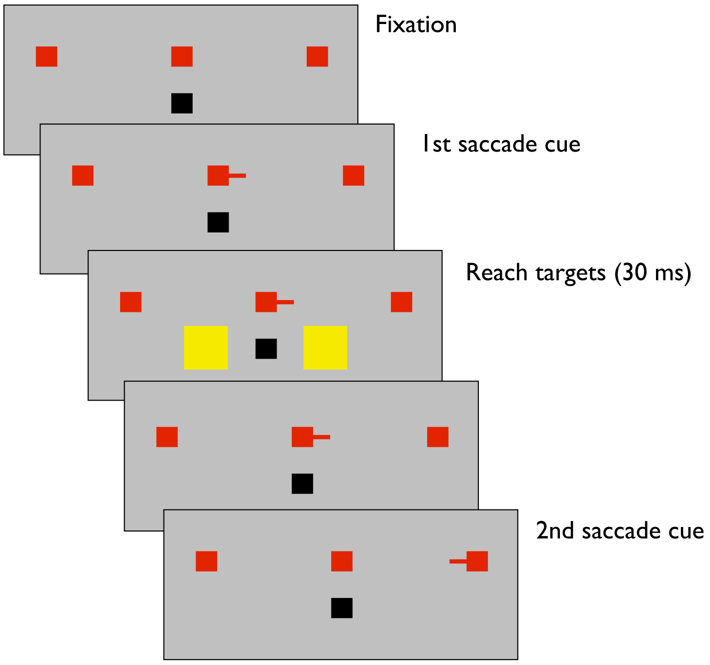


Figure 2. Task and stimuli used in Experiment 3. Participants looked at the red eye fixation. When arrow pointing left or right appeared, participants made a saccade to the red object on that side. During saccade planning two reach targets were flashed briefly. After finishing saccade, second saccade cue directing back to the display center appeared. Only after doing second saccade back participants were allowed to reach to one of the two selected objects.

METHOD

Experiment 1 – Gaze positions. In Experiment 1 we replicated the previously observed finding (Scherberger, Goodale & Andersen, 2003), that eye position affects reach target selection. Trial sequence is shown in **Figure 1**. During each trial participant looked at the fixation for the eye, which was indicated by the red square (size 0.5°), drawn at one randomly selected location out of five possible (-10°, -5°, 0°, 5° or 10° from the left to the right with respect of the display center). Five degrees bellow the fixation for the eye a row of seven blue squares (size 1.2°) was presented. Participants had to align their finger with the fixation for the hand – central one out of seven blue squares, marked by smaller black square inside of it (size 0.5°). Other six squares were always at positions 15°, 10° or 5° to the left and right of the fixation for the hand.

After a 1.5 second delay (on average, standard deviation – 0.3 seconds), two of the blue squares (located 5° to the left and right of the fixation for the hand) changed their color into yellow. Participants were asked to select one of the two targets for reaching. We manipulated reaching target selection by manipulating the onset asynchrony of the reaching targets. Both targets could light up simultaneously (SOA 0), or with 50, 100 or 150 ms SOA (either left or right target lighting up first). It has been shown previously, that manipulation of the reaching target asynchrony modulates reaching target selection, with higher probability to select targets that were presented first (Scherberger, Goodale & Andersen, 2003; Horstmann & Hoffmann, 2005). In order to assure that participants followed the task on every trial, we included a control condition on 25% of trials in which only one of two targets was presented and participants had to reach to that target.

Eight participants (5 female), aged between 18-27 years completed 600 trials of the task. All participants did a practice block of 60 trials before the task.

Experiment 2 – Briefly flashed targets. The task in this Experiment was identical as in the Experiment 1, except for the following differences. We again measured reaching preferences while we manipulated gaze position. However, for the purposes of the Experiment 3, we introduced 2 changes – two yellow reaching targets were always presented simultaneously and both reach targets were shown only for 50 ms instead of staying onscreen through the trial. We did this experiment to confirm that same effect on reaching target selection also holds for the specific stimulus conditions that we planned to use in Experiment 3.

Twelve participants (7 female), aged between 21-31 years completed 180 trials of the task.

Experiment 3 – Saccade planning. After establishing that gaze position modulates reach target selection for targets that are presented briefly, we addressed our main question: does saccade planning affect reach target selection?

Figure 2 shows a schematic illustration of the task and stimuli used. In this task participants looked at the red square which indicated fixation for the eye (size 0.8°) presented at the center of the display. Two potential saccade targets (also red squares) were shown through the trial – 10° to the the left and to the right side of the fixation for the eye. Participants aligned their right hand index finger on a fixation for the hand – black square presented 5° bellow the fixation for the eye. After a fixation period of 1.5 seconds (average fixation duration, standard deviation 0.3 seconds), first saccade cue – a small red arrow (length 0.8°) pointing from the center of the fixation for the eye – appeared. Participants were asked to quickly look at either the left or the right saccade target depending to which side saccade cue indicated. 600 ms later first saccade cue disappeared and second saccade cue appeared instructing participants to look back to the fixation for the eye. Thus, participants made two saccades - one directed toward the cued object, and another one directed back to the fixation.

Sometime during the preparation of the first saccade – from 50 to 350 ms after the first saccade cue appeared – two yellow reaching targets (size 1.2°, distance from the fixation was either 4 °or 6° for both targets) were briefly flashed (for 30 ms) to the left and right of the fixation position for the finger. Participants were asked to select one of the two targets to which they want to reach, however they were not allowed to start their reaching yet. 1600 ms after the first saccade cue appeared (or 1000 ms after the second saccade cue) short beep was presented and only then participants were allowed to point to the reach target they chose to.

Thus, to sum up, participants looked at the center of the display, then saccade cue appeared. At some time during saccade planning two reach targets were flashed and participants had to select one of them. After finishing instructed saccade, participants looked back to the center of the display, and only then they were allowed to make a reach to a selected target. Thus, at the time the reach is initiated, the eye is at the central fixation, the only manipulation being that two reach targets were flashed sometime during the saccade planning.

Eight participants (4 female), aged between 22-27 years completed at least 400 trials of the task. All participants did a practice block before the task.

Experiment 4 – Stop task. Central cue instructed saccade direction in Experiment 3. In order to make sure that our observed effects are due to saccade planning and not due to the saccade cue pointing towards one direction, we introduced a stop task in Experiment 4. This Experiment was identical to Experiment 3 except for the following modifications. Eye fixation square and two potential saccade targets were green instead of red. Two reach targets were presented between 20 and 300 ms after the first saccade cue onset. On 20% of trials, 80 ms after the first saccade cue appeared, eye fixation square changed it's color from green to red, instructing participants to cancel their saccade. Instead, on those stop trials participants had to keep fixating at the central fixation square through the trial.

Nine participants (3 females) aged between 22 and 28 years, completed at least 500 trials of the task.

Experiment 5 – Reach planning. In this experiment we investigated whether reach planning affects saccade target selection. Overall task design was similar to Experiment 3 except with order of movements being reversed. After trial started participants looked at the central fixation for the eye (red square). They aligned their finger with a black fixation square for the hand, bellow fixation for the eye. Two potential reach targets – black squares 10° to the left and the right of the fixation for the hand were presented through the trial. First reach cue instructed participants to which of the two objects to reach. Second reach cue, appearing 600 ms after the first one, instructed participants to reach back to the fixation for the hand. During first reach planning two yellow saccade targets were briefly flashed (30 ms). After hearing the beep (1600 ms after the appearance of the first reach cue), participants looked at the selected saccade target location.

Eight participants (4 females), aged between 23-28 years completed at least 360 trials of the task. All participants did a practice block before the task.

Aparatus. All stimuli were displayed on ELO CRT Open-Frame 17", with a 65 Hz refresh rate. Screen was mounted on a table, at an angle of approximately 30° to the surface. Touch display was located 50 cm away from the subject, but we adjusted this distance slightly for each participant for a comfortable reach. Reach onset and offset times, and reach start and end coordinates were defined as mouse clicks by a company provided drivers. Eye movements were recorded with a tower mount Eyelink 1000 system. Recordings were made at 1000 Hz. Eye movement accuracy was measured through each trial, and failed trials (failure to foveate the target, eye drifted away from the fixation, blinks) were discarded and repeated during the experiment. Stimulus presentation and response recording were controlled with psychophysics toolbox for Matlab.

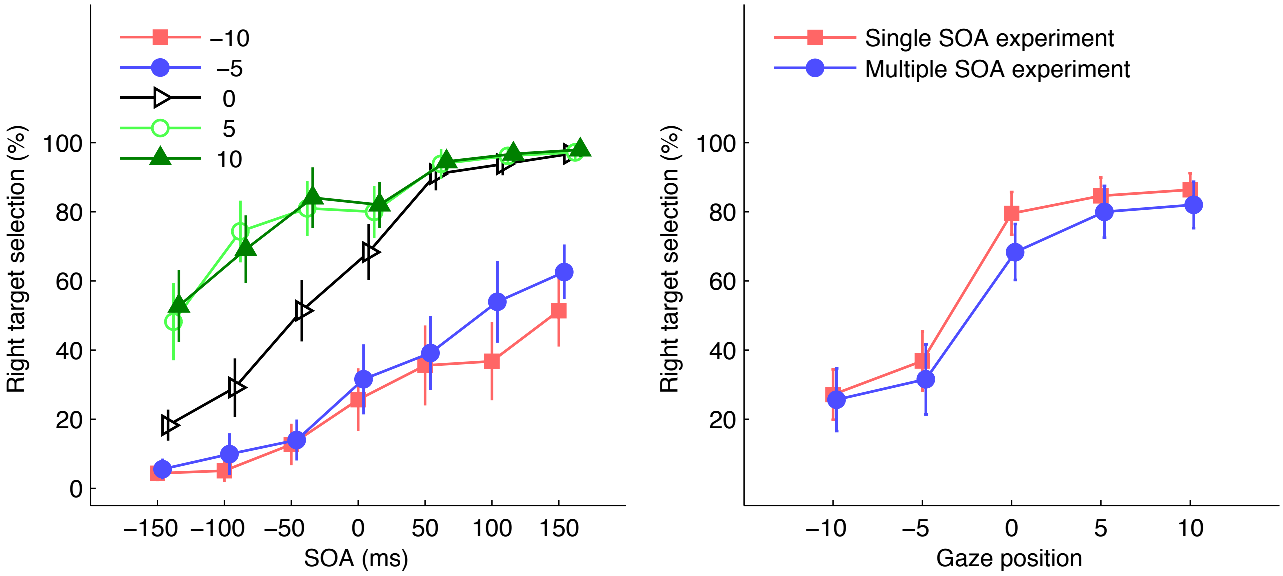


Figure 3. Reach target selection preferences for different gaze position and SOA conditions. **(A)** Proportion of right targets selected when SOA between left and right target was varied (x-axis, negative values - left target presented first) and when gaze position was manipulated (different lines, negative - gaze leftward of the fixation). **(B)** Proportion of right targets selected for the SOA 0 condition (both reach targets appear simultaneously) in Experiment 1 with multiple SOAs and Experiment 2 with single SOA condition.

RESULTS

Eye position effects. Results of Experiment 1 are shown in **Figure 3A**. In Experiment 1 two factors could affect reach target selection – eye fixation position and reach target SOA. First, changing eye fixation position altered reach target selection – participants were more likely to select right targets if eye position was to the right of the center of the display (right target was selected on 82% and 83% of trials for eye fixation positions at 5° and 10° to the right), and left targets if eye position was to the left (right target selected on 25% and 31% of trials for eye fixation positions at 5° and 10° to the left), and slightly more likely to select right targets if eye fixation position was at the center of the display (right target selected on 64% of trials). This last finding – bias for selection of right targets with eye fixation position at the center of the display – can be explained by the hand used in the experiment, as this bias reverses if participants use their left hand instead of the right (Scherberger, Goodale & Andersen, 2003).

Secondly, manipulating SOA also affected the reach target selection. Participants were more likely to select the right target if it was presented before the left one appeared.

If right target appeared 150 ms before the left one, participants selected right target on 78% of trials, whereas if left target appeared before the right one, participants selected the right target on only 23% of trials. Again, a rightward bias was observed during trials when both targets appeared simultaneously (right target selected on 58% of trials in SOA=0 condition).

A repeated measures ANOVA with two factors – fixation position and SOA – confirmed that these factors affected reach target selection (eye position effect: F(4,168)=32.57, p<0.01; SOA effect F(6,168)=50.68, p<0.01).

Briefly shown targets. For the purposes of the following experiments (Experiments 3 through 5), we performed an additional experiment – in this task we manipulated the gaze position while participants had to select one out of two reach targets that were presented, but in contrast to Experiment 1, both targets were presented only simultaneously (SOA=0), and were shown only briefly (for 30 ms). **Figure 3B** shows results of this experiment – participants' preference to select the reach target were affected by the eye position. Once again participants were more likely to select right targets if they looked at the center of the display or to the right of it, and less likely if they looked to the left. Repeated measures ANOVA with eye position as a factor was significant (F(4,11)=29.50; p<0.01). Additionally, target selection preferences in Experiment 1 (SOA=0 in that experiment, see **Figure 3B**), and Experiment 2 were not different (all p>0.25). This means that same dynamics underlie target selection regardless whether both targets are present on the screen through the selection, or whether selection is carried out on briefly presented targets.

Saccade preparation effects. In the third experiment, we investigated whether saccade preparation affects reach target selection. In this task participants prepared saccade to a target (average saccade latency – 330 ms), and two reach targets were briefly flashed while participants prepared a saccade. Participants selected right target for reaches on 77% of trials in which saccade was directed to the right and were less likely to select the right target if saccade was directed to the left (43% of trials). Next, we measured whether saccade planning affected reach target selection. For this we calculated selection preference index. First, we divided all trials into three saccade-target asynchrony groups depending on when reach targets were presented with respect to saccade onset: trials in which reach targets were presented within the first third of the saccade latency (early in the saccade planning) were assigned to the first saccade-target asynchrony group, trials

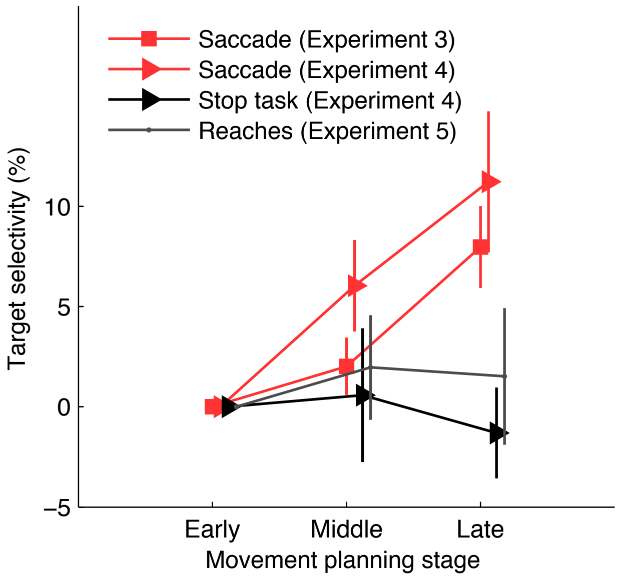


Figure 4. Target selectivity for different experiments as a function of movement planning. Positive ordinate values - increased probability to select target at the side of the planned saccade (in Experiment 3 and 4, red lines) before the saccade onset. Two conditions in Experiment 4 are shown - target selectivity when saccade was allowed (red triangles) and target selectivity when saccade had to be cancelled (stop-task, black triangles). Experiment 5 - saccade target selectivity while reaches were planned. Error bars - standard error of the mean.

with reach targets presented during the 2nd third of the saccade latency were assigned to the second group, and trials with reach targets presented late during saccade planning were assigned to the third group. After this, we calculated selection preferences – proportion of trials in which participants chose left target when saccade was directed to the left, and right target when saccade was directed to the right. Next we examined how these reach preferences changed over time, by subtracting selection preference for reach targets presented early in the saccade planning, from selection preferences during middle and late saccade planning stages. To sum up, if participants were more likely to select target presented at the side to which they made a saccade during late saccade planning stages as compared to early ones, we should observe an increase in selection preference index, and if they become less likely to select that reach target then a decrease should be observed. As can be see in the **Figure 4**, reach preferences increased before saccade – the closer to the saccade onset the reach targets appeared, the more likely participants were to select reach target on that side of the display. Before saccade onset, increase in reach selection preferences was statistically significant (t-test, t(8)=3.19, p=0.01). Additionally, selection preferences did not differ for the trials when saccades were made to the left, and trials when saccades were made to the right (two-way ANAOVA, factor of target presentation asynchrony significant F(2,14)=4.04, p<0.05; factor of hand not significant F(1,14)=0.11, p=0.75).

Stop task. In Experiment 3, task saccade cue was a small arrow directed either left or right, thus it is possible that the increase in reach selection preferences was purely due to visual stimulation effects – cue pointing to one side could bias selection preference to that side. We conducted a stop task to control for this effect. In this task once again participants made saccade to instructed side, but on 20% of the trials eye fixation changed the color to red and participants had to cancel the saccade they were planning. We found the effect of saccade direction on reach preferences to be consistent even in these conditions. If participants made saccade to the right, they chose the right reach target on 70% of trials, and if they made saccades to the left, they chose right reach target on only 38% of trials. There was also an effect of saccade preparation – the closer to the saccade onset reach targets appeared, the more likely participants were to select the reach target on that side (t(8)=3.04, p<0.01; **Figure 4**).

On trials when the stop signal appeared, reach preferences were similar to the cases when cue pointed right (54% of right targets selected), and when the cue pointed left (51% of right targets selected). Additionally, cue-reach target asynchrony did not have an effect on reach preferences (t(8)=-0.44, p=0.66). These two results argue against the interpretation that the cue might bias the observed effects, and confirm that saccade planning was crucial in affecting reach preferences.

Reaches preparation effects. In this task, we investigated whether reach target selection was affected specifically by saccades, or was it just a general effect due to action planning. We reversed the instruction and requried participants to reach to a cued location, while we presented two targets for the saccade during reach planning. If our observed selection preference increase is due to the fact that any action directed to a part of space might bias another action to be executed to that part of the space, then we should observe that planning reaches should bias the saccade target selection in the same way as planning saccades influenced reach target selection. However, this was not the case. When participants reached to the right targets, their saccades were directed right on 67% of trials, and when they reached to left target, their saccades were directed right on 59% of trials, and this difference was not significant statistically (t(7)=-0.65, p=0.54). Additionally, reach planning did not affect saccade preferences either (**Figure 4**) – participants' saccade selection preference did not change as a function of the reach planning stage (t(7)=0.44; p=0.66). Thus, this experiment demonstrated that the previously observed selection preference effect was valid only for saccade planning, but not for reach planning.

DISCUSSION

The main purpose of the study was to investigate the effects of saccade planning on reach movement decisions. In a series of experiments we measured reaching preferences while we manipulated eye position. In Experiments 1 and 2, in accordance with previous studies (Scherberger, Goodale & Andersen, 2003; Scherberger & Andersen, 2007), we demonstrated that reaching target selection is influenced by the current eye position by showing that participants were more likely to choose targets closer to the current gaze direction. In Experiments 3 and 4, we measured reaching target selection while participants planned eye movements. We found that participants were more likely to select reach objects at the direction they planned their saccade to. The main finding of our study is that reaching goal selection was influenced by eye position approximately 100 ms before saccade started. In an additional stop task, we were able to rule out that the cue indicating the direction of the saccade is biasing reach decisions. Participants were not biased to either side when the stop signal appeared, as compared to when no stop signal appeared. And lastly, on reversing the conditions, we found that reach planning does not affect saccade target selection in a similar way.

The results from our first series of experiments are in agreement with the findings of Scherberger, Goodale & Andersen (2003). While these authors were interested in investigating reference frames used for reach target selection (and found effects of head based reference frame and effects of gaze position on reach target selection), we were interested in effects of saccade preparation on reach preferences. For this task we modified the original paradigm used by Scherberger and colleagues by introducing an additional condition with briefly flashed targets. While this modification showed comparable effects to the original task used by Scherberger and colleagues, it allowed us to investigate fine temporal dynamics of saccade preparation effects on reach target selection.

The fact that the representation of the target for reaches is already updated during the planning of a saccade has not yet been demonstrated. Medendorp and Crawford

(2002) have shown that target representations are updated after saccade movements (see also Beurze et al, 2006). The reason for such updating of information, as these authors suggest, is that reach targets are represented in gaze centered coordinates. This means that every eye movement would necessitate updating of visual representation used for reaches. However, rather than updating of visual information only after the saccade onset, it would be beneficial to take into account saccade planning. There are several advantages in updating the target information during the saccade planning itself instead of after it. First, naturally the eye is coupled or anchored to the future reach goal (Neggers & Bekkering, 2000; 2001). And the fact the the reach usually follows the eye movement makes it to some extent necessary that the hand "knows" where to reach next even if the eye movement is not executed yet. The other reason is that reaching is often done in a series of movements (e.g. packing a suitcase) or very fast reaching movements (e.g. catch an object). As suggested previously (e.g. Scherberger et al., 2003), these kinds of reaching movements would be slow and not efficient, if target coordinates are only available after the saccadic onset.

Neurophysiological literature seem to support this inference as well. Two different areas in parietal cortex have been described as involved in saccade and reach planning. Interestingly, both of these areas – lateral intraparietal area suggested to be involved in eye movement planning and parietal reach region suggested to be involved in reach planning (Snyder, Batista & Andersen, 1997) – represent saccade and reach targets in gaze centered coordinates (Batista, Buneo, Snyder and Anderson, 1999). While eventually such gaze centered maps have to be transformed to coordinate frames that the hand movement planing system can use to initiate the action, it is likely that gaze centered representations dominate early stages of movement planning (Cohen & Andersen, 2002). Such a neural architecture of reach target selection is consistent with our results as it suggests that signals of the eye movement plan are already signaled to the parietal reach region. Therefore it seems plausible that the hand knows where the future eye position will be and is able to prepare the future reach in time.

Surprisingly neither attention nor the cue indicating the future eye movement affected reach decision as much as the planning of eye movements did. It has been shown previously that reach planning and execution leads to attention shifts to the movement goal location (Deubel & Schneider, 2003; Deubel, Schneider & Paprotta, 1998; Baldauf & Deubel, 2009; 2010). However, in our task, planning the reach did not affect saccade preferences suggesting that attention shifts associated with reach planning were not sufficient to alter saccade goal selection. Thus, our results demonstrate that reach preferences were updated specifically during saccade planning, and suggest that this effect can not be explained by attention. Similar conclusion could also be drawn from the stop task – as stopping saccade planing did not affect reach target selection. However, so far it is not known whether attention is shifted to planned – but cancelled – saccade locations.

Lastly, we observed that movement planning effects on movement goal selection had specific direction, i.e. information about reach, saccade planning and attentional shifts was not direction unspecific. Rather, we observed a clear saccadic bias for reach target selection, and no bias from reaches to saccade target selection. This effect is interesting in the light that strong eye-hand coupling has been observed previously (such as gaze anchoring effect, Neggers & Bekkering, 2000). However, interactions between saccade and reach planning could occur at different stages of movement planning – for example, it has been observed that fixation neurons in superior colliculus increase their firing rates during reach execution (Reyes-Puerta, Philipp, Lindner & Hoffmann, 2010), suggesting that this last effect occurs at a stage closer to saccade execution than at any of the early stages that are implemented in the parietal cortex.

In summary, we found evidence that human beings were more likely to select reach objects in the direction they planned their saccade to, and the strength of this effect increases during saccade planning. We tested whether this effect is specific to the planning and execution of eye movements and found that neither the cue indicating the direction of the eye movement (stop task) nor the reversed task (reach to cued location and selection saccade target) could explain this effect.

ACKNOWLEDGEMENTS

This study was supported by the Deutsche Forschungsgemeinschaft (GRK 1091).

REFERENCES

Baldauf, D. & Deubel, H. (2009). Attentional selection of multiple goal positions before rapid hand movement sequences: an ERP study. *Journal of Cognitive Neuroscience, 21*, 18-29.

Baldauf, D. & Deubel, H. (2010). Attentional landscapes in reaching and grasping. *Vision Research, 50*, 999-1013.

Batista, A.P., Buneo, C.A., Snyder, L.H. & Andersen, R.A. (1999). Reach plans in eye-centered coordinates. *Science, 285*, 257-260.

Bekkering, H., Adam, J.J., van den Aarssen, A., Kingma, H., & Whiting H.T. (1995). Interference between saccadic eye and goal-directed hand movements. *Experimental Brain Research, 106*, 475-484.

Beurze, S.M., Van Pelt, S., & Medendorp, W.P. (2006). Behavioral reference frames for planning human reaching movements. *Journal of Neurophysiology, 96*, 352-362.

Carey, D.P., Coleman, R.J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex, 33*, 639-652.

Cohen, Y.E., & Andersen, R.A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience, 3*, 553-562.

Desmurget, M., Epstein, C.M., Turner, R.S., Prablanc, C., Alexander, G.E., & Grafton, S.T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience, 2*, 563-567.

Deubel, H. & Schneider, W.X. (2003). Delayed saccades, but not delayed manual aiming movements, require visual attention shifts. *Annals New York Academy of Sciences, 1004*, 289-296.

Deubel, H., Schneider, W.X., & Paprotta, I. (1998). Selective dorsal and ventral processing: evidence for a common attentional mechanism in reaching and perception. *Visual Cognition, 5*, 81-107.

Gaveau, V., Pélisson, D., Blangero, A., Urquizar, C., Prablanc, C., Vighetto, A., & Pisella, L. (2008). Saccade control and eye-hand coordination in optic ataxia. *Neuropsychologia, 46*, 475-486.

Hayhoe, M. (2000). Vision using routines: a functional account of vision. *Visual Cognition, 7*, 43-64.

Horstmann, A., & Hoffmann, K.-P. (2005). Target selection in eye-hand coordination: Do we reach to where we look or do we look to where we reach? *Experimental Brain Research, 167*, 187-195.

Johansson, R.S., Westling, G., Backstrom, A., & Flanagan, J.R. (2001). Eye-hand coordination in object manipulation. *The Journal of Neuroscience, 21*, 6917-6932.

Land, M.F., Mennie, N., & Rusted, J. (1999). The roles of vision and eye movements in the control of activities of daily living. *Perception, 28*, 1311-1328.

Medendorp, W.P., & Crawford, J.D. (2002). Visuospatial updating of reaching targets in near and far space. *Neuroreport, 13*, 633-636

Neggers, S.F.W., & Bekkering, H. (2001). Gaze anchoring to a pointing target is present during the entire pointing movement and is driven by a non-visual signal. *Journal Neurophysiology, 86*, 961-970.

Neggers, S.F.W., & Bekkering, H. (2000). Ocular gaze is anchored to the target of an ongoing pointing movement. *Journal of Neurophysiology, 83*, 639-651.

Prablanc, C., Echallier, J.F., Komilis, E., & Jeannerod, M. (1979). Optimal response of eye and hand motor systems in pointing at visual target. *Biological Cybernetics, 35*, 113-124.

Reyes-Puerta, V., Philipp, R., Lindner, W., Hoffmann, K.-P. (2010). Role of the rostral superior colliculus in gaze anchoring during reach movements. *Journal of Neurophysiology, 103*, 3153-3166.

Scherberger, H., & Andersen, R.A. (2007). Target selection signals for arm reaching in the posterior parietal cortex. *Journal of Neuroscience, 27*, 2001-2012.

Scherberger, H., Goodale, M.A., & Andersen, R.A. (2003). Target selection for reaching and saccades share a similar behavioral reference frame in the macaque. *Journal of Neurophysiology, 89*, 1456-1466.

Snyder, L.H., Batista, A.P., & Andersen, R.A. (1997). Coding of intention in the posterior parietal cortex. *Nature, 386*, 167-170.

Snyder, L.H., Calton, J.L., Dickinson, A.R., Lawrence, B.M. (2002). Eye-hand coordination: saccades are faster when accompanied by a coordinated arm movement. *Journal of Neurophysiology, 87*, 2279-2286.

Soechting, J.F., Engel, K.C., Flanders, M. (2001). The Duncker illusion and eye-hand coordination. *Journal of Neurophysiology 85*, 843-854.

CHAPTER VI

STUDY 5: Predictive remapping of attention across eye movements

Nature Neuroscience (2011), 14, 252-256.

Predictive remapping of attention across eye movements

Martin Rolfs[1,2,*], Donatas Jonikaitis [3], Heiner Deubel [3], Patrick Cavanagh [1]

[1] Université Paris Descartes, Laboratoire Psychologie de la Perception, 45, rue des Saints-Pères, 75006 Paris, France

[2] New York University, Department of Psychology, 6 Washington Place, 10003 New York, NY, USA

[3] Ludwig-Maximilians-Universität, Department Psychologie, Leopoldstr. 13, 80802 München, Germany

Contribution: The author of this PhD thesis designed, ran experiments and analysed the results.

ABSTRACT

Many cells in retinotopic brain areas increase their activity when saccades (rapid eye movements) are about to bring stimuli into their receptive fields. While previous work has attempted to look at the functional correlates of such predictive remapping, no study has explicitly tested for better attentional performance at the future retinal locations of attended targets. We find that briefly before the eyes start moving, attention drawn to the targets of upcoming saccades shifts also to those retinal locations that the targets will cover once the eyes have moved, facilitating future movements. This finding shows that presaccadic visual attention shifts serve both to improve presaccadic perceptual processing at the target locations, and to speed subsequent eye movements to their new postsaccadic locations. Predictive remapping of attention provides a sparse, efficient mechanism for keeping track of relevant parts of the scene when frequent, rapid eye movements provoke retinal smear and temporal masking.

* Correspondence: martin.rolfs@gmail.com

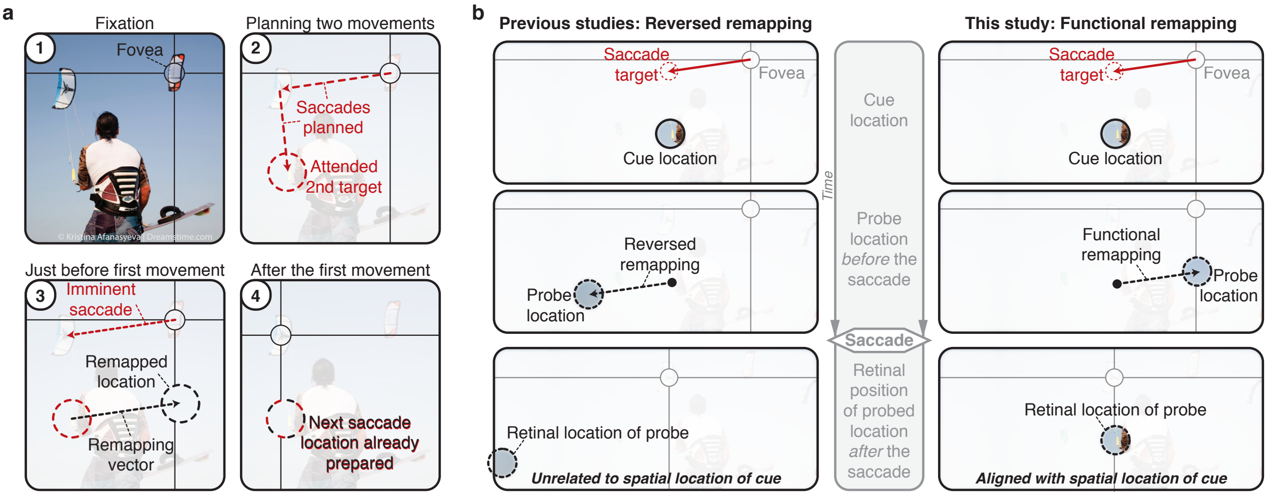


Figure 1. Predictive remapping across eye movements. (**a**) If two saccades are planned, first from the red to the blue kite and then to the kite handles visible near the surfer's left elbow, the second target (red circle) is attended in parallel to the first[9-11]. Remapping triggers a predictive activation of cells responding to the future retinotopic location of the second target, offset from its current location in the direction opposite the saccade vector (black circle)[16]. We show that this predictive activation is accompanied by an attention shift to that retinotopic location, specifying the location for the subsequent saccade. (**b**) The functional direction of remapping. Two previous studies have targeted behavioral correlates of remapping[18,19], but actually studied a reversal of remapping that has no functional correlate, as explained here (see also **Supplementary Figure 1**). In these studies, the effect of a spatial cue[18] (or, equivalently, an adaptor[19]) on subsequent pre-saccadic tests was assessed at a location offset from the cue location in the same direction as the saccade vector (middle left panel). This location is the opposite to the actual remapped location (middle right panel) and corresponds instead to the future world-centered location of the cue's current retinal location. After the saccade, this reversed remapped location covers retinotopic cortex that is far from the spatial location of the cue. Here, we reveal behavioral consequences of functional remapping, to a location that aligns with the cue location after the saccade.

INTRODUCTION

The visual system has to deal with large displacements of the image on the retina every time the eyes move to bring potentially relevant target objects onto high-acuity foveal vision. In stark contrast to what we see when a camera is quickly swept across a visual scene, these retinal image shifts escape conscious perception[1]. More importantly, we do not lose track of those parts of the scene that are of current interest and may be the targets of future eye movements. The inability to perceive changes in unattended parts of the scene, strikingly demonstrated in the paradigms of inattentional blindness and change blindness[2,3], shows that attention restricts this displacement problem to a small number of locations[4]. Some hundred milliseconds before an eye movement[5,6], visual attention is focused at the upcoming target locations[7-11], shifting the activations in saccade and attention areas of the brain[12]. These activations can be considered pointers specifying the locations of currently attended objects, whether targets of upcoming saccades or not, enabling both the planning of actions toward them and enhanced processing at those locations[13]. Here we show that these attentional “pointers” to saccade targets are updated by a predictive remapping process briefly before the eyes start moving. This process shifts attention in the direction opposite the saccade to locations that correspond to the current targets neither in retinotopic nor in world-centered coordinates, anticipating, before the eyes arrive, the locations the targets will have on the retina after the saccade lands. Our results here lend strong behavioral support to the proposal that predictive remapping[14,15]—the fact that many cells in retinotopically organized brain areas show anticipatory responses if a pending saccade will bring a stimulus into its receptive field (**Fig. 1a**)—is a critical and surprisingly rapid mechanism for keeping track of the locations of attended targets as the eyes move[16].

The discovery of predictive remapping launched intense scientific activity exploring the different brain areas and pathways involved, and revealing the requirements for this process to occur[4,17]. Up to now, however, only two studies targeted behavioral correlates of remapping[18,19] and neither of these tested the appropriate locations to determine the functional correlates of remapping (see **Fig. 1b** and **Supplementary Fig. 1**). Ours is the first study to directly investigate the consequences of remapping of eye movement targets on pre-saccadic perception and post-saccadic action. We adapted the classic double-step saccade task[20,21] that has been the central paradigm of the physiological studies of remapping. In this task, observers make two consecutive eye movements to pre-specified target locations, and critically, the vector for the eye movement to the second target is not given by its current retinal location, but by its updated location when the first saccade has been executed (**Fig. 1a**). If this vector is pre-computed and attention deployed to that retinal location prior to the first saccade, the second saccade will be prepared even before the first lands. This paradigm tests the appropriate locations for functional remapping (**Fig. 1b**) and allowed us to provide strong evidence for two key roles of this predictive process: updating the retinal location of attended parts of the scene and so facilitating subsequent movements to them.

The discovery of predictive remapping launched intense scientific activity exploring the different brain areas and pathways involved, and revealing the requirements for this

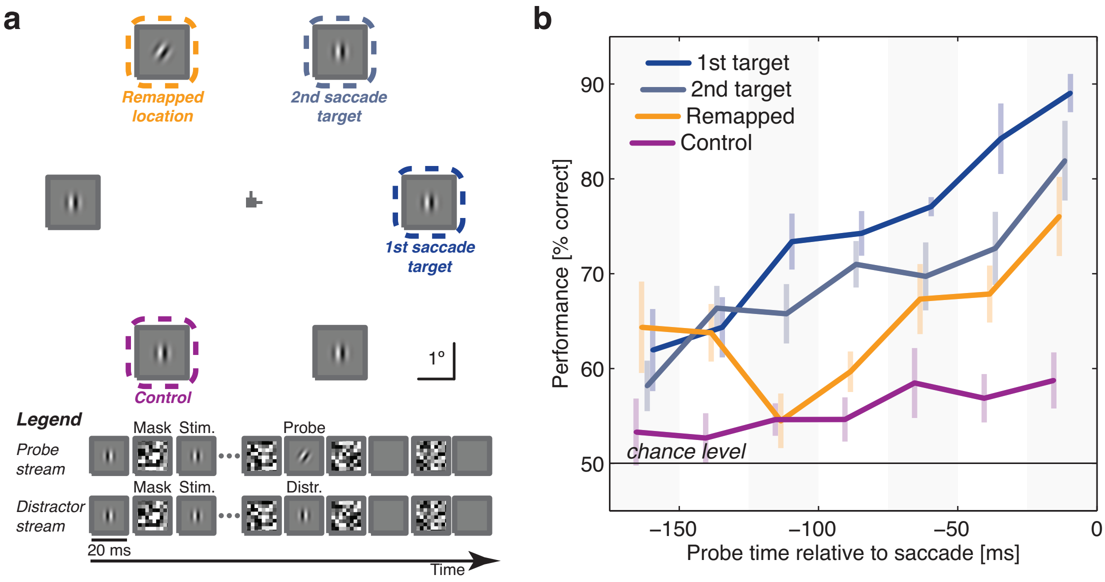


Figure 2. Predictive remapping of attention in the double-step task. (**a**) Stimulus layout. Six stimuli, arranged in a regular hexagon, displayed a flickering stream of grating-mask pairs. Following a central movement cue, subjects quickly made two eye movements, the first one left or right (here, right), the second one up or down (here, up). Fifty to 400 ms after the movement cue, one of the six gratings changed orientation (probe stream; here at remapped location), whereas all others remained vertical (distractor streams). After the eye movements, subjects reported the direction of tilt they had seen (\ or /), regardless of its location. Using performance in this task, we measured the deployment of attention at four locations (dashed frames), during the latency of the first saccade. (**b**) Performance as a function of probe offset relative to the saccade, superimposed for the probe locations tested. Error bars are s.e.m.

process to occur[4,17]. Up to now, however, only two studies targeted behavioral correlates of remapping[18,19] and neither of these tested the appropriate locations to determine the functional correlates of remapping (see **Fig. 1b** and **Supplementary Fig. 1**). Ours is the first study to directly investigate the consequences of remapping of eye movement targets on pre-saccadic perception and post-saccadic action. We adapted the classic double-step saccade task[20,21] that has been the central paradigm of the physiological studies of remapping. In this task, observers make two consecutive eye movements to pre-specified target locations, and critically, the vector for the eye movement to the second target is not given by its current retinal location, but by its updated location when the first saccade has been executed (**Fig. 1a**). If this vector is pre-computed and attention deployed to that retinal location prior to the first saccade, the second saccade will be prepared even before the first lands. This paradigm tests the appropriate locations for functional remapping (**Fig. 1b**) and allows us to provide strong evidence for two key roles of this predictive process: updating the retinal location of attended parts of the scene and so facilitating subsequent movements to them.

RESULTS

We assessed the dynamics of perceptual performance in a difficult visual discrimination task to examine the allocation of attention in a stimulus array (**Fig. 2a**) while subjects prepared a sequence of two saccades. We probed several locations in space at different times following the onset of the central movement cue indicating the locations of the two targets. The probe was a tilted Gabor grating, briefly presented for 20 ms at the end of a flickering stream of vertical gratings. This procedure allowed for high resolution of temporal probes of visual performance, a gold standard for the measurement of attentional deployment. As we will show, this fine scale temporal structure is necessary to reveal the short-lived perceptual consequences of pre-saccadic remapping. After having executed the two successive eye movements, observers reported the direction of the tilt (clockwise or counterclockwise), regardless of its location. We ensured that the perceptual task could only be solved when observers deployed attention to a particular location by adjusting the stimulus tilt in a pre-test such that observers were 82% correct at the two target locations for probes presented 150 ms after the movement cue, thus, within about 100 ms before the saccade. On each trial (each observer ran a minimum of 3000 trials), we probed one of four different locations (highlighted in **Fig. 2a**): The first saccade target (blue), the second saccade target (gray), its remapped location (orange), or its opposite location (purple), representing a neutral control location. Note that the remapped location of the second saccade target corresponds to the retinal position that the second saccade target will have only following the first saccade. It does not match either the spatial or retinal location of the second target prior to the saccade.

We plotted the average performance of nine observers as a function of the timing of the probe presentation relative to the first saccade, superimposed for all four probe locations tested (**Fig. 2b**). A test whether performance at each of these locations changed significantly across time is provided in the supplementary material (**Supplementary Fig. 2**). We found the expected advantage in discrimination performance at both the first and second saccade target locations[9-11] increasing from around 150 ms before the first saccade[5,6], with a somewhat more shallow slope for the advantage at the second saccade target. More interestingly, we found a dramatic increase in performance at the remapped location

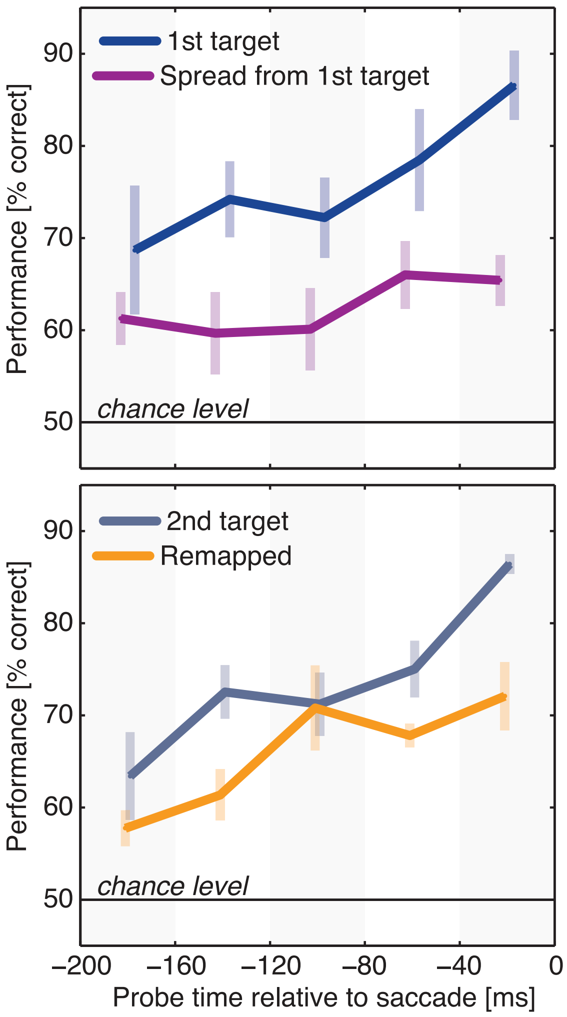


Figure 3. Controlling for the spread of attention in the double-step task. We repeated the double-step task in a new set of subjects, now also probing the location adjacent to the first saccade target to test whether attentional benefits extend around saccade targets, an alternative interpretation of the effect at the remapped location. Performance is shown as a function of probe offset relative to the saccade. Attention did not spread around saccade targets. Instead, it shifted specifically to the remapped location of the second saccade target. Error bars are s.e.m.

for the second target, emerging just 75 ms before the saccade. This benefit reached a magnitude comparable to that observed at the second saccade target itself and all nine observers showed it consistently (analyzed at a resolution of 75 ms to counteract the additional noise). In fact, across observers, the performance at the remapped location in the last 75 ms preceding the saccade correlated significantly with the performance at the second saccade target in the same time window (r=.91, P<.001), suggesting that the two allocations are strongly linked: an observer who successfully allocates attention to the second target also allocates substantial attention to its predicted post-saccadic location. Note that, prior to the saccade when this benefit is seen, the remapped location does not correspond to the second saccade target location in either retinotopic or world-centered coordinates. Contrary to the time course of perceptual facilitation at the second saccade target, performance at the remapped location revealed a significant drop almost to chance level in the time between 125 to 100 ms before the saccade (while attention is allocated to the saccade targets), excluding the possibility that the pre-saccadic enhancement is a general attentional cuing effect resulting from the movement cue. The stable performance at the

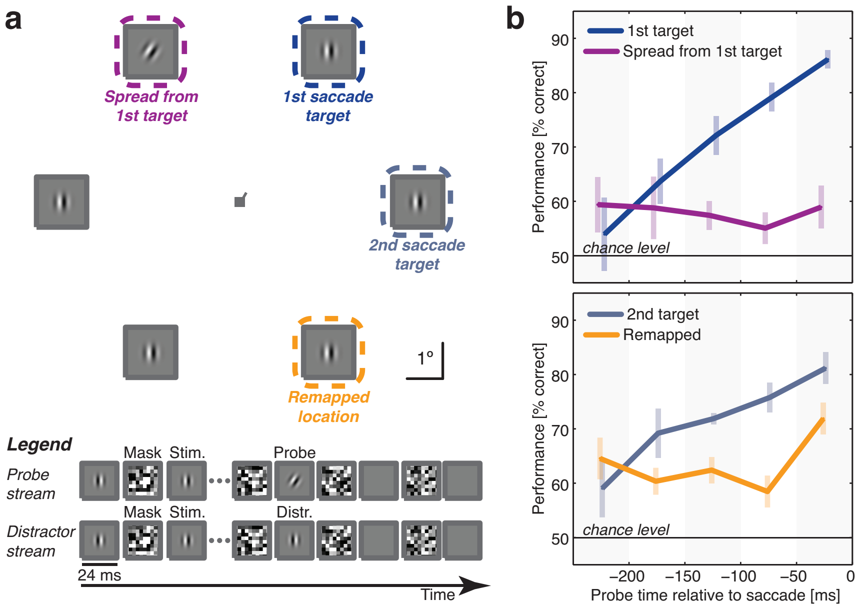


Figure 4. Controlling for cue-based facilitation in the double-step task. (**a**) In this version of the double-step task, we used only one cue, excluding the possibility of a cue-based attentional facilitation at the remapped location. The single cue indicated the first saccade target (any of the six; here upper right); the second saccade target was always the next stimulus in clockwise direction (here, right). We measured the deployment of attention at four locations (dashed frames), during the latency of the first saccade. Testing the location adjacent to the first saccade target, this experiment also again tested whether attentional benefits extend around saccade targets, an alternative interpretation of the effect at the remapped location (see also **Fig. 3**). (**b**) Performance as a function of probe offset relative to the saccade. Again, briefly before the saccade attention shifted specifically to the remapped location of the second saccade target. Error bars are s.e.m.

control location shows that the observed benefits do not represent a spatially nonspecific increase in performance, a question that we address directly in a later section.

The remapped location for the second target corresponds to the position this target will have on the retina following the first saccade. Activity in the saccade control regions of the brain is required at this location to send the second saccade to its target once the first saccade has landed. In the absence of this remapped activity, the second target could be rediscovered following the first saccade (assuming it is still present), however, if its location has been successfully remapped to the appropriate location, the second saccade should be ready to execute as soon as the first saccade lands. Indeed we can estimate from our data that the second saccade has a minimum latency benefit of 19.2±14.8 ms (corresponding to a 9.2±7.1% difference in second saccade latency; mean ± 95% confidence interval) when there was evidence that an observer had successfully shifted his or her attention to the remapped location (e.g., correctly identified the probe stimulus orientation at

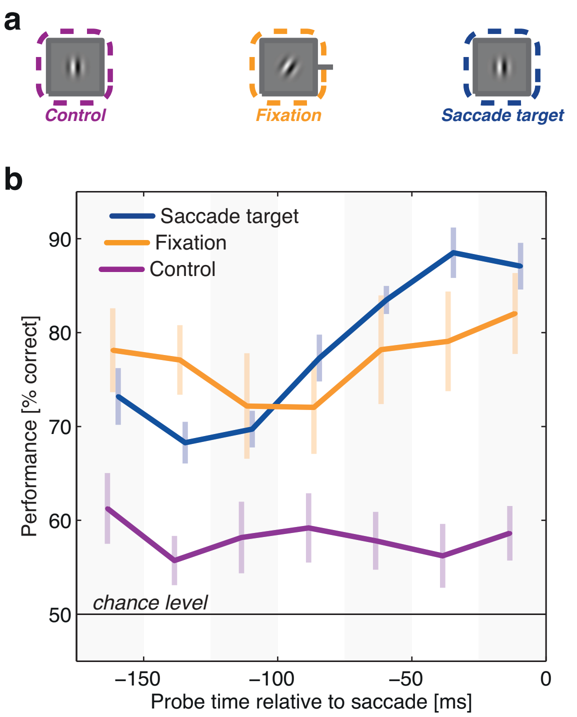


Figure 5. Predictive remapping of attention to the fovea. (**a**) Stimulus layout in the single step task. We presented three stimuli, arranged at equal distances in a line. Otherwise the paradigm was identical to that in the double-step task (**Fig. 2a**). Following a movement cue (here, right), subjects quickly made an eye movement to the indicated target and reported the direction of the tilted stimulus regardless of its location. (**b**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are s.e.m.

that location; see **Online Methods**). This effect was most pronounced just before the saccade: taking only trials when observers correctly identified a probe presented in the last 25 ms before the saccade (rather than the whole pre-saccadic period as in the main analysis), the conditional benefit was 28.3±23.0 ms. Thus, an attention shift to the remapped location before the first saccade was associated with a speeded execution of the second saccade, or equivalently, the preprogramming of the second saccade was associated with a deployment of attention to the remapped location before the eyes moved to its first target. A similar speeding of the second saccade was of course also seen for trials where observers successfully identified the target at the pre-saccadic location of the second target (9.9±6.6 ms) but not at all seen contingent on performance at other locations (first target: −10.3±7.1 ms; control location: −29.2±32.7 ms). As previously mentioned, attention must be allocated first to the target before it can be transferred to the remapped location. The remapped location cannot be computed without first localizing its current location.

Although the specificity of these effects is striking and consistent with the remapping of attention to the future location of targets on the retina, we have to rule out two alternative explanations. The benefit at the remapped location may have arisen simply from (1) an attentional spread to locations adjacent to the saccade targets, or (2), a strategic deployment of attention to the cued side of the display. In two separate control experiments, we ruled out both. To test for the spatial extent of attentional benefits around saccade targets, we repeated the double-step experiment but, in addition to testing the saccade target locations as well as the remapped location of the second saccade target, we now also examined visual performance at a new control location, the one adjacent to the first saccade target that was not the target of the second saccade. If attentional benefits extend around saccade targets, this control location should also show a change in performance across time, because it is next to the first saccade goal. The results demonstrate that it did not. Performance at the first saccade target increased strongly across time (**Fig. 3**; see **Supplementary Fig. 3** for a significance test), starting more than 150 ms before the first saccade, while at the adjacent location controlling for attentional spread, it remained consistently low across that whole interval. The other results replicated those of the first experiment: Performance at the second saccade target location also showed a strong increase (lower panel of **Fig. 3**); and at the remapped location of the second target, we again found a significant performance increase now occurring about 100 ms before the first saccade is executed.

To also exclude the possibility that the local performance increase at the remapped location resulted from a strategical deployment of attention to the pre-cued side of the display, we ran a second control experiment. In this single-cue version of the double-step experiment (**Fig. 4a**), a central cue indicated the target of the first saccade (any of the six locations in the display) while the second target was always the next location in clockwise direction. Otherwise it was identical to the control experiment described above. Again, performance at the first saccade target increased strongly across time (**Fig. 4b**; see **Supplementary Fig. 4** for a significance test), starting some 150 ms before the first saccade, while at the adjacent location controlling for attentional spread, it remained constantly low throughout that whole period. Performance at the second saccade target location also showed a strong increase (lower panel of **Fig. 4b**). At the remapped location of the second target, we again find a significant performance increase now occurring just 50 ms before the first saccade is executed. The spatiotemporal specificity of this effect shows that it is not a result of attentional spread around the saccade target locations. Moreover, because probe locations were balanced around the saccade targets and because the movement cue pointed nowhere near the remapped location, our results can neither be explained by strategical or cue-based deployment of attention, which in any case may occur only early during the preparation of a saccade[6].

In our first three experiments, we showed that before a saccade, attention to a second saccade target is updated in a retinotopic frame of reference. Using the same general paradigm, we next studied the dynamics of attention at the remapped location for a single saccade target: this remapped location is at (or near) the fovea[22], where the target will land after the saccade. Although this situation is maximally ecologically valid (the fovea is the future retinotopic location of every imminent saccade target), it has so far remained untested in neurophysiological studies of remapping. Probing attention at the fovea is difficult, because the presentation of a probe stimulus at the fovea is likely to interfere with the preparation of an eye movement. Using constantly flickering stimuli, our paradigm avoids this issue by masking the transient caused by the probe (**Supplementary Figs. 2–5a,b**). The display contained three horizontally aligned and equally spaced object locations (**Fig. 5a**): Fixation, saccade target (denoted by a line pointing away from fixation), and a control location at the opposite side. We plotted the average performance of nine observers as a function of probe time before the saccade (**Fig. 5b**; see **Supplementary Fig. 5** for a significance test). Performance strongly increased at the saccade target as the eye movement neared. Although performance was always very high at fixation, allowing for less variation across time, it showed the same time course as the benefit for the remapped location in the double-step task, with a continuous increase starting around 75 ms before the saccade. We observed no variation of performance at the control location, again excluding the possibility of a nonspecific presaccadic performance increase.

DISCUSSION

We studied the functional correlates of predictive remapping of targets of saccadic eye movements[16]. Using a sensitive perceptual probe, we assessed the dynamics of spatial attention prior to a saccade without interrupting saccade programming. The probe revealed a robust increase in visual performance at the remapped, future retinal locations of a sequence of movement goals, occurring less than 100 ms before the eye started moving. This benefit was short-lived and spatially constrained to the remapped locations and thus explained by a local attentional facilitation (rather than other well-established changes in visual performance such as perceptual learning[23], lateral or temporal facilitation[24,25]). Moreover, it did not result from a general spread of attention deployed to the saccade targets themselves. In fact, the perceptual benefit at the remapped location was associated with a decrease of saccade latencies to subsequent targets, emphasizing the functional consequences of remapping of attention.

Predictive remapping has often been associated with phenomenal, visual stability across saccades[4,13,17,26]. Although the proposal that remapping helps maintain feature information in world-centered coordinates[19] has been challenged recently[13,27], our data suggest that pre-saccadic shifts of activations that index only the locations of attended targets may be sufficient for visual stability. In fact, our data provide immediate behavioral evidence for the recent proposal that these shifting attentional pointers are the essence of trans-saccadic remapping[13], providing an efficient and sparse mechanism to keep tracks of relevant locations in space as the eyes explore the visual scene[4]. Based on efference copy (or corollary discharge) of the upcoming saccade[22,28,29], neurons in the retinotopic areas controlling saccades and attention pre-activate in anticipation of a soon-to-arrive stimulus[14,15]. This activation projects to the corresponding locations in lower level visual areas[30,31], alerting those parts of the retinotopic visual cortex that will be analyzing targets of interest after the saccade. The results presented here reveal two functional consequences of the predictive remapping process, the attentional benefits at the remapped location just prior to the saccade (subserving attentional facilitation of world locations, once the saccade has landed[18,32]), and preprogramming of future action.

Supplementary information contains four Supplementary Figures.

Acknowledgements This work was supported by the 7th Framework Program of the European Commission (Marie Curie International Outgoing Fellowship 235625 awarded to M.R.), by Deutsche Forschungsgemeinschaft (GRK 1091, as a fellowship to D.J.), and by a Chaire d'Excellence grant to P.C. We thank C. Buß for help with data acquisition.

Author Contributions M.R., D.J., H.D., and P.C. designed the experiments. M.R. and D.J. conducted the experiments and analyzed the data. M.R. and P.C. wrote the manuscript. P.C. and H.D. supervised the project. All authors discussed the results and commented on the manuscript.

REFERENCES

1. Castet, E., Jeanjean, S. & Masson, G.S. Motion perception of saccade-induced retinal translation *Proc. Natl. Acad. Sci. U.S.A.* **99,** 15159–15163 (2002).

2. Mack, A. & Rock, I. *Inattentional blindness* (Cambridge, MA: MIT Press, 1998).

3. O'Regan, J.K., Rensink, R.A. & Clark, J.J. Change-blindness as a result of 'mudsplashes'. *Nature* **398**, 34, 1999.

4. Wurtz, R.H. Neuronal mechanisms of visual stability. *Vision Res.* **48**, 2070–2089, 2008.

5. Deubel, H. The time course of presaccadic attention shifts. *Psychol. Res.* **72**, 630–640, 2008.

6. Montagnini, A. & Castet, E. Spatiotemporal dynamics of visual attention during saccade preparation: Independence and coupling between attention and movement planning. *J. Vis.* **7**(14):8, 1–16, 2007.

7. Deubel, H. & Schneider, W.X. Saccade target selection and object recognition: Evidence for a common attentional mechanism. *Vision Res.* **36**, 1827–1837, 1996.

8. Kowler, E., Anderson, E.Dosher, B. & Blaser, E. The role of attention in programming saccades. *Vision Res.* **35**, 1897–1916, 1995.

9. Baldauf, D. & Deubel, H. Properties of attentional selection during the preparation of sequential saccades. *Exp. Brain Res.* **184**, 411–425, 2008.

10. Gersch, T.M., Schnitzer, B.S., Sanghvi, P.S., Dosher, B. & Kowler, E. Attentional enhancement along the path of a sequence of saccades. *Visual Cogn.* **14**, 104–107, 2006.

11. Godijn, R. & Theeuwes, J. Parallel allocation of attention prior to the execution of saccade sequences. *J. Exp. Psychol. Hum. Percept. Perform.* **29**, 882–896, 2003.

12. Awh, E., Armstrong, K.M. & Moore, T. Visual and oculomotor selection: links, causes and implications for spatial attention. *Trends Cogn. Sci.* **10**, 124–130, 2006.

13. Cavanagh, P., Hunt, A. A., Afraz, A. & Rolfs, M. Visual stability based on remapping of attention pointers. *Trends Cogn. Sci.* **14**, 147–153, 2010.

14. Duhamel, J.-R., Colby, C.L. & Goldberg, M.E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* **255**, 90–92, 1992.

15. Sommer, M.A. & Wurtz, R.H. Influence of the thalamus on spatial visual processing in frontal cortex. *Nature* **444**, 374–377, 2006.

16. Gottlieb, J.P., Kusunoki, M. & Goldberg, M.E. The representation of visual salience in monkey parietal cortex. *Nature* **391**, 481–484, 1998.

17. Berman, R. & Colby, C.L. Attention and active vision. *Vision Res.* **49**, 1233–1248, 2009.

18. Mathôt, S. & Theeuwes, J. Evidence for the predictive remapping of visual attention. *Exp. Brain Res.* **200**, 117–122, 2010.

19. Melcher, D. Predictive re-mapping of visual features precedes saccadic eye movements. *Nat. Neurosci.* **10**, 903–907, 2007.

20. Becker, W. & Jürgens, R. An analysis of the saccadic system by means of double step stimuli. *Vision Res.* **19**, 967–983, 1979.

21. Hallett, P.E. & Lightstone, A.D. Saccadic eye movements to flashed targets. *Vision Res.* **16**, 107–114, 1976.

22. Collins, T., Rolfs, M., Deubel, H. & Cavanagh, P. Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *J. Vis.* **9**(5):29, 1–9, 2009.

23. Karni, A. & Sagi, D. Where practice makes perfect in texture discrimination: Evidence for primary visual-cortex plasticity. *Proc. Natl. Acad. Sci. U.S.A.* **88**, 4966–4970, 1991.

24. Polat, U. & Sagi, D. Lateral interactions between spatial channels: Suppression and facilitation revealed by lateral masking experiments. *Vision Res.* **33**, 993–999, 1993.

25. Solomon, J.A. The effect of spatial cues on visual sensitivity. *Vision Res.* **44**, 1209–1216, 2004.

26. Melcher, D. & Colby, C.L. Trans-saccadic perception. *Trends Cogn. Sci.* **12**, 466–473, 2008.

27. Knapen, T., Rolfs, M., Wexler, M. & Cavanagh, P. The reference frame of the tilt aftereffect. *J. Vis.* **10**(1):8, 1–13, 2010.

28. Guthrie, B.L., Porter, J.D. & Sparks, D.L. Corollary discharge provides accurate eye position information to the oculomotor system. *Science* **221**, 1193–1195, 1983.

29. Sommer, M.A. & Wurtz, R.H. A pathway in primate brain for internal monitoring of movements. *Science* **296**, 1480–1482, 2002.

30. Chen, Y., Martinez-Conde, S., Macknik, S.L., Bereshpolova, Y., Swadlow, H.A. & Alonso, J.M. Task difficulty modulates the activity of specific neuronal populations in primary visual cortex. *Nat. Neurosci.* **11**, 974–982, 2008.

31. Macknik, S.L. & Martinez-Conde, S. Chapter 81: The Role of Feedback in Visual Attention and Awareness. in *The Cognitive Neurosciences* (4th Edition, ed.) 1165–1179 (MIT Press, 2009).

32. Golomb, J.D., Chun, M.M., and Mazer, J.A. The native coordinate system of spatial attention is retinotopic. *J. Neurosci.* **28**, 10654–10662, 2008.

ONLINE METHODS

Participants. Nine observers (age 19-32, 2 female, 7 right-eye dominant, 7 right-handed, 2 authors) were tested in Paris for the two main experiments. Nine observers (age 22-28, 2 female, all right-eye dominant, 8 right-handed, 1 author) were tested in Munich for the two double-step control experiments (7 in the single-cue and 6 in the two-cue control). Observers had normal or corrected-to-normal vision and gave informed consent before study participation. The experiments were conducted in accordance with the Declaration of Helsinki.

Setup. Observers sat in a silent and dimly lit room with the head positioned on a chin rest. Stimuli were presented at 63 cm distance on a 22" Sony GDM-F520 screen (1050x1400 pixels, 100 Hz vertical refresh rate). The dominant eye's gaze position was recorded and available online using an EyeLink 2000 Desktop Mount (SR Research, Osgoode, Ontario, Canada). Stimulus presentation and response collection was controlled by an Apple MacPro computer and implemented in MATLAB (MathWorks, Natick, Massachusetts, USA), using standard toolboxes[33-35].

Double-step experiment. During each trial a green fixation dot (0.3x0.3°) was presented at the center of a uniform gray display. Six object locations were highlighted by green square outlines (1.5 x 1.5°) that were arranged at 5° distance of central fixation to form the corners of a regular hexagon. In each of these boxes, a flickering stream of stimuli was presented, alternating between vertical Gabor patches (2.5 cpd, 100% contrast, random phase on each presentation) and white noise, each presented for 20 ms. After a normally distributed random interval (*M* = 1000 ms, *SD* = 300 ms, cutoff at 3.3 *SD*), a saccade cue appeared consisting of two lines (0.2° long, one left or right, one up or down) pointing away from the fixation dot. Participants performed this saccade task as quickly and accurately as possible. Fifty to 400 ms after the onset of the saccade cue, one of the Gabors changed orientation. After this probe presentation, all Gabor patches disappeared and noise patches flickered on and off at 25 Hz. After finishing the saccade task, participants reported by a button press whether the probe was tilted clockwise or counterclockwise, regardless of its location (i.e., we never asked for the probe location itself). In each trial, the probe appeared randomly at either the first saccade goal, the second saccade goal, the remapped location of the second saccade goal (left or right to the second saccade goal) or at an irrelevant location (same distance from the first saccade goal as remapped location, but in the other direction). If participants failed to look at both target locations within 1500 ms, a feedback was given and the trial was repeated later in the block. No feedback was given for the perceptual task.

Participants ran a minimum of 3000 trials in six one-hour sessions. Before each session we obtained three 82% orientation discrimination thresholds for probe patches presented in the upper (25.1±8.8°; *M*±*SD* of tilt at threshold, across participants), middle (16.7±5.3°) and lower (25.0±6.8°) parts of the visual field using interleaved QUEST staircases[36] in the same task. Probes were presented only at the saccade target locations and in a time window of 150-200 ms after saccade cue onset. Auditory feedback on performance in the perceptual task was provided.

Double-step control experiments. Designed to control for attentional spread from saccade targets as an explanation of our remapping effect, both the two-cue and the single-cue control experiments were identical to the double step experiment except for the following differences. Stimuli were presented at 70 cm distance on a 22" Lacie Electron 22 Blue screen (1024x1280 pixels, 85 Hz vertical refresh rate) and eye movements were recorded using an EyeLink 1000 tower mount. Probes were presented either at the first saccade target, the second saccade target, the remapped location of the second target (next to it in clockwise direction) or at a control location, the location adjacent to the first saccade target in counter-clockwise direction. Due to the different refresh rate, stimuli in the flickering streams changed at 21.5 Hz; hence, the probe duration was 23.5 ms. In addition, in the single-cue control, a single cue indicated the first saccade goal (any of the six stimulus locations), the second saccade goal was always the next target in clockwise direction.

Participants ran a minimum of 1920 trials in four one-hour sessions in the single-cue control and a minimum of 3000 trials in six one-hour sessions in the two-cue control. In the the two-cue control, orientation discrimination thresholds for probe patches presented in the upper, middle, and lower parts of the visual field were 14.6±5.4°, 13.5±5.1°, 14.5±5.5°, respectively. In the single-cue control, separate orientation discrimination thresholds were obtained for the first and the second saccade target and for each of them separately for the upper (12.5±7.5° at first and 18.0±9.5° at second saccade target), the middle (11.9±3.7° at first and 23.2±5.4° at second target), and the lower (8.0±2.1° at first and 19.3±5.9° at second target) visual field. Discrimination thresholds obtained for the first and second saccade targets were also used for the control location (adjacent to first saccade target) and the remapped location (adjacent to second saccade target), respectively.

Single-step experiment. The single step task was different only in the following ways. Three object locations were highlighted, one at the center of the screen (fixated at trial start) and two at an horizontal distance of 6°. The saccade cue was a 0.5° line pointing away from either the left or the right side of the central square, denoting the saccade target. Failure to look at the target within 1000 ms triggered a feedback and the trial was repeated later in the block.

Participants ran a minimum of 2000 trials in four one-hour sessions. In the pre-test, two separate orientation discrimination thresholds were obtained, one for probes at fixation (17.0±5.7°), one for the saccade target (13.3±7.6°). Probes at fixation were presented 150-200 ms before saccade cue onset, while this location was still attended.

Data pre-processing. Saccade detection was based on a velocity-based algorithm[37]. Response saccades were defined as the first saccade that left a circular fixation region and landed inside a target-centered circular region (radii of 2°). We rejected trials with blinks, no response saccades starting within 100 to 400 ms after saccade cue onset, saccades larger than 1° before a response saccade, or saccades to the remapped location (circular region with radius of 2°) within 500 ms after the response saccades. We included a total of 23318 trials (or 86.4%) in the double-step experiment, a total of 10532 trials (or 78.4%) in the double-step control experiment, and a total of 15409 trials (or 85.6%) in the single-step experiment in data analyses.

Data analysis. We used a permutation method[38] to generate confidence intervals testing whether performance changed across time before a saccade (**Figs. 2b**, **3b**, **4b**, and **5b**). The method is based on the idea that temporally invariant variables are indistinguishable from their random permutations across time. In an observer's original data set, each response (correct or incorrect) is associated with a particular probe time. We randomly reassigned responses to the probe times (without replacement) for each observer separately and, subsequently, computed an average surrogate time course of performance as for the original data. We repeated that 1,000 times and computed means and 95% confidence intervals from these surrogate samples. If the average performance differs from the time course of the original data, we can be confident that performance varies as a function of time. The results of these analyses are shown in **Supplementary Figs. 2**, **3**, **4**, and **5**.

Estimating latency benefits contingent on high performance at a given location. We know (a), the distribution of second saccade latencies for trials where an observer's perceptual report of a probe presented at a given location was correct, f_c, or incorrect, f_i. Neglecting lapses, f_i is composed only of trials with low perceptual performance (incorrect guesses), whereas f_c is composed of trials with high perceptual performance, $f_{c|high}$ and correct guesses $f_{c|low}$. We wish to decompose f_c. To do this, we first fitted an ex-Gaussian distribution $F_i(t;\ \mu_i,\ \sigma_i,\ \tau_i)$ to f_i. Because, by definition, $F_{c|low}(t;\ \mu_{c|low},\ \sigma_{c|low},\ \tau_{c|low}) = F_i(t;\ \mu_i,\ \sigma_i,\ \tau_i)$, we fitted f_c with a mixture of of $p\ F_i(t;\ \mu_i,\ \sigma_i,\ \tau_i)$ and a second ex-Gaussian $(1-p)\ F_{c|high}(t;\ \mu_{c|high},\ \sigma_{c|high},\ \tau_{c|high})$, where $p = p_i/p_c$, i.e., the proportion of correct trials that were guesses. The reported latency differences between high and low performance at a given location represent the difference between the means of the distributions, $(\mu_{c|low} + \tau_{c|low})-(\mu_{c|high} + \tau_{c|high})$. Because of relatively low performance, few trials were available for fitting $F_{c|high}$ for the control location and the procedure did not converge for four observers. Results for that condition were computed over the remaining five subjects. Note that the four remaining observers showed slightly longer latencies for correct trials at the control location, in agreement with the average data. These estimates imply that attending to a stimulus and correct performance go hand in hand, which is certainly not the case. That is, even if the probe location was attended, presumably decreasing saccade latency, observers were correct only on a proportion of trials. And, conversely, if the probe location was not attended (predicting longer saccade latencies), subjects may still have seen and correctly reported the probe. Therefore, this procedure results in a conservative estimate of the real latency difference between high and low performance trials.

33. Brainard, D.H. The Psychophysics Toolbox. *Spat. Vis.* **10**, 433–436, 1997.

34. Pelli, D.G. The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spat. Vis.* **10**, 347–442, 1997.

35. Cornelissen, F.W., Peters, E.M. & Palmer, J. The Eyelink Toolbox: Eye tracking with MATLAB and the Psychophysics Toolbox. *Behav. Res. Meth. Inst. Comp.* **34**, 613–617, 2002.

36. Watson, A.B. & Pelli, D.G. QUEST: A Bayesian adaptive psychometric method. *Percept. Psychophys.* **33**, 113–120, 1983.

37. Engbert, R. & Mergenthaler, K. Microsaccades are triggered by low retinal image slip. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 7192–7197, 2006.

38. Rolfs, M., Engbert, R. & Kliegl, R. Crossmodal coupling of oculomotor control and spatial attention in vision and audition. *Exp. Brain Res.* **166**, 427–439, 2005.

Supplementary Information

Inventory:

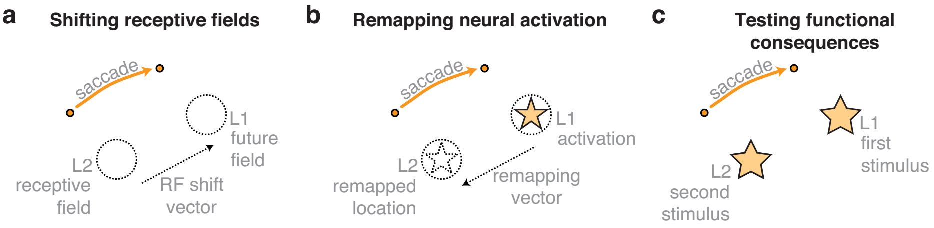
Supplementary Figure 1. This figure illustrates the appropriate procedure for testing how pre-saccadic remapping supports the updating of attended target locations.

Supplementary Figure 2. For the double-step experiment, this figure depicts the statistical tests of performance changes across time (panel a) and shows that the metrics and latency of the first saccade are largely independent of probe location and timing (panels b and c).

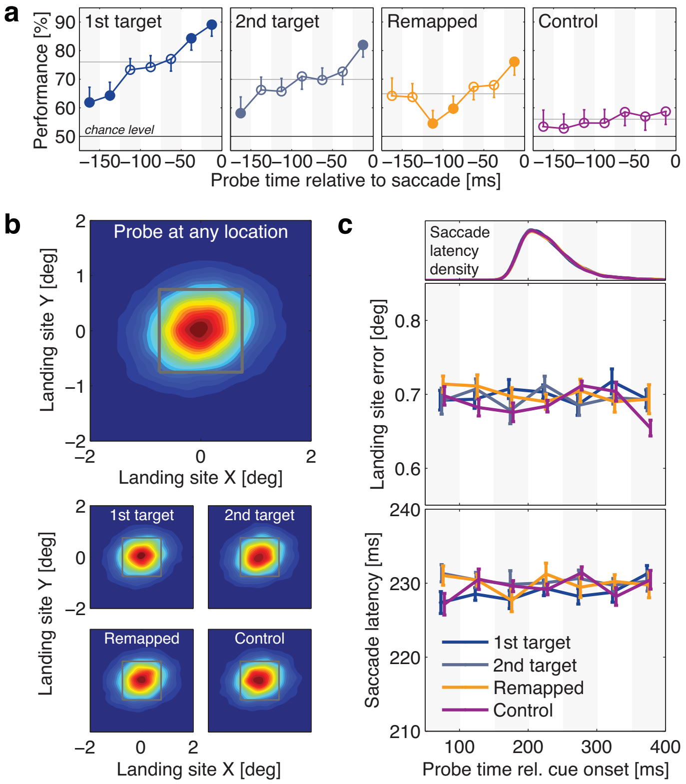
Supplementary Figure 3. For the two-cue double-step control experiment, this figure depicts the statistical tests of performance changes across time (panel a) and shows that the metrics and latency of the first saccade are largely independent of probe location and timing (panels b and c).

Supplementary Figure 4. For the single-cue double-step control experiment, this figure depicts the statistical tests of performance changes across time (panel a) and shows that the metrics and latency of the first saccade are largely independent of probe location and timing (panels b and c).

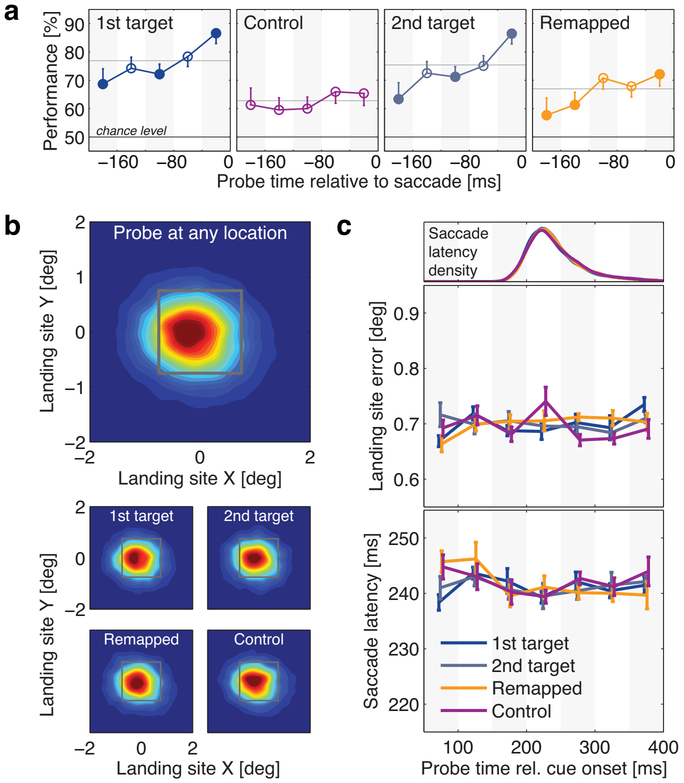
Supplementary Figure 5. For the single-step experiment, this figure depicts the statistical tests of performance changes across time (panel a) and shows that the metrics and latency of the saccade are largely independent of probe location and timing (panels b and c).



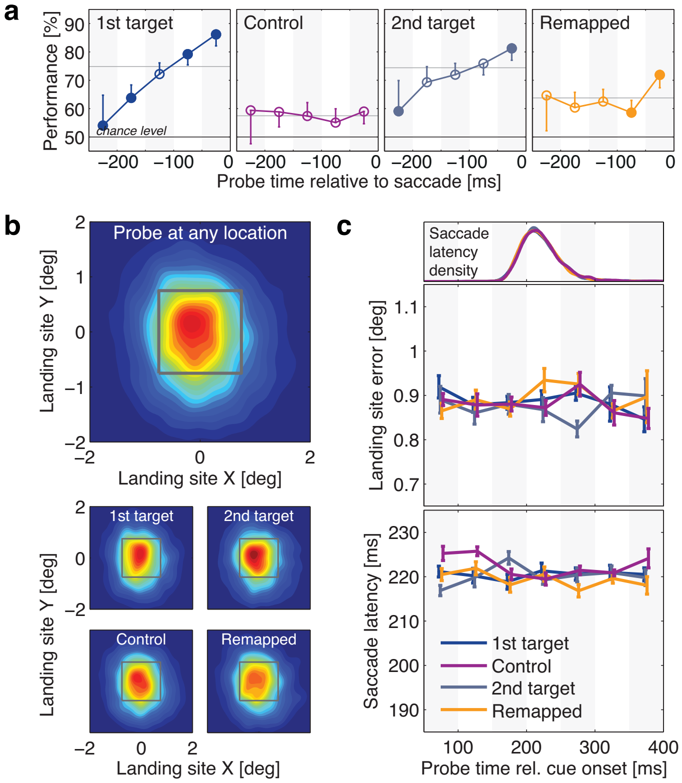
Supplementary Figure 1. Testing the functional consequences of pre-saccadic remapping. Pre-saccadic remapping[14-16] can be described either as shifting receptive fields (RFs) or the remapping of neural activation. These are functionally equivalent even though the shifts appear to be in opposite directions. Importantly, the direction of shift for the RF description has led in some cases to an inappropriate choice of stimulus locations for behavioral tests. (**a**) Shifting RFs. Just before a saccade, cells with a classical RF at a particular location in space, L2, become receptive to stimulation at the "future field" location, L1, which is shifted away from the classical RF in the *same* direction as the saccade vector (RF shift vector). (**b**) Remapping neural activation. In these remapping studies, the link from stimulus location to active cell location therefore shifts in the opposite direction. Specifically, a briefly presented attended target at L1 activates cells that encode that target's expected retinal location after the saccades. The RF shift in **a** is a shift of an explanatory construct, whereas the activation shift in **b** is the observable effect. It is what really happens to cell activity and the remapping vector for this activation shift *opposes* the saccade vector. This is the direction consistent with efference copy and the direction that allows target locations to be appropriately updated across saccades, because these sweep across the retina in the direction opposite the saccade. (**c**) To test remapping of an attended target, the probe needs to be at the location shifted opposite to the saccade. In our study, we measured the remapping of attention for an attended peripheral stimulus (the 2nd saccade target; here at L1) to its retinotopic location after the saccade (here, L2). If the test is presented at a time when activation is remapped to that location, attentional benefits are observed. The two previous studies that addressed behavioral correlates of pre-saccadic remapping[18,19] used the opposite stimulus order, first presenting a cue[18] or an adaptation stimulus[19] at a location equivalent to L2 in panel c, then a probe at L1. This reversed remapping shift, L2→L1 follows the direction of the shifting receptive fields as in panel a but not the direction of remapped activation that is critical to the updating function of remapping. Functional remapping occurs in their experiments for both stimulus locations. Their first stimuli, the adaptation or cue at L2 in panel **c**, gets remapped, but back from L2 opposite the direction to L1, onto locations where nothing at all is presented. It also occurs from their second stimulus, the probe, at location L1 in panel **c**, that will remap activation back to the first stimulus location L1 where the cue or adaptation has already been presented and removed. The direction of activation transfer is opposite to the direction of influence they intended to test and described in their articles but in both cases, they report significant effects. So the reversed remapping from probe to cued or adapted location appears to carry benefits and was the appropriate description of the results of these two papers. Thus, even though the remapping direction is reversed in these articles, they may have found an interesting contribution of remapping onto already existing activity and certainly their results were intriguing and significant. They did not however, study the functional remapping phenomenon in its actual context of supporting the updating of an attended target location as we have here.



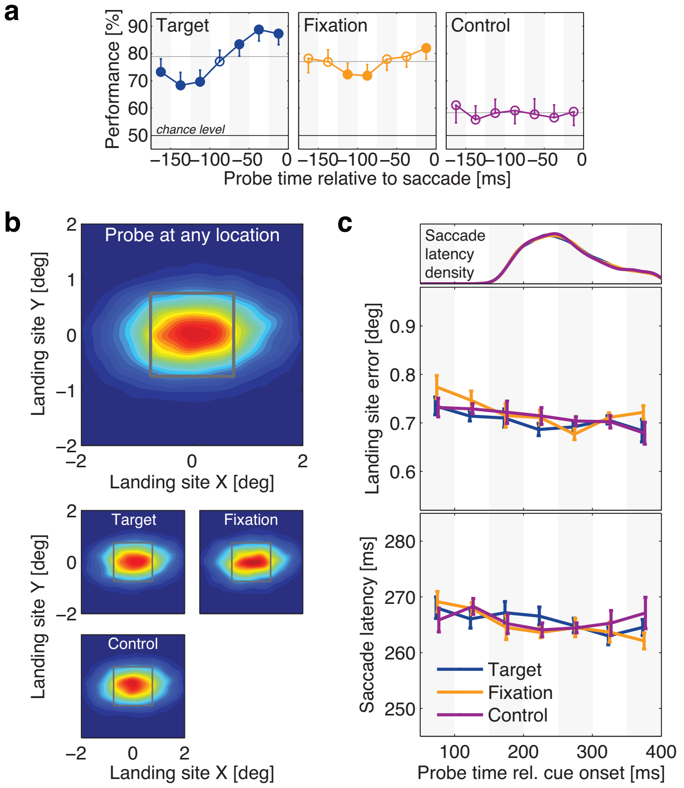
Supplementary Figure 2. Supplementary analyses for the double-step experiment, providing significance tests for the performance changes across time and showing that the metrics and latency of the first saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see Experimental Procedures). Filled symbols highlight significant deviations. (**b**) Landing sites of the first saccade relative to the first saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all conditions collapsed, the lower four panels show data for each probe location separately. (**c**) Mean landing site error of the first saccade (Euclidian distance from the first target's center; upper panel) and its latency (lower panel) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are standard errors of the mean. The middle panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 230±24 ms (*M*±*SD*, across observers) for first saccades and 226±29 ms for second saccades.



Supplementary Figure 3. Supplementary analyses for the two-cue double-step control experiment, providing significance tests for the performance changes across time and showing that the metrics and latency of the first saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see Experimental Procedures). Filled symbols highlight significant deviations. (**b**) Landing sites of the first saccade relative to the first saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all conditions collapsed, the lower four panels show data for each probe location separately. (**c**) Mean landing site error of the first saccade (Euclidian distance from the first target's center; upper panel) and its latency (lower panel) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are standard errors of the mean. The middle panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 242±15 ms (*M*±*SD*, across observers) for first saccades and 240±32 ms for second saccades.



Supplementary Figure 4. Supplementary analyses for the two-cue double-step control experiment, providing significance tests for the performance changes across time and showing that the metrics and latency of the first saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see Experimental Procedures). Filled symbols highlight significant deviations. (**b**) Landing sites of the first saccade relative to the first saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all conditions collapsed, the lower four panels show data for each probe location separately. (**c**) Mean landing site error of the first saccade (Euclidian distance from the first target's center; upper panel) and its latency (lower panel) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are standard errors of the mean. The middle panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 221±10 ms (*M*±*SD*, across observers) for first saccades and 222±34 ms for second saccades.



Supplementary Figure 5. Supplementary analyses for the single-step experiment, providing significance tests for the performance changes across time and showing that the metrics and latency of the saccade are largely independent of probe location and timing. (**a**) Performance at the probed locations as a function of probe offset relative to the saccade. Error bars are 95% confidence intervals testing whether performance differed from the average (gray lines) (see Experimental Procedures). Filled symbols highlight significant deviations. (**b**) Landing sites of the saccade relative to the saccade target (gray outline), plotted in 2D-density plots. The upper panel shows data from all probe locations collapsed, the lower three panels show data for each probe location separately. (**c**) Mean landing site error of the saccade (Euclidian distance from the first target's center; upper panel) and its latency (lower panel) as a function of probe location (different lines) and probe time relative to the onset of the saccade cue. Error bars are standard errors of the mean. The middle panel shows the distribution of saccade onsets relative to the onset of the cue (i.e., saccade latencies). The four distributions overlap almost completely. The average overall saccade latency was 265±35 ms (*M*±*SD*, across observers).

PUBLICATIONS

Jonikaitis, D., & Deubel, H. (2011). Independent allocation of attention to eye and hand targets in coordinated eye-hand movements. *Psychological science, 22*, 339-347. (Presented in Chapter 3).

Rolfs, M., Jonikaitis, D., Deubel, H., & Cavanagh, P. (2011). Predictive remapping of attention across eye movements. *Nature Neuroscience, 14*, 252-256. (Presented in Chapter 6)

Jonikaitis, D., Schubert, T., & Deubel, H. (2010). Preparing coordinated eye and hand movements: Dual task costs are not attentional. *Journal of Vision, 10 (14)*, Article 23. (Presented in Chapter 4)

Other two studies (presented in Chapters 2, 5) are either prepared manuscripts or under review.