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A vision to reach for: the interplay between visual perception and visually-guided movements

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"*Vision without action is merely a dream. Action without vision just passes the time. Vision with action can change the world*." **Joel A. Barker**

Abstract

Throughout everyday life we are surrounded by a multitude of stimuli we can look at, reach to, and visually perceive in many different ways. However, we cannot perceive, look at, or reach to all stimuli simultaneously. We have to make a selection to perceive and interact with the world in a useful way. The selection for perception, saccades and reaches is the consequence of activation and competition on specific priority maps. Where we select to perceive influences the selection for action, and vice versa. For example, a movement trajectory is influenced by the presence of a physically salient distractor. Previous research has mainly focused on the interplay between visual perception and eye movements. However, less is known regarding how reaching movements are influenced by visual perception and eye movements. The studies in this thesis were designed to get a better understanding of the mechanism by which visually guided reaching movements are influenced by the motor and sensory component of the visual system.

In the first study, I investigated whether the target selection for saccades and reaches occur independently. I analyzed trajectories of simultaneously performed saccades and reaches. If the target selection for both effectors were independent, I expected to observe no difference in the movement trajectory depending on the other effector's target location. However, I found that movements curved away from the other effector's target location for both reaches and saccades.

Previous research showed that the top-down task set can trigger an active suppression of physically salient distractors during selection for perception and saccades. By actively suppressing the distractor location the attraction of visual perception and saccades can be avoided. It was unclear whether this mechanism also transferred to reaching movement planning. In the second study, I investigated whether the influence of a physically salient distractor on reaching movements is task-dependent. I compared trajectories of reaches towards a target when a physically salient distractor was present between two tasks. In the first task the target had to be searched. In the second task the target was cued. Hence, the target certainty was low in the first task but high in the second task. We hypothesized that only in the second task, when the target certainty was high, the distractor could be actively suppressed during reach planning, avoiding attraction towards the distractor's location. I found reaching movements to curve away from the physically salient distractor in the search-to-reach task but not in the cued reach task.

Stimuli associated with reward influence where we perceive, look and reach. A large body of research has delved into the mechanisms of how reward influences perception and saccades. However, the mechanisms of how reward influences reaching movements is not well understood. In the third study I wanted to clarify two open standing points: (i) is the attraction

of reaches towards reward the result of an association between reward and a color or between reward and reaching to a color? (ii) Is the attraction of reaches towards reward dependent on an initial attraction by physical salience? To this end I designed a task in which a non-physically salient distractor signaled the possibility of earning either low or high reward. I found that reaching movements curved towards the non-salient, reward signaling distractor. Note that reaching towards the reward signal was never necessary nor useful as it would lead to the omission of reward. Furthermore, the attraction by reward was enhanced in short latency reaches.

The results of these studies show that the planning of reaching movements is influenced by the selection for perception and saccades. The interplay between the selection of visual perception and visually-guided action fit within a priority framework where activation on different priority maps is transferred. Under certain circumstances, the transfer of activation results in competition on the movement priority map during movement planning. The competition affects movement parameters and is responsible for the observed interplays between perception and action.

Contents

I Synopsis

1. Introduction

Lucy is sitting behind her desk. Instead of working she looks at her phone every other minute. Yesterday she met someone special and she is hoping that they will reach out. Suddenly, she grabs hold of herself and decides to start working. She wants to move her mouse to wake up the sleeping computer. Yet, when she starts reaching, she catches herself reaching to her phone, makes a correction and grabs the mouse. The trajectory of the reach towards her mouse deviated more towards her phone than the trajectory of Lucy's reach to her mouse before she met the special person. In that way, the trajectory of a movement, be it a hand or eye movement, can reveal aspects of the cognitive process underlying target selection. This example illustrates that where people want to perceive can influence the movement trajectory. Also other movement parameters, such as movement latency, duration, and endpoint location, are likely to be affected by where people want to perceive. On the other hand, where people want to move to can influence where they perceive. Perception, i.e. perceptual performance, is increased at the target location of a movement, even before the movement is initiated. Hence, there is an interplay between perception and action, but why and how do we select a target to perceive or move to in the first place?

Selection for perception and action

The world around us is filled with an abundance of stimuli we can look at, reach to, and process visually in many different ways. Think of Lucy sitting in her office and all the ways she could perceive and interact with objects in her immediate vicinity. For example, she could perceive her desk as a whole or study its legs more closely, she could look at the left or right corner of the desk, and she could put her hand on the desk or grab one side. Evidently, the possibilities to perceive and interact with the world are infinite at any moment. However, we have only two eyes that usually fixate one and the same location, we usually have one dominant hand we use to interact with objects and we are not able to visually perceive every object in the world in detail at the same time. Hence, a selection has to be made in perception and action so that we can properly perceive and interact with the world.

We cannot perceive all aspects of each object in our surroundings at the same time. When Lucy is reading a message on her phone, chances are she will not notice an email notification on her laptop. The visual perceptual system is constrained by resource limitations (Broadbent, 1958). Hence, to enable a fluent and efficient functioning of the perceptual system, the selection of some objects at the expense of others is necessary. To select an object at a location the sensory information is regulated by enhancing the signal corresponding to that location (Carrasco, 2011; Dosher & Lu, 2000). In that way, the processing of visual information at a certain location is prioritized and perceptual performance at that location is increased. The prioritization can be

driven by e.g. saliency, top-down goals, memory, or reward (Failing & Theeuwes, 2018; Theeuwes, 2019). The selection mechanism is often referred to as attentional selection.

Goal-directed actions, such as saccades and reaches, are constrained by physical limitations. Lucy cannot reach to her phone and computer mouse with one hand at the same time. She has to make a choice. Neither can she make a saccade to fixate both locations together. Thus, one target has to be selected to move to in order to interact with the world in a useful way. This is achieved by increasing the activation on an eye or hand movement priority map corresponding to a movement plan or vector to the target location e.g. computer mouse (Cisek & Kalaska, 2010; Zelinsky & Bisley, 2015). When only one location is activated on the map, there is no competition between movement plans. When a movement is initiated at this moment, it would go to the target in an efficient way. However, also another object's location (i.e. distractor, e.g. phone) could be activated on the map. This might be driven by e.g. saliency, memory, or reward. If a movement would be initiated while two locations in close spatial proximity are highly active, the resulting movement vector would be directed in between the two locations. Ideally, a movement is executed when the competition between the two movement plans is resolved. This can be achieved by decreasing the activation at the non-target location relative to the target location. However, when a movement is initiated before competition is resolved, e.g. because of time pressure, it does not mean the movement needs to end up in between the two locations. The competition can also be resolved while a movement is ongoing. If this happens, a movement that first goes into the direction in between the target and the non-target, would eventually end up at the target. The trajectory of this movement would show a deviation towards the non-target relative to a movement that would have been initiated when the competition was resolved. However, the trajectory can also deviate away from the non-target (Moehler & Fiehler, 2014; 2017). This happens when there is a greater inhibition of the non-target location on the movement priority map (McSorley, Haggard, & Walker, 2004; Tipper, Howard, & Houghton, 2000). The over-inhibition shifts the peak activation on the map away from the target in the opposite direction from the non-target. When a movement is initiated at that moment, it will be directed to the opposite side of the target than where the non-target is. In case the over-inhibition is resolved during movement, the movement will eventually end up at the target. Note that the focus lies on movement trajectories; however, competition on the movement priority map can also influence other movement parameters such as latency, duration, and endpoint location (Castiello, 1996; Failing, Nissens, Pearson, Le Pelley, & Theeuwes, 2015; Nissens, Failing, & Theeuwes, 2017).

Selection for visual perception and visually guided movements, such as saccades and reaches, relies on the activation of a location on a visuo-spatial priority map (Cisek & Kalaska, 2010). Correlates of priority maps for visual perception have been found in the intermediate layers of the superior colliculus (SC), the intraparietal cortex (IPC) and the frontal eye fields (FEF; White et

al., 2017; Thompson & Bichot, 2005; Bisley & Goldberg, 2010). Eye movement priority maps have been found in the FEF, the superior colliculus, and LIP that represents space in an egocentric reference frame (Paré & Wurtz, 2001; Snyder et al., 2000). A reaching movement priority map that represents locations relative to the direction of gaze and the position of the arm, is located in the medial intraparietal area (MIP), also known as the parietal reach region (PRR; Buneo, Jarvis, Batista, & Andersen, 2002). Other regions that have been proposed to act as reach priority maps are the anterior intraparietal area and the ventral intraparietal area (Zelinsky & Bisley, 2015). Priority signals can originate from different sources which are assumed to be initiated in different brain regions. Stimulus salience might originate from early visual cortex and saliency maps in the superficial layers of the superior colliculus (Itti & Koch, 2001). The neural origin of top-down influences are not well understood and might not necessarily be traced back to one neural substrate. However, some evidence has suggested that the anterior cingulate and orbitofrontal cortex play a role in top-down instruction-related value-sets (Kennerley, Behrens, & Wallis, 2011).

Two lines of behavioral research show that selection for visual perception and visually guided movements influence each other. First, selecting a saccade or reach target during movement planning influences visual perception by increasing perceptual performance at the target location. Second, the prioritization of a location for visual perception, driven by e.g. saliency, top-down goals, memory, or reward, influences target selection during movement planning resulting in affected movement parameters, such as reach or saccade trajectory, latency, duration and endpoint.

The influence of action on perception

Planning a visually-guided, target-directed action increases visual performance at the target location. This has typically been studied using a dual-task paradigm comprising a visual discrimination task and a movement task (Deubel & Schneider, 1996). The movement task is simply to make a saccade and/or reach as quickly as possible after the movement target is cued. The discrimination task is to detect a briefly presented probe character among 11 distractors. The location of the probe is unknown before its onset, therefore, it is not beneficial to anticipatory prioritize a certain location for visual perception. The probe is detected more often at the movement target location from around 200ms before movement onset. Thus, perceptual performance is increased, i.e. prioritized at the movement target location shortly before movement onset. This has been found for both eye and hand movements (Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011). When an eye and hand movement are planned simultaneously to two separate locations, perceptual performance is increased at both locations (Hanning, Aagten-Murphy, & Deubel, 2018; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011). The obligatory enhancement of visual perception at a

saccade target is often termed as the pre-saccadic shift of attention (Deubel, 2008; Harrison, Mattingley, & Remington, 2012).

The influence of perception on action

The enhancement of visual processing at a location affects the planning of a visually-guided action as is evidenced by changes in the movement trajectory, latency, duration and endpoint, driven by e.g. physical salience, reward, or memory. Visual processing can be enhanced at a location driven by the task at hand, i.e. top-down goals. However, there are other factors such as physical salience, selection history, reward and memory that can lead to an enhanced visual processing of a location that is different from the current top-down goals. These non-top-down related factors are often investigated in visual search tasks where e.g. participants have to report the orientation of a line segment within a square presented among circles. As such, the top-down goal is to enhance visual processing at the location of the square. On some trials, features of one of the circles are different so that visual processing is enhanced at its location independent of the top-down goals, i.e. attentional capture, but driven by other factors (Theeuwes, 2019). Enhancement of visual processing at a non-target, distractor location leads to an increase in the time to find the target. For example, when all but one of the distractor shapes is in the same color, visual processing will be enhanced at the location of the differently colored shape. Because visual processing resources are limited the enhancement at the distractor will go at the expense of visual processing at other locations such as the target. This will result in a delay of the moment at which visual processing is enhanced at the target. Other stimulus features that can attract visual processing independent of the task at hand are an association with reward (Anderson, Laurent, & Yantis, 2011; Failing & Theeuwes, 2017), selection history (Theeuwes, 2019), or memory (e.g. when a location or color needs to be reported after performing the search task; Olivers, Peters, Houtkamp, & Roelfsema, 2011).

Movement planning is affected by where visual processing is enhanced. Saccades and reaches are attracted towards a physically salient distractor when the target has to be searched (Kerzel & Schönhammer, 2013; Moher & Song, 2013; Moher, Anderson, & Song, 2015; Neyedli & Welsh, 2012; Song & Nakayama, 2006; Song & Nakayama, 2008; Van der Stigchel, 2010; Van der Stigchel, Meeter, & Theeuwes, 2006; Welsh, 2011; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999; Wood et al., 2011). For example, the trajectory of reaches towards a target deviate more towards a physically salient compared to non-salient distractor (Howard & Tipper, 1997; Kerzel & Schönhammer, 2013; Tipper, Howard, & Jackson, 1997; Welsh, Elliott, & Weeks, 1999; Welsh & Elliott, 2004; Wood et al., 2011). Saccades more often end up at a distractor that is associated with a high compared to low monetary reward during search (Failing et al., 2015). Also, saccades end up more often at a distractor associated with high compared to low threat during search (Nissens et al., 2017). However, sometimes movements deviate from distractors.

Saccadic trajectory deviates towards a physically salient or reward associated distractor when saccadic latency is short but deviates away from the distractor when saccadic latency is high (Hickey & Zoest, 2012, McSorley, Haggard, & Walker, 2006, 2009; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). Reach trajectories deviate away from physically salient distractors and distractors of which the location has to be remembered (Moehler & Fiehler, 2017). In a variation of the dual task paradigm, where the perceptual and saccade target are cued, saccades curve away from the perceptual target location (Moehler & Fiehler, 2014). Thus, saccades curve away from a location where visual perception is enhanced due to task demands. As mentioned before, distractor stimuli influence movement planning by activating a movement vector on the movement priority map that correspond to their location. If the target and distractor location are both activated when a movement is initiated, the resulting movement will be attracted towards the distractor. If the distractor location has been inhibited, the resulting movement will deviate away from the distractor or will not be affected by the distractor. Together, the enhancement of visual perceptual processing at a location seem to result in the activation of that location on the movement priority map, and, as such, affect movement planning. However, especially regarding reaching movements, the mechanisms by which the enhancement of visual processing affect movement planning is not well understood.

The interplay between visual perception and visually guided movements

The selection of a movement target enhances visual processing at that location. And the enhancement of visual processing at a location affects the selection of a movement target by activating that location on the movement priority map. Several theories have been proposed to explain the interplay between visual perception and visually guided movements. (i) According to the visual attention model (VAM; Schneider, 1995), visual attention is the unitary mechanism behind selection-for-perception and selection-for-action. Enhancing visual processing at a location and planning goal-directed action both require a shift of attention to the targeted location. VAM assumes that both selection processes rely on one and the same capacity-limited attentional resource, i.e. both processes are firmly coupled. Allocating attention to a location facilitates both perceptual performance and the planning of a goal-directed movement to that location. Hence, planning of a goal-directed movement to a location will lead to the enhancement of visual processing at that location. And enhancing visual processing at a location will facilitate action planning at that location. (ii) The premotor theory of attention (Rizzolatti, Riggio, Dascola, & Umiltá, 1987) assumes that the enhancement of visual processing at a location is a direct and necessary consequence of movement planning, i.e. a movement has to be planned (but not necessarily executed) to a location in order to shift covert attention to that location. As the VAM, the premotor theory assumes a strong interplay between visual perception and visually guided

movements. However, where the VAM assumes that visual attention is necessary for movement planning, the premotor theory assumes that movement planning is necessary for visual attention.

(iii) An alternative explanation is given in terms of priority maps (Cisek & Kalaska, 2010; Todd & Manaligod, 2018; Zelinsky & Bisley, 2015). As mentioned before, selection for visual perception and visually guided movements are driven by the activation on different priority maps, i.e. neural representations of visual space. Priority at a location can be enhanced driven by physical salience, value, selection history, task instructions, etc. (Todd & Manaligod, 2018). The priority map for visual perception is thought to guide the allocation of covert attention, influence the allocation of overt attention, i.e. eye movements (Zelinsky & Bisley, 2015), and influence hand movements. This is a consequence of connections between the priority maps for visual perception, eye movements and reaching movements. To drive this point further, a location that is activated on the visual perception priority map driven by e.g. saliency, will also be activated on the eye movement priority map and vice versa. For example, if a movement target and a salient distractor are presented, both locations will be activated on the visual perception priority map that in turn influences the activation on the eye movement priority map. During movement planning, competition between the target and distractor location will be resolved by inhibiting the distractor location and enhancing the target location. The competition will influence the parameters such as the trajectory of the upcoming movement. The high activation of the target location on the movement priority map right before movement execution will influence the activation on the visual perception priority map. This spread of activation results in enhanced visual performance at the target location of the upcoming movement.

Summary of rationale and objectives

The studies in this thesis were designed to get a better understanding of the mechanisms of the interplay between perception and visually guided reaching movements. Previous research mainly focused on the interplay between visual perception and eye movements, i.e. overt and covert attention. In general, factors, such as physical salience, memory, reward, selection history, etc., that attract visual perceptual resources also influence eye movement planning. It almost seems as if selection for visual perception and visually guided eye movements are driven by the same mechanism (VAM) or that the first is the consequence of the latter (premotor theory of attention). Either way, the motor and sensory component of the visual system are very strongly coupled. If the brain wants to optimize where to fixate, eye movements should be attracted to the location where visual perception is enhanced in order to bring that location into the fovea. However, the same rationale does not necessarily transfer to goal directed reaching movements. For example, to pick up a rose, one possibly wants to enhance visual perception at a potential thorn location. It would even be beneficial to fixate that location. However, it would not be beneficial to reach toward that location. Reaching to a location where visual perception is

enhanced is not always useful. Nonetheless, previous research has shown that factors that attract visual perception also influence reaching movement planning. The studies in this thesis were designed to get a better understanding of the mechanism by which visually guided reaching movements are influenced by visual perception and eye movement planning.

The first study was designed to investigate the coupling between eye and reaching movement planning. Does the target selection for the eye and hand operate totally independently? Previous studies showed that visual perception is enhanced at the target location of an eye and reaching movements (Deubel, 2008; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011), even when the saccade and reach target are two separate locations. This has been seen as evidence for a separate selection process for saccades and reaching. The first study was designed to explore to what extent both selection processes are separate. To this end I investigated the trajectory and end point location of saccades and reaches that were performed simultaneously to the same or separate locations. If both selections mechanisms would be totally independent, the reach parameters should not be affected by whether a saccade is performed to the same or different location and vice versa.

The second study was designed to investigate whether the influence of physically salient stimuli on reaching movement planning is task-dependent. Previous research showed that attraction of visual perceptual resources and eye movements towards a physically salient distractor can be avoided under certain top-down task sets (Lamy & Egeth, 2003; Lamy, Leber & Egeth, 2004; Theeuwes & Burger, 1998). An active suppression of the distractor can take place shortly after the distractor is presented avoiding attraction. Examples of task properties that define the top-down task set are time of cueing, and expectancies, relevancy and feature overlap of the target and distractor. However, it is unknown if active suppression also takes place in the planning of reaching movements. The second study was designed to explore if attraction of a physically salient distractor can be avoided depending on the top-down task set, i.e. if it is task-dependent. The certainty of where the target would be presented was manipulated. Reach trajectories towards the target were analyzed. We hypothesized that active suppression of the distractor would take place in reach planning only when the certainty of the target location was high. When the certainty of the target location was low, we expected reaching movements to be attracted towards the physically salient distractor. When the certainty of the target was high, we expected reaching movements to deviate away from the physically salient distractor.

The third study was designed to investigate the influence of reward on reaching movements. Previous studies showed that a stimulus associated with reward can attract reaching movement trajectories (Chapman, Gallivan, Wong, Wispinski, & Enns, 2015; Moher, Anderson, & Song, 2015; Wirth, Dignath, Pfister, Kunde & Eder, 2016). However, from these studies it was unclear (i) whether an initial attraction by physical salience is necessary for reward to attract reaches, or

(ii) whether previously rewarding the act of reaching towards the reward associated stimulus is necessary. In the third study we investigated whether a non-physically salient distractor that signaled reward influences reaching movements. Moreover, reaching towards the reward distractor was never necessary nor useful. We analyzed whether the trajectory of a reach towards a target was influenced by the presence of a non-salient distractor that signaled the possibility of earning high or low reward.

2. Summary of Published, Peer-Reviewed Articles

Study 1: Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements

People naturally look where they reach. Eye and hand movements are highly coordinated in time and space. In natural tasks, people coordinate eye and hand movements in a seemingly obligatory fashion (Pelz, Hayhoe, & Loeber, 2001). Also on the level of target selection there is a tight coupling between eye and hand movements (Gorbet & Sergio, 2009; Moher & Song, 2016; Donkelaar, 1997; see also Gopal & Murthy, 2015). In the brain there is some overlap in activation during the planning of eye and hand movements. Neurophysiological and imaging studies showed overlapping brain activation (Battaglia-Mayer, Babicola, & Satta, 2016; Beurze, de Lange, Toni, & Medendorp, 2009; Gallivan, McLean, Smith, & Culham, 2011; Levy, Schluppeck, Heeger, & Glimcher, 2007; Magri, Fabbri, Caramazza, & Lingnau, 2019), and distinct activation (Gallivan et al., 2011; Magri et al., 2019; Tosoni, Galati, Romani, & Corbetta, 2008; Van Der Werf, Jensen, Fries, & Medendorp, 2010) during the planning of saccades and reaches.

Behavioral research that describes the planning of eye and hand movements as an attentional selection mechanism found conflicting results (Hanning et al., 2018; Jonikaitis & Deubel, 2011; Khan, Song, & McPeek, 2011; Malienko, Harrar, & Khan, 2018). In a dual-task study, participants had to perform a saccade, reach, or simultaneously saccade and reach to cued locations while discriminating a target probe before movement onset. Jonikaitis and Deubel (2011) found that discrimination performance was not deteriorated at the target location of simultaneous, but spatially separate saccades and reaches compared to a single saccade or reach. Perceptual performance can be enhanced independently to eye and hand target locations without costs. They argued that this is evidence for separate attentional resources and separate attentional selection mechanisms for the eye and hand. In contrast, Khan, Song, and McPeek (2011) found that discrimination performance was not enhanced at the target location of simultaneous, and spatially overlapping saccades and reaches compared to a single saccade or reach. This shows that there was no additional enhancement in perceptual performance by performing a saccade and reach to the same location compared to only one. They argued that this is evidence for an overlapping attentional resource for eye and hand movements.

Study 1 (Nissens & Fiehler, 2018) was designed to investigate the extent to which the target selection for eye and hand movements influence each other. Participants performed a simultaneous eye and hand movements to the same or separate locations. Figure 1 illustrates the sequence of trial events. The targets were cued by a line presented above fixation. The blue line indicated the saccade target and the yellow line the reach target (counterbalanced between

participants). All combinations of eye and hand target location were counterbalanced. Participants were encouraged to perform the movements as quickly and accurately as possible after cue onset.

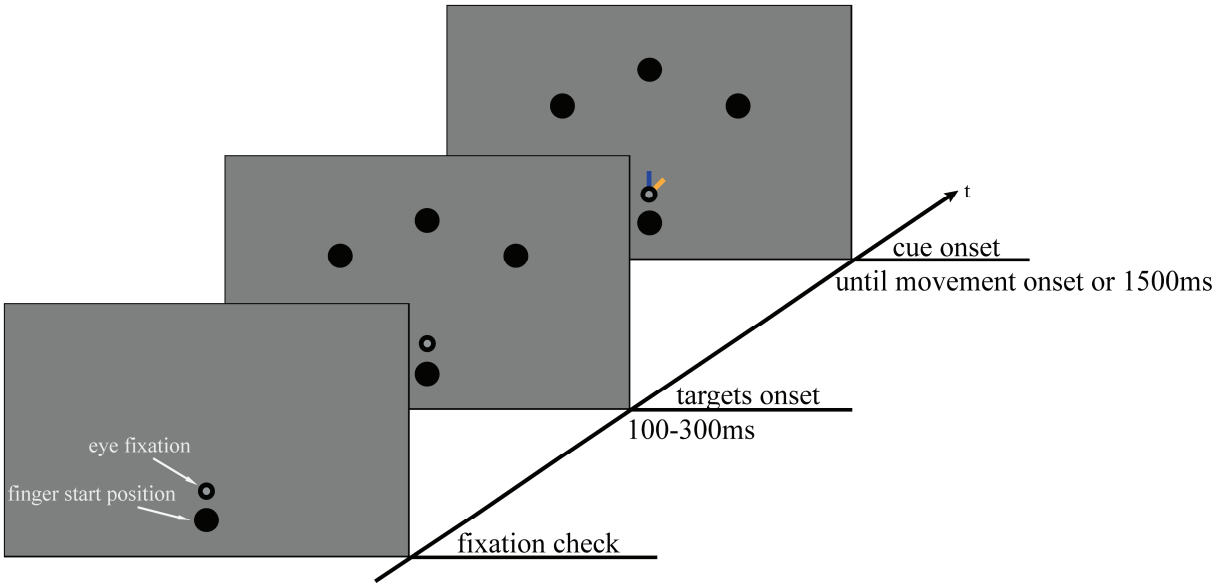

Figure 1. Sequence of trial events.

We asked whether the movement parameters, trajectory and endpoint location, of one effector was influenced by the relative target location of the other effector. We hypothesized that if target selection for the eye and hand were separate, there should be no influence of where a reach is performed on the saccade movement parameters and vice versa. On the other hand, if the target selection for the eye and hand overlaps on some level, we would expect an influence of the target location of one effector on the movement parameters of the other effector. We found that the trajectory of a vertically performed saccade curved more to the left when it was performed simultaneously with a reach to the right compared to a reach to the left (see Figure 2A). Similarly, the trajectory of a vertically performed reach curved more to the left when it was performed simultaneously with a saccade to the right compared to the left (see Figure 2B). Furthermore, the endpoint location of saccades and reaches were shifted away from the location of the simultaneously performed but spatially separate reach or saccade, respectively. The movement parameters of one effector are influenced by the relative target location of the other effector. Our findings suggest that the target selection for eye and hand movements is overlapping to some extent.

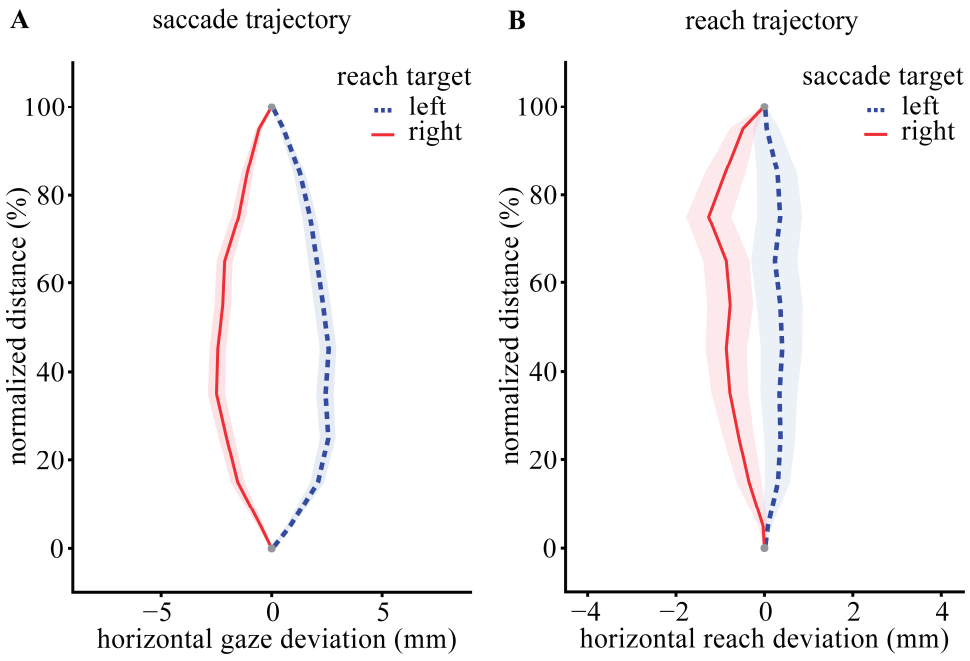

Figure 2. A: normalized trajectory of saccades to the central target for conditions in which a simultaneous reaching movement was performed to the left or right of the central target. B: normalized trajectory of reaching movements to the central target for conditions in which a simultaneous saccade was performed to the left or right of the central target. Shaded areas around the mean trajectories represent within-subject 95% confidence intervals (Cousineau 2005).

Study 2: The attractiveness of salient distractors to reaching movements is task-dependent

Physically salient distractors can attract visual perceptual processing and eye movements during search. However, this attraction can be avoided (Lamy & Egeth, 2003; Lamy, Leber & Egeth, 2004; Theeuwes & Burger, 1998) by active suppression of the distractor shortly after distractor onset. Active suppression occurs under certain task settings, i.e. top-down task sets. The top-down task set is influenced by, for example, time of cueing, expectations, and relevance of the distractor. For example, cuing the target before the onset of the search display can omit attraction of visual perceptual resources by a salient distractor (Yantis & Jonides, 1990). Attraction of visual perceptual resources and eye movements by a distractor is also avoided in blocks with a high proportion of distractor trials (Geyer, Müller & Krummenacher, 2008). However, it is unknown whether the mechanism of fast active suppression also takes place during reaching movement planning.

Study 2 (Nissens & Fiehler, 2020) was designed to investigate whether the attraction of reaching movements by physically salient distractors is task-dependent. Does active suppression of a physically salient distractor take place during reaching movement target selection? Two tasks were designed to manipulate the level of certainty of the target location. If the certainty of the target location is low, active suppression of the distractor cannot take place. If the certainty of the target location is high, active suppression of the distractor can take place. In both tasks participants were instructed to reach towards a diamond presented among three circles. See figure 3A for the

sequence of trial events. Participants were instructed to remain fixation while reaching. All shapes were in the same red color in the baseline condition. In the low physical salience (LPS) distractor condition one of the distractors was pink, i.e. a color that was close in color space to the red color (Figure 3B, left). In the high physical salience (HPS) distractor condition one of the distractors was in blue, i.e. a color that was further away in color space from the red color (Figure 3B, right). In the search-to-reach task (Figure 3A, left), the target had to be searched and reached to. In the cued reach task (Figure 3A, right), the target was cued and had to be reached to. The certainty of the target location was low in the search-to-reach task and high in the cued reach task. Therefore, active suppression of the distractor could take place in the cued reach task but not the search-to-reach task. We hypothesized that the reach trajectory would curve towards the HPS distractor in the search-to-reach task. However, we expected the trajectory to curve away from the HPS distractor in the cued reach task if active suppression of the distractor does take place during the reaching movement target selection.

We conducted three experiments. In experiment 1 participants performed the search-to-reach task. In experiment 2 participants performed the cued reach task. On some trials one of the distractors was in the LPS or HPS color. We found that the reach trajectory of movements performed to the target curved towards the HPS distractor in experiment 1 but not in experiment 2.

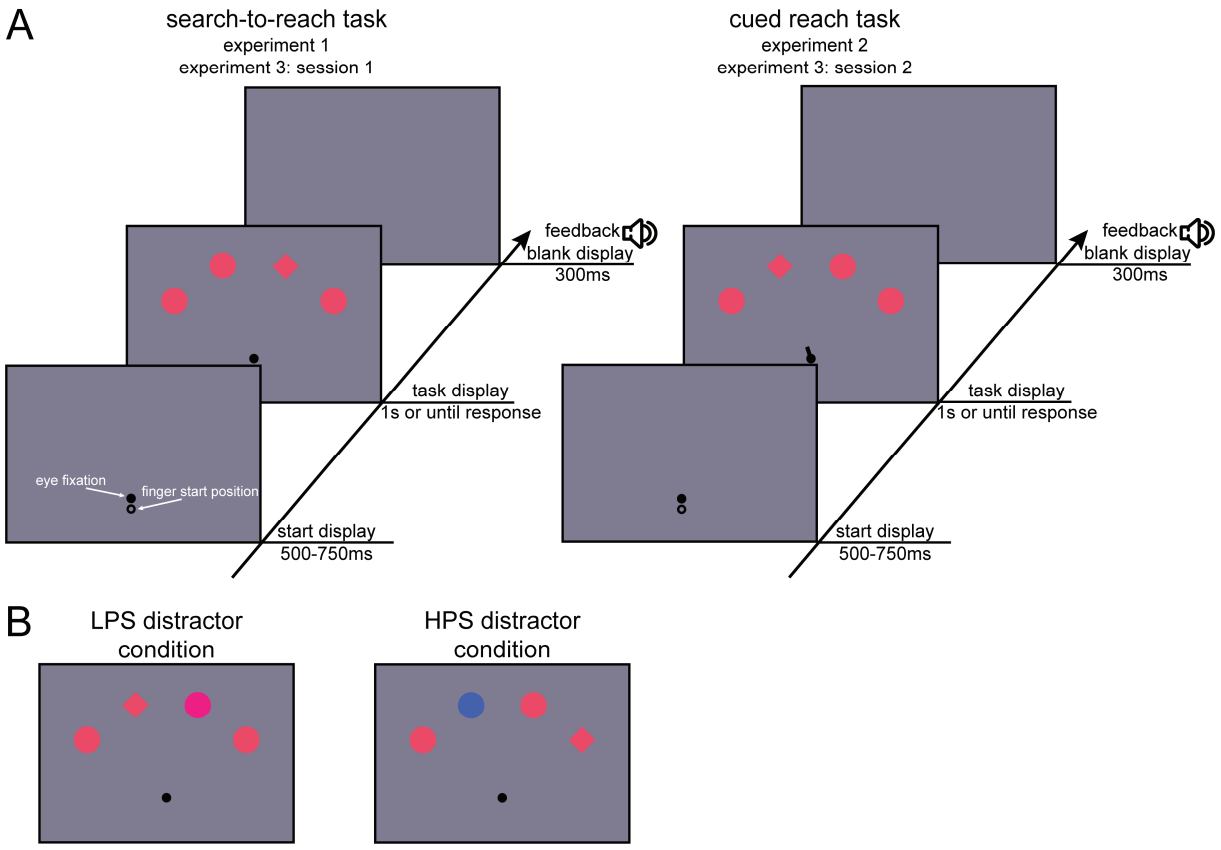

Figure 3. Experimental procedure. (A) Sequence of trial events. (B) Example task display for the Low Physical Salience (LPS) distractor condition (left) and High Physical Salience (HPS) distractor condition (right).

To directly compare the effect of a highly physically salient distractor on reaching movements in a search-to-reach task and a cued reach task, we ran a within-subjects design in experiment 3 where participants were invited to perform both experimental tasks on two separate days. In one session participants performed the search-to-reach task and on the other day the cued reach task. On some trials one of the distractors was in the HPS color. We found that the trajectory curved more towards the HPS distractor in the search-to-reach task than in the cued reach task (see figure 4). Relative to the baseline, the trajectory curved towards the HPS distractor in the search-to-reach task but not in the cued reach task. In summary, when the certainty of the target location was low, reaching movements were attracted towards the HPS distractor. When the certainty of the target location was high, reaching movements were unaffected by the presence of the HPS distractor. Note that we expected reaching movements to curve away from the HPS distractor if active suppression would take place during reach planning. We suggest that active suppression of the HPS distractor still takes place but not on the level of reach target selection.

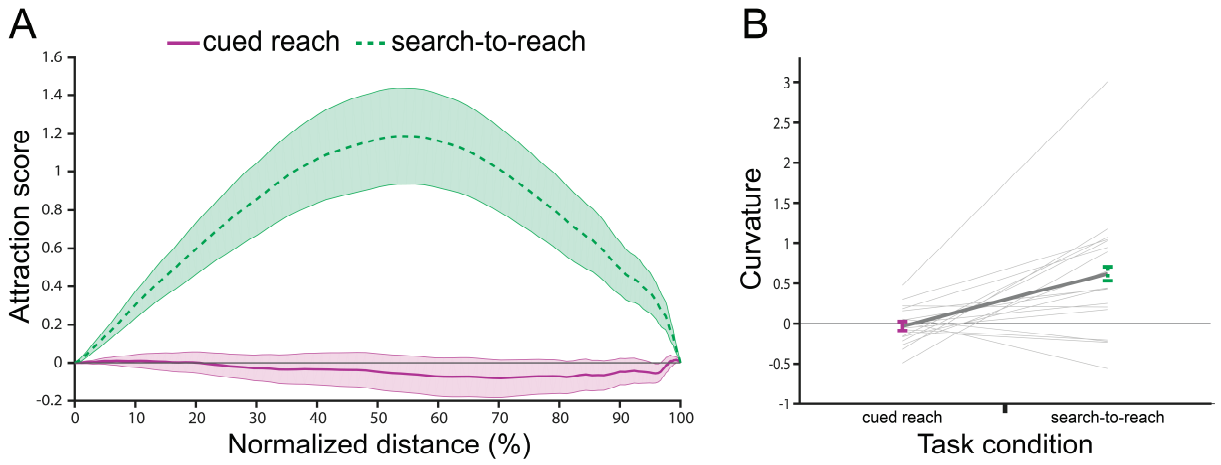

Figure 4. Results of experiment 3. (A) Distractor attraction scores along the normalized movement amplitude. The green line shows the attraction score for the High Physical Salience (HPS) distractor in the search-to-reach task. The purple line shows the attraction score for the HPS distractor in the cued reach task. Positive values indicate that the finger position deviated toward the distractor compared to baseline. (B) Curvature for the cued reach task (purple) and search-to-reach task (green). Positive values indicate that the reaching movement deviated towards the HPS distractor. All error bars reflect between-subjects SEM.

3. Summary of Article in Revision

Study 3: Reaching movements are attracted by stimuli that signal reward

Current goals and physical salience can influence visual perception and movement parameters. However, stimuli associated with value also influence action and perception. For example, the presence of a distractor signaling reward or threat increases response times and attracts saccades towards its location during search (Failing, Nissens, Pearson, LePelley, & Theeuwes, 2015; Failing & Theeuwes, 2017; Nissens, Failing, & Theeuwes, 2017; Schmidt, Belopolsky, & Theeuwes, 2015). Reward also influences reaches. In previous studies an association between a certain color and reward was established by giving reward after reaching to that color. On subsequent trials in the same (Chapman, Gallivan, Wong, Wispinski, & Enns, 2015; Wirth, Dignath, Pfister, Kunde & Eder, 2016) or different (Gallivan et al., 2015; Moher, Anderson & Song, 2015) blocks the distractor was in the color associated with reward. Reach trajectories were attracted towards the reward-associated distractor. Two points remain unclear: (i) Reaching towards the reward color was reinforced on some trials. Therefore, it is unclear whether the attraction by the reward color was due to a learned association between the color and reward or the action of reaching towards the color and reward. Is it the color itself or the act of reaching toward the color that gains priority? (ii) The reward associated distractor was physically salient (Moher et al., 2015) or presented with only one alternative shape (Chapman et al., 2015; Wirth et al., 2016). Therefore, it is unclear whether the attraction of reaching movements toward a stimulus associated with reward relies on an initial attraction by physical salience. Does a reward associated stimulus attract reaching movements when it is not physically salient, i.e. presented among multiple differently colored shapes?

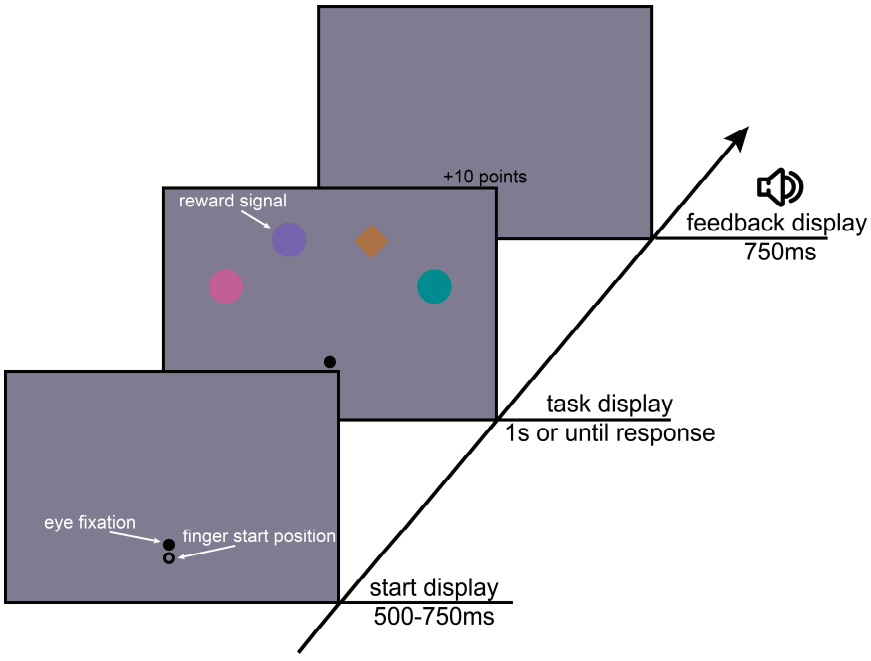

Figure 5. Sequence of trial events.

In an attempt to elucidate these open questions, the third study was designed (see Appendix). We investigated whether a stimulus signaling reward, that is never a target nor physically salient, can influence reaching movements. In our experiment participants had to reach towards a diamond shape without making eye movements. See figure 5 for the sequence of trial events. Four differently color shapes, three circles and one diamond, were presented above fixation. On some trials participants could earn high or low reward. This was signaled by the color of one of the distractor shapes. The target was never in one of the two reward signaling colors. On baseline trials, none of the reward signaling colors were present. Reward was only given on high or low reward trials, when participants reached to the correct shape, in time, without making eye movements. Participants received feedback about how much reward they earned after each trial. We found that reaching movements trajectories curved toward the high reward signaling distractor (Figure 6A). This effect was larger on trials where reach latency was short (Figure 6B) compared to long (Figure 6C). Thus, stimuli signaling reward attract reaching movements even when (i) reaching towards the reward color was never necessary nor useful and (ii) the reward signaling distractor was not physically salient.

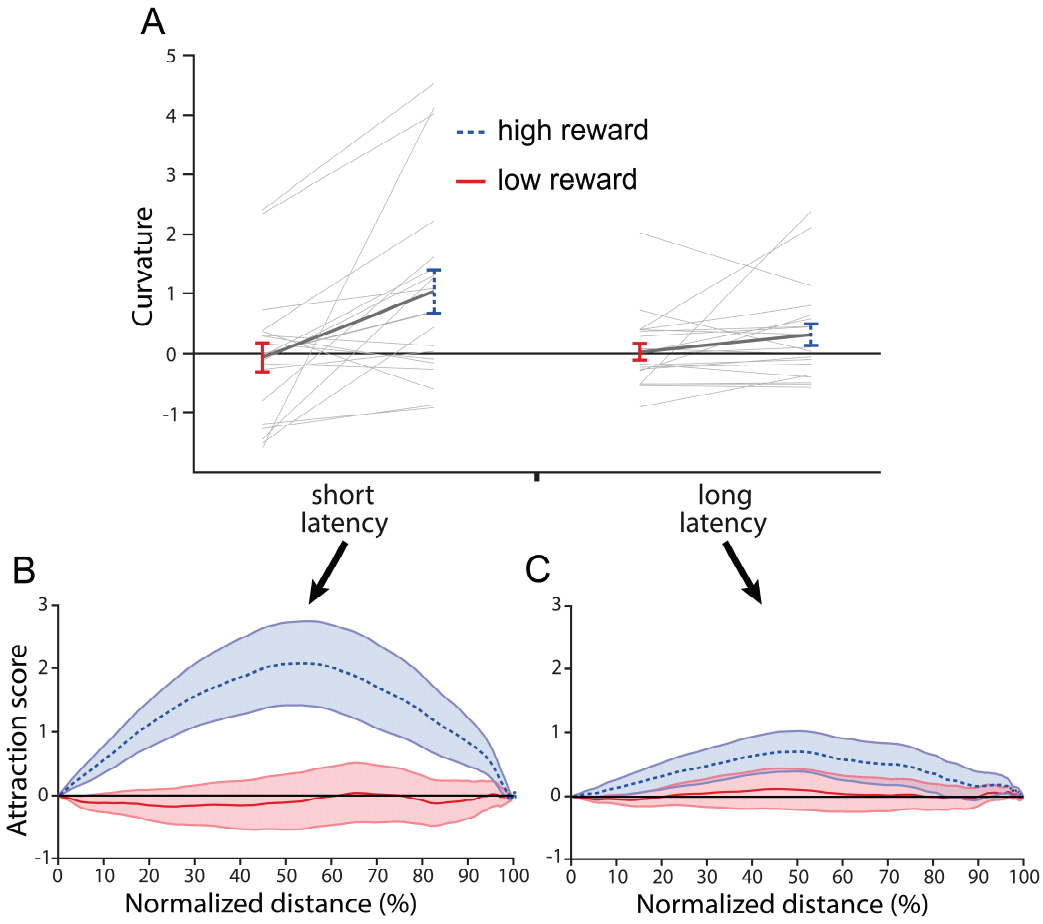

Figure 6. (A) The magnitude of reach curvature by reward signaling value of the distractor separately for short latency trials (left) and long latency trials (right). Positive values denote curvature towards the distractor. Distractor attraction scores along the normalized movement amplitude by reward signaling value of the distractor for short latency trials (B) and long latency trials (C). Positive values denote attraction towards the distractor. All error bars reflect SEM.

4. Discussion

In the present thesis I examined the interplay between visual perception and visually guided movements, in particular the mechanisms by which visually guided reaching movements are influenced by visual perception and eye movements.

Interplay between eye and hand movements

In study 1 we investigated whether the targets are selected separately for eye and hand movements (Nissens & Fiehler, 2018). Therefore, we examined movement parameters of simultaneously performed saccades and reaches. If the target selection processes for both effector systems were totally separate we would expect no influence of the target location of one effector on the movement parameters of the other effector. However, we found that movement curvature and end point deviated away from the target location of the other effector for both eye and hand movements. Our results provide evidence that the target selection process of both effectors overlap to some extend during visually guided movement planning.

Neurophysiological research showed that a target location can be activated on both the saccade and reach priority map at the same time. When a cue later reveals whether an eye or hand movement is required, the activation is further increased on the corresponding movement priority map and inhibited on the other movement priority map (Calton, Dickinson, & Snyder, 2002; Cui & Anderson, 2007). Moreover, when two target locations are presented, both locations will be activated on the movement priority map. When a cue later reveals which is the actual target location, the activation of the actual target location is increased and the activation of the non-target location is inhibited (Cisek & Kalaska, 2005; Powel & Goldberg, 2000; see also Kim & Basso, 2008). We argue that upon cue presentation in study 1, both eye and hand target location are activated on both the saccade and reach priority map. To select the correct target, the hand target location is inhibited on the saccade priority map and vice versa on the reach priority map. The shift in the trajectory and end point location of one effector is a consequence of the inhibition of the other effector's target location.

Task-dependent interplay between visual salience and hand movements

Research has shown that the attraction of visual perceptual resources and eye movements by a physically salient distractor can be avoided under certain top-down task sets, i.e. it is task dependent. Attraction is avoided by actively suppressing the salient distractor on the priority map before it attracts perceptual resources or saccades. However, it is unknown whether this mechanism also takes place on the reach priority map and influences hand movements. In study 2 (Nissens & Fiehler, 2020), a salient distractor was presented while participants had to reach towards a target. We found that when the location of the target had to be searched and was

uncertain, the reaching movement curved away from the salient distractor. When the location of the target was cued and certain, the reaching movements were unaffected by the salient distractor. Thus, the influence of the physically salient distractor depended on the target certainty i.e. the top-down task set.

In the search-to-reach task, the physically salient distractor is activated on the reach priority map together with the target location. Due to time pressure, the movement is initiated before the competition is resolved. This results in the reach's initial direction to be shifted towards the distractor. During reach, the distractor location is further inhibited so that the reach ends up at the target. This will result in the trajectory to be shifted towards the salient distractor. In the cued reach task, our hypothesis was that the reach would curve away from the salient distractor due to active suppression of the distractor location. However, reach trajectory was unaffected by the presence of a salient distractor. We argue that the active suppression of the distractor location occurs on the visual perception priority map. The activation on the visual perception priority map is then transferred to the reach priority map. Because the distractor is not activated on the reach priority map there is no competition and no inhibition. Hence, the reach trajectory is unaffected by the presence of a salient distractor in the cued reach task.

Interplay between reward and hand movements

In study 3 we investigated the mechanism that drives reaching movements to be attracted towards stimuli associated with reward (see Appendix). Previous studies left open several points: (i) whether attraction is caused by an association between a color and reward or between the act of reaching to a color and reward, and (ii) whether an initial attraction by physical salience is necessary. Therefore, we examined reach trajectories of movements towards a target while on some trials a non-physically salient distractor signaled the possibility of earning reward. Reaching towards the reward distractor was never necessary, conversely, it would lead to the omission of reward. We found that reaching movements were attracted towards the reward signaling distractor. This effect was magnified in short latency reaches. Thus, an association between a color and reward can attract reaching movements without an initial saliency driven attraction.

We argue that the reward signaling color gains priority in the selection for action. When the shapes are presented, the reward distractor and target location are activated on the reach priority map. Especially on short latency reaches, movements are initiated before competition is resolved. The initial direction of the resulting movement will be shifted in the direction of the reward distractor. During movement the reward distractor is inhibited and the trajectory is corrected to end up at the target. The resulting movement trajectory will be curved towards the reward distractor. On long latency trials less curvature is observed due to more time to inhibit the reward distractor.

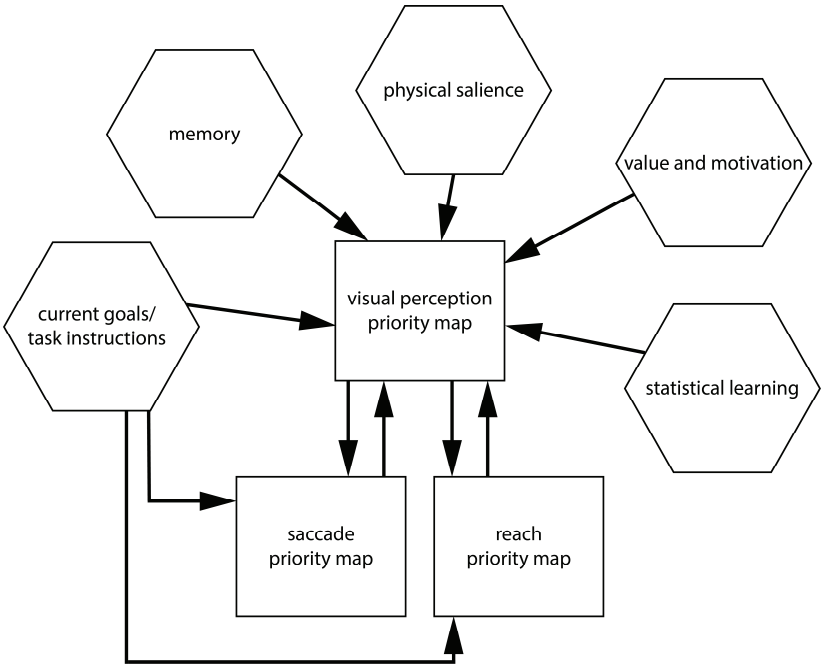

Figure 7. Schematic representation of a visuo-spatial priority framework. Priority sources (hexagons) influence the activation on the visuo-spatial priority maps. Transfer of activation between the visual perception priority map, and saccade and reach priority map.

An interplay between priority maps

The interplay between visual perception and visually guided eye and hand movements can be explained by interactions between priority maps and the competition for selection on each of them. Selection for visual perception and visually guided saccades and reaches have been argued to be the result of a competition on priority maps (Todd & Manaligod, 2018; Zelinsky & Bisley, 2015; see also Cisek & Kalaska, 2010). Activation from one priority map is transferred to another especially within one reference frame. For example, priority maps that represent space in visual coordinates. This could explain the interplay between visual perception and visually guided actions such as visually guided saccades and reaches. The transfer of activation between the visual perception priority map and movement priority maps facilitates and might be necessary for planning visually guided movements. Furthermore, transfer of activation between movement priority maps for reaches and saccades facilitates eye-hand coordination. Apart from inter priority map connections, priority signals can originate from different sources, e.g. physical salience, value, task instructions, selection history, memory, etc.. Some of these sources have been linked to certain brain areas (Todd & Manaligod, 2018; Zelinsky & Bisley, 2015). For example, physical salience might originate from the superficial layers of the superior colliculus and early visual cortex (Itti & Koch, 2001). However, the mechanism of priority sources is not well understood.

In figure 7, a visuo-spatial priority framework is outlined. The framework is an oversimplification for several reasons. (i) Each priority map has multiple instances in the brain. For example, visual perception priority maps can be found in the intermediate layers of the SC,

IPC and FEF (White et al., 2017; Thompson & Bichot, 2005; Bisley & Goldberg, 2010). Most likely different maps serve different functions. (ii) Priority sources are not well understood. The suggested priority sources that appear to be different behaviorally might stem from the same neural mechanism. For example, priority related to selection history might be overlapping with priority related to memory or task instructions. Also, the suggested priority sources are not an exhaustive list. (iii) The visual perception priority map might not be specific for visual perception but a general priority map to prioritize behaviorally relevant locations or stimuli. The general priority map does not only enhance visual perception but is also the main source for the activation on the movement priority maps. For example, in study 1 both the eye and hand target location are relevant and, thus, activated on the general (visual perception) priority map. The activation is then transferred to both the saccade and reach priority map where inhibition of the other effector's target location is necessary to perform the task. The general priority map might be the closest substrate of what is generally referred to as visual selective attention. However, I think the term attention is not necessary nor useful to explain the phenomena of the interplay between visual perception and visually-guided movements.

At the beginning of my doctoral research in Giessen I viewed the interactions between perception and action through an attentional framework. However, along the way it became increasingly difficult to unite all the literature I was presented with under this framework. I modified the meaning of attention, narrowing it down to something that resembles the working of priority maps and the increase of activation in visual cortex. It became apparent that the term attention was more of a burden than a meaningful mechanism. Attention is used to explain very different phenomena (Hommel et al., 2019; Krauzlis, Bollimunta, Arcizet, & Wang, 2014). Occasionally, it covers up phenomena that we can't explain well. This ultimately refrains us from asking the right questions and increasing our understanding of behavioral phenomena and how the brain works. I think it is better to avoid the use of the term attention. Let us talk about more clearly defined mechanisms and neural substrates. It is better to have a clearly defined mechanism that is partially wrong than an ill-defined mechanism that explains everything. Only clearly defined mechanisms can be criticized in a constructive way, be improved and move science forward.

Future directions

In the present thesis several aspects of the interplay between visual perception and visually guided movements were studied. Yet, there are several open standing questions. We showed that a reward signaling stimulus attracts reaching movements even when reaching towards it was never necessary nor useful. One might wonder what would happen if one distractor signaled threat. Previous studies have shown that threat signaling stimuli do attract visual perceptual resources and eye movements (Nissens et al., 2017; Schmidt et al., 2015). Manual approach behavior

towards a stimulus associated with threat could be harmful in real life. Therefore, we would expect an avoidance of stimuli associated with threat. A potential mechanism could be that a threat signaling stimulus triggers an inhibition at its location on the reach priority map. We ran an experiment analogous to the one in study 3 with the color of one of the distractors signaling threat instead of reward. The color of one of the distractors signaled high (50%) or low (5%) probability of getting an unpleasant electrical stimulation if participants did not reach to the target in time. To our surprise, reaching parameters were not significantly affected by the presence of a threat signaling distractor. Future experiment are needed to elucidate under which circumstances and what effect stimuli associated to threat influence reach planning. One suggestion would be to run an experiment as in study 3 where the color signals the intensity (instead of probability) of the electrical stimulation. Also, a color could be associated with threat in a color-threat conditioning block before the experimental block (Schmidt et al., 2015).

Physically salient and reward associated distractors influence visually guided reaching movements. However, in these experiments the distractor is typically presented within reach, i.e. peripersonal space. The question arises whether stimuli that are physically salient or associated with reward also attract reaching movements if they are not reachable, i.e. in extrapersonal space. Virtual reality provides a way to present stimuli in extrapersonal space with great control of the experimental environment. For example, the location of a distractor could be manipulated by varying its depth while keeping all other coordinates constant. In this way we can get an understanding whether stimuli that are visually salient but non-reachable also influence reaches. I expect movements to be influenced by non-reachable salient stimuli when the target is selected on a visuo-spatial reach priority map, i.e. in visually guided reaching.

Conclusion

The work presented in this thesis delved into the mechanism under which the planning of reaching movements is influenced by visual perception and eye movements. Study 1 showed that when a saccade and reach are planned simultaneously they affect each other. Study 2 showed that under certain circumstances physically salient stimuli do not affect reach parameters. Study 3 showed that reward associated stimuli affect reach parameters. Overall, the results fit into a priority framework where activation on a general, visual perception priority map is influenced by different sources such as physical salience, value, memory and current goals. The activation between the general and movement priority maps is transferred which benefits visually guided movement planning and eye-hand coordination. Under certain circumstances, the transfer of activation results in competition on the movement priority map during movement planning. The competition affects movement parameters and is responsible for the observed interplay between perception and action.

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II Publications

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RAPID REPORT | *Control of Coordinated Movements*

Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements

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Nissens T, Fiehler K. Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements. *J Neurophysiol* 119: 118–123, 2018. First published October 11, 2017; doi:10.1152/jn.00618.2017.—Simultaneous eye and hand movements are highly coordinated and tightly coupled. This raises the question whether the selection of eye and hand targets relies on a shared attentional mechanism or separate attentional systems. Previous studies have revealed conflicting results by reporting evidence for both a shared as well as separate systems. Movement properties such as movement curvature can provide novel insights into this question as they provide a sensitive measure for attentional allocation during target selection. In the current study, participants performed simultaneous eye and hand movements to the same or different visual target locations. We show that both saccade and reaching movements curve away from the other effector's target location when they are simultaneously performed to spatially distinct locations. We argue that there is a shared attentional mechanism involved in selecting eye and hand targets that may be found on the level of effector-independent priority maps.

NEW & NOTEWORTHY Movement properties such as movement curvature have been widely neglected as important sources of information in investigating whether the attentional systems underlying target selection for eye and hand movements are separate or shared. We convincingly show that movement curvature is influenced by the other effector's target location in simultaneous eye and hand movements to spatially distinct locations. Our results provide evidence for shared attentional systems involved in the selection of saccade and reach targets.

saccades; reaching; eye-hand coordination; attention; movement curvature

INTRODUCTION

Eye and hand movements are both spatially and temporally highly coordinated. When planning a simultaneous eye and hand movement the target location for each movement has to be selected. Movement target selection involves attentional allocation at the target location. Given the high level of coordination between eye and hand movements the question arises whether eye and hand targets are selected by a shared attentional system or separate attentional systems. A number of neurophysiological and imaging studies have found support for largely independent systems by showing distinct preparatory activity in posterior parietal brain regions for eye and hand movements (Tosoni et al. 2008; Van Der Werf et al. 2010). Furthermore, it has been suggested that movement goals for saccades and reaches are represented in separate brain areas of the posterior parietal cortex (Dickinson et al. 2003). Other studies have reported a tight coupling between selection of targets for eye and hand movements (Gorbet and Sergio 2009; Moher and Song 2016; van Donkelaar 1997; see also Gopal and Murthy 2015). Moreover, overlapping brain activation has been observed in areas of the parietal and prefrontal cortex for eye and hand movement planning (Beurze et al. 2009; Levy et al. 2007), arguing against separate attentional systems. Further support comes from recent studies in nonhuman primates suggesting an effector-independent priority map for target selection in the superior colliculus (Song and McPeek 2015; Wolf et al. 2015).

Behavioral work in humans investigating attentional allocation to target locations of an upcoming hand, eye, or simultaneous hand and eye movement has also revealed conflicting results. Using a dual-task paradigm, Jonikaitis and Deubel (2011) asked participants to discriminate a target probe while preparing an eye, hand, or combined eye and hand movement to the same or a different location. They found that combined eye and hand movements to different locations did not deteriorate discrimination performance at either target location compared with a single eye or hand movement. This suggests that attention can be allocated independently to spatially distinct eye and hand target locations without any costs. Thus, the authors propose separate, effector-specific attentional systems for target selection. In contrast, Khan et al. (2011) used a similar dual-task paradigm and found that discrimination performance was not enhanced when participants performed a simultaneous eye and hand movement to the same target location compared with a single movement. Hence, there seems to be no additive effect of making combined compared with a single movement to one location. Therefore, they argue for an attentional system shared across effectors.

Movement properties of the eyes and hand, such as movement end point and trajectory, provide a sensitive measure for attentional allocation. Deviations in movement trajectory are a result of competing movement vectors, often explained in terms of population coding (McSorley et al. 2004; Tipper et al. 1997). In a motor map each neuron codes an individual movement vector toward the corresponding location. Movements are initiated toward the average of the vectors in the

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motor map. When two vectors are activated by a target and a distractor stimulus, presented in close spatial proximity, the average vector lies in between the target and the distractor. Competition between the two vectors has to be resolved to make a movement toward the target location instead of an intermediate location. This is done by inhibiting the neurons that code for the vector toward the distractor, resulting in a shift of the average vector away from the distractor. When competition is resolved, the inhibition of the distractor vector will cause the movement to curve away from the inhibited vector.

Regarding deviations in trajectories as a consequence of attentional allocation, the population coding theory assumes the presence of a movement vector in the direction of the attended location. This is in line with the premotor theory of attention (Rizzolatti et al. 1987), which claims that the mechanisms behind spatial attention and movement programming are the same. Thus, in the case of attentional allocation toward a nontarget location, competition between the movement vector toward the target and the movement vector toward the attended location has to be resolved by inhibiting the vector toward the attended location. In this way allocating attention to a nontarget location will lead to trajectories that curve away from the nontarget location (Sheliga et al. 1995; Van der Stigchel and Theeuwes 2007). In sum, examining the trajectories of eye and hand movements can provide novel insight into attentional mechanisms of target selection (for reviews on hand movements see Song 2017; Song and Nakayama 2009; for reviews on eye movements see Van der Stigchel 2006, 2010).

In the present study, we investigated the trajectories of simultaneously performed eye and hand movements to elucidate whether eye and hand targets are selected by a shared or separate attentional systems. To this end, we examined how movement curvature of one effector is influenced by a simultaneous movement of the other effector when moving to different locations. If the eye and hand targets are selected by a shared attentional system, we expect the hand movement to curve away from the eye target location and the eye movement to curve away from the hand target location.

MATERIALS AND METHODS

Participants. Twenty-seven volunteers with reported normal or corrected-to-normal vision participated in the experiment. Eight participants were excluded due to less than 20% of trials meeting the inclusion criteria in one of the conditions of interest (see *Analyses*), and one participant was excluded due to data corruption, resulting in a final sample of 18 participants (11 men, mean age 25). The sample size was estimated using GPower (Faul et al. 2007) based on the effect size of reach curvature observed after testing 11 participants ($d_z = 0.7$), with α error probability = 0.05, and power = 0.90. This resulted in a sample size estimate of 19 participants. We tested 18 participants to counterbalance the relationship between the color of the cue and effector type between participants (power = 0.89). All participants were right-handed according to the Edinburgh Handedness Inventory (89.3 ± 13.5; Oldfield 1971). Participants gave written, informed consent before the experiment and received course credits or financial compensation. The study was approved by the Giessen University ethics committee and was in accordance with the Declaration of Helsinki (2008).

Experimental setup and stimuli. Stimuli were created in OpenSesame (Mathôt et al. 2012) and presented on a vertically positioned Iiyama Vision Master Pro 510 monitor (1,024 × 768 pixels, 85 Hz). Reach movements were recorded with an optoelectronic motion tracking system (Optotrak Certus, Northern Digital, Waterloo, ON, Canada) that registered an infrared marker placed on the fingernail of the right index finger with a sampling rate of 100 Hz. Monocular movements of participants' right eye were recorded via a head-mounted video-based EyeLink II (SR Research, Mississauga, ON, Canada) with a sampling rate of 500 Hz. A decimal keyboard was placed to the left, in front of the participants. Participants' head was positioned on a chin rest at a distance of 47 cm from the screen. The hand of the participant was visible throughout the experiment, which was performed in a dimly lit room.

The task display (see Fig. 1) consisted of an eye fixation circle [0.7 vd (visual degrees radius)] presented 3.5 vd below screen center and, thereunder, a finger start position circle (1.2 vd radius). The three target circles were positioned on an imaginary circle (7 vd radius) around fixation: the central one vertically above fixation, the other two 45 angular degrees to the left and right from the central one. The cues were a blue and an orange line (0.7 vd long) around fixation pointing in the direction of the eye and finger target circle respectively (color and effector relationship was counterbalanced across participants).

Procedure. The task of the participant was to simultaneously move the eyes and the index finger of the right hand to the same or different target locations as quickly and as accurately as possible. Targets occurred at three possible locations. Each combination of eye and hand target location was presented, leading to nine (3×3) possible trial types. Each block consisted of 45 trials, i.e., five repetitions of each trial type. Participants first performed a practice block with feedback about their accuracy on each trial. A trial was evaluated correctly if the eye and hand ended up at their respective target location (gaze distance from eye target <2.5 vd and finger position <20 mm from hand target) within 1,500 ms. After the first practice block, performance was evaluated. If the overall accuracy was above 80%, participants proceeded with the experiment. Otherwise, they had to practice until they reached 80% accuracy or performed three practice blocks. The experiment consisted of 10 experimental blocks in total. Participants performed 50 repetitions of each trial type. During the experimental block feedback about accuracy was only given at the end of each block. The experiment consisted of 500 trials and took ~1.5 h.

Each trial started with the presentation of a fixation/start screen. After the participant pressed the 0 button on a decimal keyboard eye drift correction was performed and the finger start position was evaluated. The trial continued only if participants fixated within 2 vd from the eye fixation circle and their finger was positioned less than 5 mm away from the finger start position. Otherwise, "check failed" was displayed and the trial was restarted. After a successful drift correction and correctly registered finger start position, the three possible targets were presented and stayed on until the end of the trial, i.e., targets were always visible during movement. After a variable interval of 100–300 ms the eye and finger target cues were presented, until the end of the trial, prompting participants to simultaneously

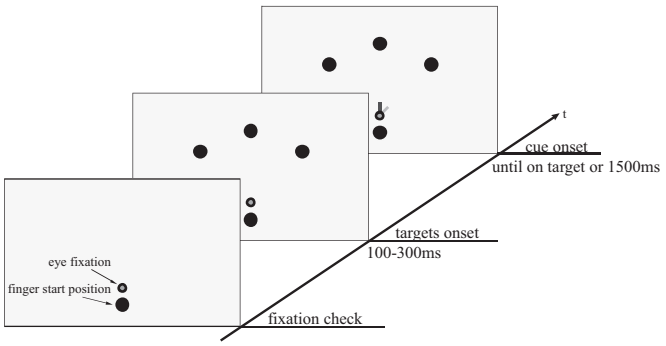

Fig. 1. Sequence of trial events. Participants had to make a simultaneous saccade and reaching movement to different cued locations after cue onset. The dark gray line indicated the saccade target and the light gray line the reach target.

move their eyes and finger as quickly and as accurately as possible to the correct locations. The trial was finished 200 ms after participants fixated on the eye target (gaze distance from target <2.5 vd) and touched the finger target on the screen (finger position <20 mm from target) or 1,500 ms after cue onset.

Analyses. An automatic algorithm implemented in *pygaze* (Dalmaijer et al. 2014) was used to detect saccades starting and end point using minimum velocity and acceleration criteria of 35 vd/s and 9,500 vd/s^2, respectively. Reach data were rotated online so that x and y were aligned to the horizontal and vertical axis of the monitor screen and, consequently, z was the axis perpendicular to the monitor screen. The rotated raw data was used to calculate all reach parameters (movement onset, offset, curvature, and trajectory). The starting point of a reach was defined as the first sample of four consecutive vector velocity readings greater than 20 mm/s where there was a total acceleration of 20 mm/s^2 across the four points. The end point of a reach was defined by the point in time when the velocity dropped below 20 mm/s (see Chapman and Goodale 2010).

The task was designed in such a way that we could examine the influence of the movement direction (left vs. right) of the one effector on the curvature of the vertical movement of the other effector. Previous research has shown that vertical movements are less noisy, more consistent, and more suited to reveal influences of attention on movement curvature than diagonal ones (e.g., Viviani et al. 1977). Consequently, to examine the influence of hand movements on eye movements we only analyzed trials where the eye movement was made to the central target and where the hand moved either to the left or right target. We examined the influence of eye movements on hand movements likewise. Hence, we only analyzed trials where one effector moved to the central target and the other effector moved to a lateralized target (conditions of interest). Trials of the remaining conditions served as catch trials and were not included in the analyses. All statistical analyses were conducted using JASP (JASP Team 2017). Normality was confirmed for all reported t-tests (Shapiro-Wilk, $P \geq 0.07$). According with our hypothesis, we corrected our results on movement curvature and end point angular deviation for multiple comparisons by adjusting alpha to the Šidák corrected alpha value of $\alpha_{SID} = 0.02532$ [$\alpha_{SID} = 1 - (1 - \alpha)^{1/m}$; with $\alpha = 0.05$ and $m = 2$; Šidák 1967]. Furthermore, we corrected for an interim analysis that was performed at sample size 11. We used a linear spending function with overall $\alpha = 0.02532$ and $\varphi = 1$, which resulted in $\alpha_{cor} = 0.01585$ for the full sample (calculated using WinDL created by Reboussin et al. 2000). With corrections for multiple testing and interim analysis incorporated, we rejected the null-hypothesis when the P value was smaller than $\alpha_{cor} = 0.01585$.

From the conditions of interest, we excluded trials where the first eye movement did not end within 2.5 vd distance from the eye target (32.3%), where the first hand movement did not end within 20 mm distance from the hand target (9.2%), and where the latency of the first movement was shorter than 80 ms (5.4%). Over all criteria, 40.4% of trials were excluded, leaving 2,146 trials for data analyses.

Eye and hand movement curvature was determined as the area enclosed by the movement trajectory and a straight line running from the movement starting point to the end point (Ludwig and Gilchrist 2002). The area to the left of the straight line was given a negative value and summed with the area to the right of the straight line. The area was normalized by dividing it by the squared amplitude and multiplying it by 100 (Koenig and Lachnit 2011). Movement trajectories (Fig. 2), shown for illustrative purposes, were scaled to the same starting point and rotated to the same end point. The horizontal deviation over 10% fractions of the movement amplitude was calculated for each participant, effector (eye and hand) and other effector's target location (left and right). The trajectory was corrected for participants' individual movement behavior by subtracting the trajectory on congruent trials (eye and hand movement both to the central target).

RESULTS

To investigate the effect of the hand target location on eye movements during simultaneous eye and hand movements, we hypothesized that vertical saccades will curve more to the right when a simultaneous hand movement was executed to the left target compared with the right. Based on our directed hypothesis, we ran a one-sided t-test which revealed that saccades curved more to the right when the hand target was on the left compared with the right, $t(17) = 6.670$, $P < 0.001$, $\alpha_{cor} = 0.01585$, $d_z = 1.6$. Hence, saccades curved away from the location of the hand target (Figs. 2*A* and 3*A*).

Second, we investigated the corresponding effect of the eye target on hand movements and hypothesized that vertical

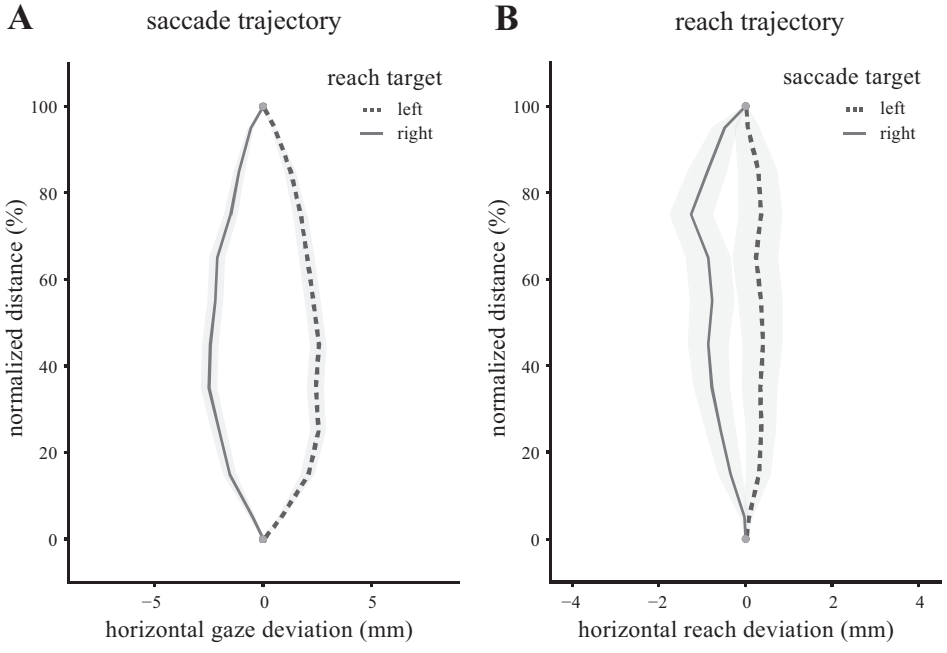

Fig. 2. *A*: normalized trajectory of saccades to the central target for conditions in which a simultaneous reaching movement was performed to the left or right of the central target. *B*: normalized trajectory of reaching movements to the central target for conditions in which a simultaneous saccade was performed to the left or right of the central target. Shaded areas around the mean trajectories represent within-subject 95% confidence intervals (Cousineau 2005).

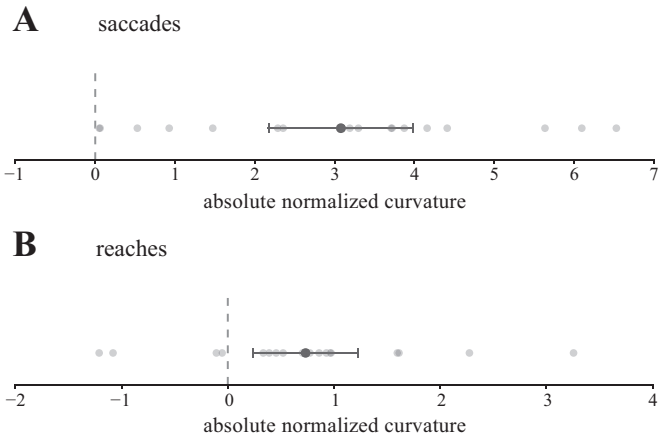

Fig. 3. Depicting the absolute normalized curvature away from the other effector's target location over participants (dark gray) and for each participant individually (light gray); separately for saccades (*A*) and reaches (*B*). Absolute normalized curvature away from the other effector's target location was calculated by subtracting the average curvature for the other effector on the right from the average curvature for the other effector on the left. Thus, positive values represent curvature away from the other effector's target location. Error bars represent within-subject 95% confidence intervals (Cousineau 2005).

reaching movements would curve more to the right when a concurrent eye movement is performed to the left, compared with the right. Indeed, we found that reaching movements curved more to the right when the eye target was on the left compared with the right, $t(17) = 2.923$, $P = 0.005$, $\alpha_{cor} = 0.01585$, $d_z = 0.7$, one-sided. As illustrated in Figs. 2*B* and 3*B*, reaches curved away from the location of the eye target.

Movement angular deviation was calculated as the angle between the line from the movement starting point to the target and the line from the starting point to the end point. Negative values were given when the end point was located to the left of the line between the movement starting point and the target. We hypothesized, for both saccades and reaches, that the movement end point will be more to the left of the target when the movement of the other effector is to the right compared with the left. Thus, to further investigate the effect of the hand target location on eye movements, we examined whether the angular deviation of the saccade end point to the target was more to the right when a concurrent hand movement was performed to the left compared with the right. Consistent with our hypothesis, we found that the saccade end point landed more to the right of the target when the hand target was on the left compared with when it was on the right, $t(17) = 3.280$, $P = 0.002$, $\alpha_{cor} = 0.01585$, $d_z = 0.8$, one-sided. Similarly, for the effect of the eye target on hand movements, we found that the angular deviation of the reach end point was more to the left of the target when the eye target was on the right compared with the left, $t(17) = 5.145$, $P < 0.001$, $\alpha_{cor} = 0.01585$, $d_z = 1.2$, one-sided. Hence, for both the eyes and the hand, the movement end point was deviated away from the other effector target location (see Fig. 4).

Movement latencies were defined as the time (in ms) between the onset of the target cue display and the onset of the movement. The saccadic latency differed depending on the movement direction of the concurrent hand movement, $t(17) = 5.007$, $P < 0.001$, $d_z = 1.2$, two-sided. Saccades were initiated slower when the hand moved into the contralateral (553 ms) than the ipsilateral (509 ms) field. We also examined whether the difference in saccadic latency was accompanied by a difference in reach latency. Reaches were initiated slower contralateral (616 ms) compared with ipsilateral [585 ms; $t(17) = 4.420$, $P < 0.001$, $d_z = 1.0$, two-sided]. Reach latency did not differ depending on the direction of the concurrent saccade, $t(17) = 0.814$, $P = 0.40$, two-sided.

Next we examined the difference in movement onset between reaches and saccades, and between conditions. We calculated the movement onset difference (MOD) by subtracting the eye movement latency from the hand movement latency. Hence, a positive value means that the eye movement was initiated before the hand movement. The eye led the hand by 71ms on average. This is similar to the MOD reported in the study by Khan and colleagues (2011) who found a latency difference of 64 ms. This difference can at least partially be attributed to the inertia of the hand (cf. Paninski et al. 2004; Moran and Schwartz 1999). The MOD did not differ significantly for vertical saccade trials with reaches to the left compared with right, $t(17) = 1.600$, $P = 0.128$, two-sided. Moreover, the MOD did not differ significantly for vertical reach trials with saccades to the left compared with right, $t(17) = 2.023$, $P = 0.059$, two-sided. Conclusively, the MOD did not differ between any of the relevant conditions.

To control for potential effects of fatigue, we split our data on saccade and reach curvature in a first experiment half, including blocks 1 to 5, and a second half, including blocks 6 to 10. Hence, we performed ANOVA's with the other effector position (left vs. right) and experiment half (first vs. second) as factors. There was no main effects of experiment half nor an interaction effect between experiment half and other effector position on saccade curvature [main effect half: $F(1,17) = 1.453$, $P = 0.245$; interaction effect: $F(1,17) = 3.197$, $P = 0.09$] or reach curvature [main effect half: $F(1,17) = 0.134$, $P = 0.719$; interaction effect: $F(1,17) = 2.979$, $P = 0.102$]. Next we tested whether task accuracy changed between the beginning and end of the experiment. We performed an ANOVA (Greenhouse-Geisser corrected) with experiment half (first vs. second) and the relevant conditions (4 levels: other

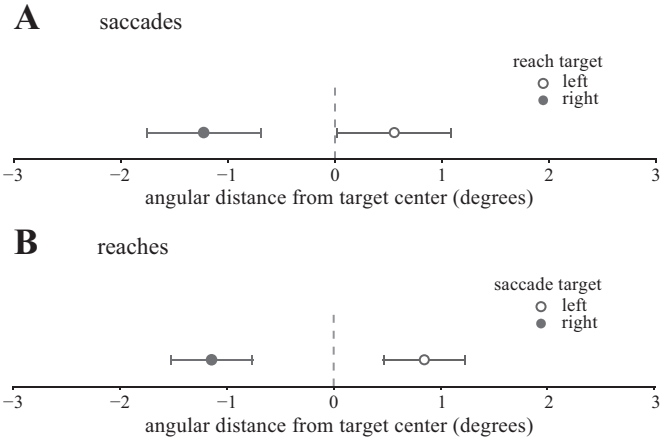

Fig. 4. *A*: mean angular distance of the saccade end point from target center (saccade accuracy) when reaching movements were performed simultaneously to the left or right. *B*: mean angular distance of the reach end point from target center (reach accuracy) when saccadic eye movements were performed simultaneously to the left or right. Error bars represent within-subject 95% confidence intervals (Cousineau 2005).

effector's target position left and right for both vertical saccade and vertical reach trials). We found no main effect of experiment half [$F(1,17) = 0.472$, $P = 0.505$] nor an interaction effect between experiment half and relevant conditions [$F(3,51) = 0.941$, $P = 0.422$]. In summary, we did not find evidence for an effect of fatigue on movement curvature, and neither did fatigue influence the effect of the other target position on movement curvature. Furthermore, overall accuracy was not affected by fatigue for the relevant conditions.

DISCUSSION

In the present study, we investigated whether targets for simultaneous eye and hand movements are selected by a shared attentional mechanism or separate attentional systems. To this end, we examined movement curvature and end point deviation of simultaneously performed saccadic eye and reaching movements. If the attentional systems for eye and hand movements are separate we would expect to see no difference in curvature depending on the other target location. In contrast, we found that both eye and hand movements curve away from the target location of the other effector when they are performed simultaneously toward different locations. Accordingly, saccade and reach end points were shifted away from the other effector's target location. Our results provide evidence for a shared attentional mechanism for selecting saccade and reach targets for coordinated eye and hand movements.

Previous research has reported contradictory evidence for shared vs. separate attentional systems for eye and hand movements. Our results add to previous findings by showing that the systems involved in planning eye and hand movements are overlapping (Beurze et al. 2009; Levy et al. 2007; Song and McPeek 2015; Wolf et al. 2015). This may facilitate a tight coupling and high coordination between both effector systems (cf. Moher and Song 2016; van Donkelaar 1997). However, in our experiment participants were able to move their eyes and hand to different locations. This suggests that some parts of the systems involved in movement planning are separate for the eyes and hand. This is in line with imaging studies that found distinct brain activation involved in planning eye and hand movements (Dickinson et al. 2003; Tosoni et al. 2008; Van Der Werf et al. 2010).

Our results are inconsistent with the psychophysical study by Jonikaitis and Deubel (2011), in which they argue in favor of separate attentional systems. The lack of deteriorated discrimination performance in combined eye and hand movements might be explained by low task difficulty [2 alternative forced choice (AFC) task]. In this light, a shared attentional mechanism might be able to allocate sufficient attention at both eye and hand target locations to perform the task as good as in the condition where only one movement is made. Similarly, we suggest that Khan et al. (2011) did find evidence for overlapping attentional systems due to higher task difficulty (4 AFC task). We argue that movement curvature is less prone to influences of task difficulty when investigating attentional mechanisms during target selection. Hence, movement curvature seems to be well suited to examine attentional mechanisms involved in movement planning and complements previous results using dual-perceptual-motor tasks.

As postulated by the population coding theory (McSorley et al. 2004; Tipper et al. 1997), a movement curving away from a competing location results from inhibition of the neurons in the motor map (i.e., effector-specific priority map) coding for the movement vector toward the inhibited location. Our findings indicate that while planning a movement to a target in one effector system, the movement vector to the other effectors' target is being inhibited. More specifically, planning a hand movement while simultaneously planning an eye movement to another location leads to competing movement plans, presumably on the effector-specific priority maps. Priority maps have been found in the frontal eye fields, lateral intraparietal area, and superior colliculus for the oculomotor system and in the anterior intraparietal area, the ventral intraparietal area, and the medial intraparietal area, also known as parietal reach region (for a review see Zelinsky and Bisley 2015) for the visuomotor reach system. We speculate that the activation of the other effector's movement vector on the effector-specific priority map results from a connection with the effector-independent priority maps as can be found in the intermediate layers of the superior colliculus (Song and McPeek 2015; Wolf et al. 2015). In more detail, both the hand and eye target location are activated on the effector-independent priority map. This activation is transferred to the effector-specific priority maps where the competition between the two activated locations is resolved by inhibition (see Herwig 2015). The inhibition of the other effector's target location on the effector-specific priority map causes the movement to curve away from the other effector's target location.

Our results show that saccades were initiated faster when the concurrent hand movement was executed to the right compared with the left. Previous research has shown that reaches toward a location ipsilateral to the moving limb are initiated faster than reaches toward a contralateral location (Fisk and Goodale 1985). In our study, reaches were initiated faster into ipsilateral compared with contralateral space. Since our task demanded simultaneous saccade and reach movements, the eyes might have waited for the hand (cf. Khan et al. 2011), which would lead to shorter saccade latencies when the simultaneous hand movement was performed to an ipsilateral compared with a contralateral target location.

In conclusion, when planning simultaneous eye and hand movements, the movement trajectory of one effector curves away and its end point is shifted away from the other effector's target location. This suggests a shared attentional system for coordinated eye and hand movements possibly based on an effector-independent priority map where both effectors' target locations are activated. This activation might be transferred to the effector-specific motor maps where the other effector's target location is being inhibited causing movements that curve away from that location.

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DISCLOSURES

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

AUTHOR CONTRIBUTIONS

T.N. and K.F. conceived and designed research; T.N. performed experiments; T.N. analyzed data; T.N. and K.F. interpreted results of experiments; T.N. prepared figures; T.N. drafted manuscript; T.N. and K.F. edited and revised manuscript; T.N. and K.F. approved final version of manuscript.

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The attractiveness of salient distractors to reaching movements is task dependent

Tom Nissens[1] · Katja Fiehler[1]

Abstract

Previous studies in visual attention and oculomotor research showed that a physically salient distractor does not always capture attention or the eyes. Under certain top-down task sets, a salient distractor can be actively suppressed, avoiding capture. Even though previous studies showed that reaching movements are also influenced by salient distractors, it is unclear if and how a mechanism of active suppression of distractors would affect reaching movements. Active suppression might also explain why some studies find reaching movements to curve towards a distractor, while others find reaching movements to curve away. In this study, we varied the top-down task set in two separate experiments by manipulating the certainty about the target location. Participants had to reach for a diamond present among three circles. In Experiments 1 and 3, participants had to search for the reach targets; hence, the target's location certainty was low. In Experiments 2 and 3, the target's location was cued before the reach; hence, the target's location certainty was high. We found that reaches curved towards the physically salient, color singleton, distractor in the search-to-reach task (Experiments 1 and 3), but not in the cued reach task (Experiments 2 and 3). Thus, the saliency of the distractor only attracted reaching movements when the certainty of the target's location was low. Our findings suggest that the attractiveness of physically salient distractors to reaching movements depends on the top-down task set. The results can be explained by the effect of active attentional suppression on the competition between movement plans.

Keywords Reaching · Attention · Movement curvature · Physical salience · Visual search · Suppression

In everyday life, we manually interact with plenty of objects (e.g., by reaching towards a target object). The path of the reaching movement can be influenced by nontarget objects in the environment. If you need to quickly pick up your USB stick from a cluttered desk, you first have to search for the USB stick and then reach towards it to grab it. Would the reach path be influenced by other objects on the desk? And would this depend on their physical salience? Would the reach path be different if you do not have to search before reaching (e.g., if another person points towards the location of the USB stick)?

Physically salient distractors can capture visual attention and eye movements. For example, a salient distractor captures attention during a visual search task leading to slower response times (Theeuwes, 1992). Moreover, saccades are directed more often towards a high physically salient (HPS) distractor during search (Godijn & Theeuwes, 2002; McPeek, 2006; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). The presence of a distractor also influences the trajectory of saccades directed towards a visual target. Short latency saccades tend to curve towards a distractor, while long latency saccades tend to curve away from a distractor (McSorley, Haggard, & Walker, 2006; see also van Zoest, Donk, & Van der Stigchel, 2012). However, it has been shown that an active suppression process can prevent a physically salient distractor from capturing attention and eye movements (Lamy & Egeth, 2003; Lamy, Leber, & Egeth, 2004; Theeuwes & Burger, 1998). For example, cueing the target before the onset of a search display can omit attentional capture by a distractor (Yantis & Jonides, 1990). Also, distractors did not capture attention or eye movements in blocks with a relatively high proportion of distractor trials (Geyer, Müller, & Krummenacher, 2008). The active suppression of the distractor can take place shortly after the distractor is presented, but only under the right top-down task set. Task properties such as time of cueing, expectancies, relevancy, and feature overlap between the target and distractor, and many more, define the top-down task set. An important component

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of the top-down task set is the level of certainty of the distractor not being a target, which is again influenced by the level of certainty about the target location. For example, when the target location is validly cued on each trial before the target and distractor is presented, there is high certainty that the stimulus presented at the cued location is the target and, importantly, that stimuli presented at noncued locations are distractors. Moreover, the higher the feature overlap between target and distractor, the lower the certainty the distractor is not a target. Only when the certainty the distractor is not a target is high at the moment the distractor is presented, the distractor can be suppressed before it captures attention or the eyes. It has been argued that distractors produce an automatic attend-to-me signal that, under the right top-down task set, can be actively suppressed to prevent actual capture (Sawaki & Luck, 2010). It is unknown if the mechanism of fast active suppression also takes place in the planning of reaching movements.

Several studies found that reach trajectories are influenced by the presence of a salient distractor (Howard & Tipper, 1997; Kerzel & Schönhammer, 2013; Tipper, Howard, & Jackson, 1997; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999; Wood et al., 2011). The influence of distractors on reach trajectories is often explained by competition between multiple movement plans (e.g., one towards the distractor and one towards the target; Cisek & Kalaska, 2005; McSorley, Haggard, & Walker, 2004; Tipper, Howard, & Houghton, 1998, 2000; see also Cisek & Kalaska, 2010; Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015; Gallivan, Chapman, Wolpert, & Flanagan, 2018; Herwig, 2015; Schneider, Einhauser, & Horstmann, 2013; Song, 2017). When competition between the two motor plans has not been resolved at the moment the reaching movement is executed, the initial direction of the movement will be diverted towards the distractor. When the competing movement plan towards the distractor is fully inhibited at the moment the reaching movement is executed, the movement's initial direction will rather be away from the distractor. It has been argued that several experimental factors such as task instructions, the action-relevance of the distractor, the timing between target and distractor, or the cueing or priming procedures can influence the dynamics of the competition between target and distractor during movement planning and execution, and, hence, influence the movement trajectory (Song & Nakayama 2009). Experimental factors can also change the top-down task set under which a reaching movement is planned and performed. One important component of the top-down task set is the level of certainty about the target location. From the literature it seems that reaching movements to a target of which the location is certain tend to curve away from a distractor (e.g., Nissens & Fiehler, 2018; Moehler & Fiehler, 2017), whereas reaching movements tend to curve towards distractors when the target location is uncertain (e.g., Kerzel & Schönhammer, 2013; Moher, Anderson, & Song, 2015; Moher & Song, 2013; Neyedli & Welsh, 2012; Song & Nakayama, 2006, 2008; Welsh, 2011; Welsh & Elliott, 2004; Welsh et al., 1999; Wood et al., 2011). However, these studies differ in many design and task features; the top-down task set (i.e., level of target certainty) is only one. Hence, it is unclear whether the top-down task set can elucidate the mechanism determining when reaching movements curve away versus towards distractors.

In the present study, we examined whether and how the top-down task set (i.e., the certainty of the target location) influences the level and direction in which reaching curvature is affected by distractor saliency. We theorize that, with low target certainty and little active top-down control, the presentation of a salient distractor will activate a movement plan to the distractor, which will compete with the movement plan to the target. This will cause the reaching movement to curve towards the distractor. However, with high target certainty and active top-down control, the movement plan to the salient distractor will be suppressed shortly after its presentation. This will cause the reaching movement to curve away from the distractor. We hypothesize that reaches curve towards a distractor when there is uncertainty about the target location (e.g., when the target has to be searched; Moher et al., 2015; Moher & Song, 2013; Song & Nakayama, 2006, 2008). Curvature away from the distractor is expected when the target location is known (e.g., when the target is cued before the start of the reach; Nissens & Fiehler, 2018). In the first experiment, we asked participants to search for and reach towards a diamond shape presented among three circles. All shapes were presented either in the same color or one circle was presented in a low physically salient (LPS) or in a high physically salient (HPS) color. In the second experiment, the design was exactly the same, with one key difference: A cue was presented together with the onset of the shapes. Hence, participants did not have to search for the target, but could simply follow the cue and reach towards the indicated location. Based on our hypothesis, we expected that reaches would curve more toward the HPS distractor compared with the LPS distractor in the search-to-reach task (Experiments 1 and 3). In contrast, reaches should curve away from the HPS distractor compared with the LPS distractor in the cued reach task (Experiments 2 and 3).

Experiment 1: Search-to-reach task

Experiment 1 aimed to investigate the effects LPS and HPS distractors have on reaching movements if participants need to search for the target in a stimulus display.

Materials and methods

Participants

Twenty volunteers with reported normal or corrected-to-normal vision participated in the experiment. Two participants were excluded due to less than 50% of the trials meeting the inclusion criteria (see below) in at least one of the conditions of interest, resulting in a final sample of 18 participants (13 females, mean age 23 years). All participants were right-handed according to the Edinburgh Handedness Inventory (M = 85.4, SD = 19.9; Oldfield, 1971). All participants performed an Ishihara test (Ishihara, 2004) to ensure normal color vision. Participants gave written informed consent prior to the experiment and received course credits or financial compensation. The study was approved by the ethics committee of the Justus Liebig University Giessen, Department of Psychology and Sports Science, and was in accordance with the 2008 Declaration of Helsinki.

Experimental setup

Stimuli were created using Psychophysics Toolbox (Kleiner et al., 2007) in MATLAB (The MathWorks, Natick, MA, USA) and presented on a VPixx VIEWPixx monitor (1,920 × 1,200 pixels, 120 Hz; VPixx Technologies Inc., Saint-Bruno, QC, Canada). To enable the conversion of LAB color space to RGB color space, the monitor was color calibrated using a Konica Minolta Spectroradiometer CS-2000 (Konica Minolta Holdings Inc., Marunouchi, Tokyo, Japan). Reach movements were recorded with an optoelectronic motion tracking system (Optotrak Certus, Northern Digital Inc., Waterloo, ON, Canada), which registered an infrared marker placed on the fingernail of the right index finger with a sampling rate of 250 Hz. The motion tracking system was controlled via MATLAB using the Optotrak Toolbox created by V. H. Franz (http://www.ecogsci.cs.uni-tuebingen.de/OptotrakToolbox). Monocular movements of participants' right eye were recorded via a head mounted video-based EyeLink II (SR Research, Mississauga, ON, Canada) with a sampling rate of 250Hz. Participants' head was positioned on a chin rest at a distance of 48 cm from the screen.

Stimuli

The experimental stimuli are depicted in Fig. 1a. The start display consisted of an eye fixation circle (0.42 vd = visual degrees radius) presented 2.5 vd below screen center. The outlined circle indicating the finger start position (0.42 vd radius) was presented 1.5 vd below the eye fixation circle. In the task display, the finger start position circle was removed and the four shapes (1.25 vd, 11mm radius), comprising three distractor circles and one target diamond, were positioned on an imaginary arc (10 vd, 88 mm radius) around eye fixation with 36 angular degrees between neighboring shapes.

All stimulus colors were defined in LAB color space which was created by the International Commission on Illumination (CIE) in an attempt to develop a perceptually uniform color space. In this color space, the distance between two colors in color space approximates the perceptual distance between those colors. LAB colors are defined in three coordinates: Lightness (≈luminance), A (green–red axis), and B (blue–yellow axis). The background (LAB: 50, 0, 0) and the shapes were isoluminant (i.e., same lightness). Eye fixation and finger start positions were in black (LAB: 0, 0, 0). The target color was red (LAB: 50, 75, 30); the low physical salience (LPS) color was reddish pink (LAB: 50, 91, 14); the high physical salience (HPS) color was blue (LAB: 50, 30, −75). The difference in chroma between the different shape colors was minimal. The distance in color space between the target color and the HPS color (114.24) was about five times the distance between the target color and the LPS color (22.63).

Procedure

The trial schedule is illustrated in Fig. 1a. The task of the participant was to reach as quickly and as accurately as possible for the diamond target shape while ignoring all other shapes and keeping their gaze on the eye fixation circle. The target appeared at any of the four shape locations with equal probability. On 50% of trials, all shapes had the same color (baseline condition). On 50% of trials one of the distractor circles was in a different color; of those trials, 50% were in the LPS color and 50% in the HPS color. The physical salient distractor circle could appear at any of the nontarget positions with equal probability.

The experiment consisted of two sessions, each consisting of 816 experiment trials, leading to a total of 1,632 trials per participant. Each session took about 60 to 90 minutes, including the setup of the participant and were performed on separate days. Participants took a break after each 102 trials. At the beginning of the first session, participants completed two practice blocks of 25 trials each. At the beginning of the second session, participants completed only one practice block of 25 trials. After each practice block the average reach latency was displayed and participants were encouraged to decrease reach latency. In the practice blocks all trials were baseline condition trials (i.e., all shapes had the same color).

Each trial started with the presentation of the start display. Then, the participants gaze and finger position were evaluated. When the participant's finger was at the start circle (finger position within 5 mm in the x, y dimension and within 3 mm in z dimension from the center of the start circle), drift correction was performed, followed by a reevaluation of the finger position to ensure the participant had not moved their finger during drift correction. If participants did not have their finger

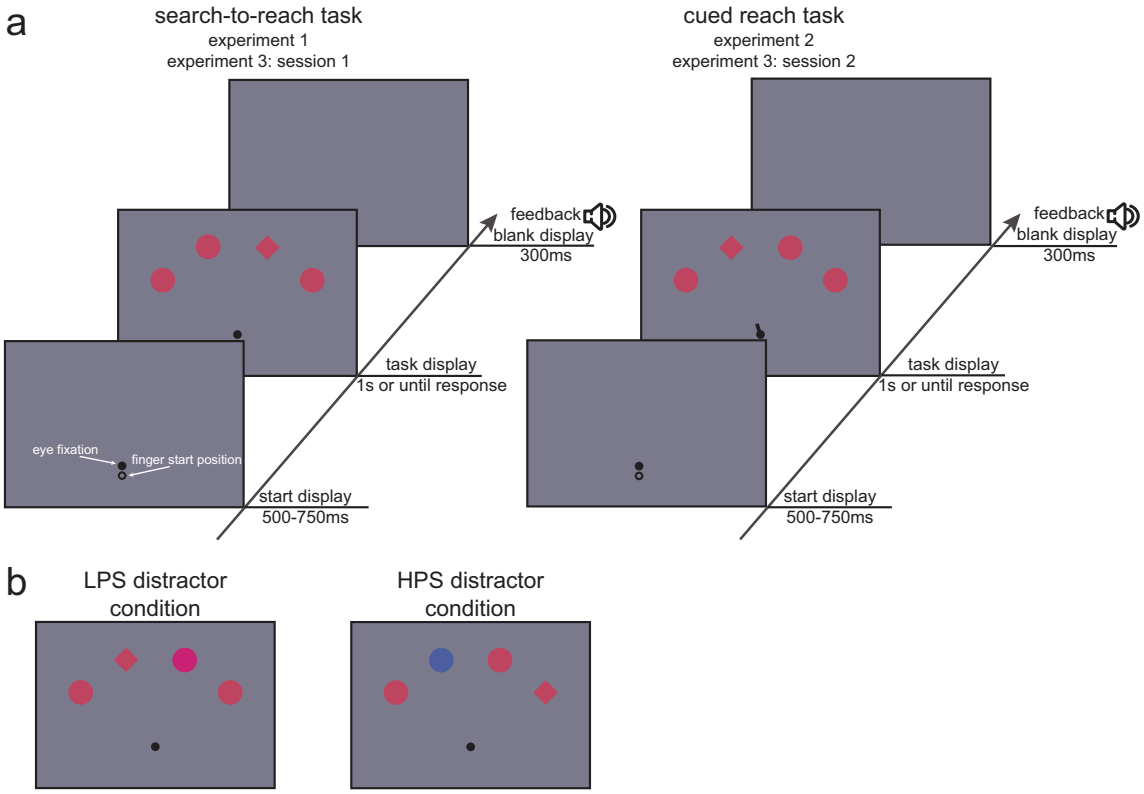

Fig. 1 Experimental procedure. **a** Sequence of trial events. Participants had to reach for a diamond shape presented among circles. In Experiment 1 and in the first session of Experiment 3, the diamond shape had to be searched and reached for. In Experiment 2 and in the second session of Experiment 3, the diamond shape was cued and had to be reached for. **b** Example task display for the low physical salience (LPS) distractor condition (left) and high physical salience (HPS) distractor condition (right). In Experiments 1 and 2, both LPS and HPS distractors were presented. In Experiment 3, only the HPS distractor was presented

at the start position after 600 ms the text "Finger not at start" was displayed until they moved their finger to the start position. If the finger position reevaluation was negative, the text "Hand moved too early. Trial restarts . . ." was displayed, and the trial was restarted. The fixation/start screen was presented for a randomized minimum time of 500 ms or 750 ms, or until gaze and finger position were evaluated positively. Next the task display consisting of the four shapes comprising three distractor circles and one target diamond was presented. Participants had to search for the diamond and then reach as quickly and as accurately as possible to it. Participants were instructed to fixate the fixation circle during the trial. Trials in which participants moved their eyes were excluded offline (see below). The task display was presented for a maximum of 1,000 ms. However, when a reach end was detected earlier the task display was removed 150ms later. A reach end was detected when the finger velocity dropped below 20 mm/s after moving more than 40 mm from the start position within 1,000 ms after the onset of the task display. Note that the reach onset detection procedure differed between the online and off-line analysis. The trial was evaluated as correct if the reach endpoint was within 28 mm from the center of the target shape. In any other case the trial was evaluated as incorrect. Participants received feedback about their performance after the offset of the task display in the form of a beep (high pitch = correct, low pitch = incorrect). The intertrial interval was 300 ms.

Analyses

Finger position coordinates were rotated online so that x and y were aligned to the horizontal and vertical axis of the monitor screen and, consequently, z was the axis perpendicular to the monitor screen. Small sections of missing reach data, due to the temporarily blocked view of the marker on the fingernail by the Optotrak, were interpolated for each dimension separately using the interp1 function within MATLAB. In the off-line analysis, the starting point of a reach was defined as the first sample of four consecutive vector velocity readings greater than 25 mm/s where there was a total acceleration of 20 mm/s^2 across the four points. The end point of a reach was defined as the point in time when the velocity dropped below 20 mm/s (see Chapman & Goodale, 2010). Saccades' start point and end point were detected online using minimum velocity and acceleration criteria of 30 vd/s and 8,000 vd/s^2, respectively.

Trials were excluded when at least one of the following criteria was reached: a saccade of >2.5 vd was detected; the reach end was more than 28 mm away from the target center;

the reach start was more than 10 mm from the finger start circle; the maximum reach velocity was >5,000 mm/s; the reach latency was <200 ms or >600 ms. Over all criteria and all participants, 7.64% of trials were excluded.

To determine whether the reaches deviated towards or away from the physical salient distractor, we calculated an attraction score (see Moher et al., 2015). The attraction score denotes the distance at a certain point along the trajectory between the baseline condition and one of the physically salient distractor conditions relative to the physically salient distractor's location, with positive value denoting deviation towards (i.e., attraction) and negative value denoting deviation away. In more detail, using only the x and y coordinates, the reach movements were rotated and shifted so that the x coordinate of the end and start point equaled zero and the y coordinate of the start point equaled zero. To normalize the reach movement, reaches were resampled to 101 samples equally spaced along the amplitude (y dimension) using the normalizeFDA function of functional data analysis (FDA) for the reach trajectories toolbox in MATLAB (see Gallivan & Chapman, 2014; Ramsay & Silverman, 2005). For each combination of target and distractor location and each distractor condition (baseline vs. LPS vs. HPS) separately, we calculated the average reach movement. Next, for each combination of target and distractor location, we subtracted the baseline reach from the LPS and HPS reach. For target and distractor location combinations where the distractor was to the left of the target, the baseline corrected reach x values were multiplied by −1. Hence, positive x values denote deviation towards the physical salient distractor and negative x values denote deviation away from the physical salient distractor. The resulting x values of the reach movement are the values of the attraction score.

To determine when during the reaching movement the distractor attracted the trajectory, we performed a cluster-based analysis (see Maris & Oostenveld, 2007; Moher et al., 2015). The t statistic for the distractor attraction score was calculated for each point along the normalized space, then the largest cluster of consecutive t values, for which $p < .05$ was detected, and the sum of the t values in that cluster were calculated. Next, the order of t values was randomly permuted 100,000 times, and the same cluster analysis was performed to get a distribution of possible cluster sizes. A kernel density estimation was used to estimate a probability density function (PDF) from the distribution of possible cluster sizes. If the observed cluster size was significant, with $p < .05$ under the estimated PDF, the portion of the reaching movement related to this cluster is reported to be affected by the distractor.

Reach curvature was calculated by averaging the attraction score values. Hence, a positive reach curvature denotes deviation towards the distractor and negative values deviation away.

Results

Main results

A one-way repeated-measures ANOVA with the factor distractor color (LPS vs. HPS vs. baseline) revealed that reaching movement curvature was influenced by the distractor color, $F(2, 34) = 5.645$, $p = .008$, $\eta_p^2 = 0.249$. Post hoc t tests revealed that reaching movement curvature was higher for the HPS distractor compared with the LPS distractor condition, $t(17) = 2.706$, $p_{holm} = 0.045$, $d_z = 0.64$. Furthermore, the movement curvature was significantly different from baseline in the HPS distractor condition, $t(17) = 2.663$, $p_{holm} = 0.045$, $d_z = 0.63$, but not in the LPS distractor condition, $t(17) = 0.693$, $p_{holm} = 0.5$, $d_z = 0.16$. Thus, reaches curved more towards the distractor presented in the HPS color compared with the LPS color (see Fig. 2b). This result was confirmed by the distractor attraction scores that were higher for the HPS than the LPS distractor condition from 6% to 69% of the reaching movement (see Fig. 2a). Hence, the reaching movement deviated stronger to the HPS distractor compared with the LPS distractor from 6% to 69% of the normalized reach amplitude.

The reach latency did not differ significantly between the distractor color conditions, $F(2, 34) = 2.458$, $p = .101$, $\eta_p^2 = 0.126$. Thus, the differences in reaching movement trajectory between the LPS, HPS, and baseline conditions are not related to differences in reach latency. However, the movement time was significantly different between the distractor color conditions, $F(2, 34) = 8.699$, $p < .001$, $\eta_p^2 = 0.339$. Post-hoc t-tests revealed that the movement time was longer when the HPS distractor was present (342 ms) compared to baseline (338 ms), $t(17) = 4.361$, $p_{holm} < .001$, $d_z = 1.03$. However, the movement time was not significantly different between LPS trials (339 ms) and HPS trials, $t(17) = 2.421$, $p_{holm} = 0.054$, $d_z = 0.57$, nor baseline, $t(17) = 1.309$, $p_{holm} = 0.208$, $d_z = 0.31$. The small increase in movement time on HPS trials compared with baseline trials is likely to be related to the increased curvature on HPS trials (see Table 1 for descriptive statistics).

Exploratory results

From the eye movement literature, it is known that the effect of distractor presence on movement properties can depend on the latency of the movement (e.g., McSorley et al., 2006) or the distance between the target and the distractor (e.g., Godijn & Theeuwes, 2002). Similar effects have been found for reaching movements showing a stronger movement curvature for distractors located close than far from the target (Moehler & Fiehler, 2017). Moreover, shorter reach latencies seem to lead to more curved trajectories in a search-to-reach task (Song & Nakayama, 2008). Based on these previous findings, we performed exploratory analyses and examined whether reach latency and/or the distance between the target and the

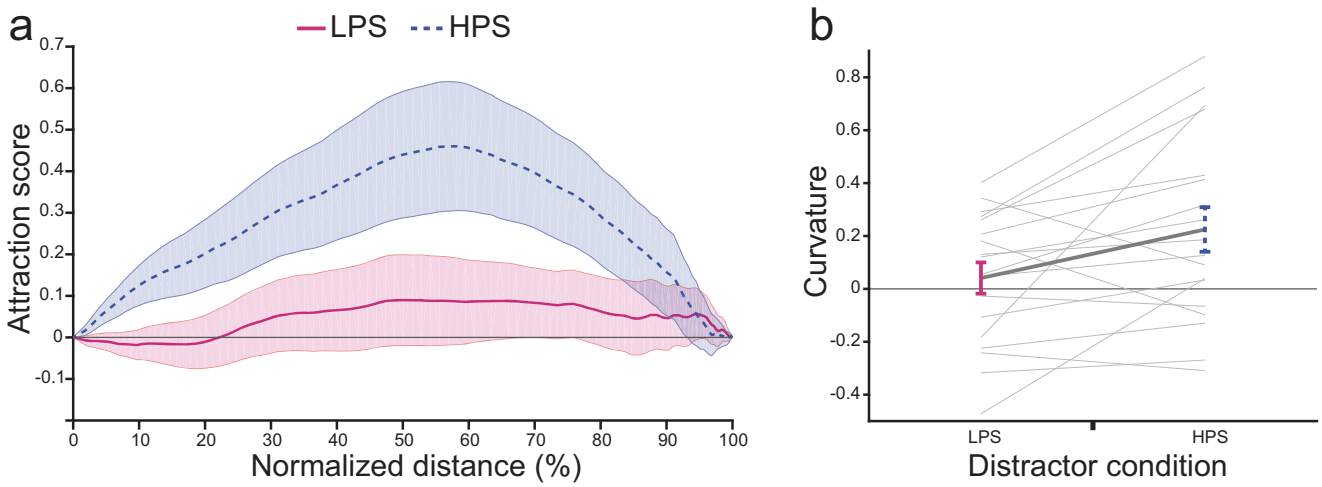

Fig. 2 Results of Experiment 1: search-to-reach task. **a** Distractor attraction scores along the normalized movement amplitude. The blue line shows the attraction score for the high physical salience (HPS) distractor condition. The red line shows the attraction score for the low physical salience (LPS) distractor condition. Positive values indicate finger position deviated toward the distractor compared with baseline. **b** Curvature for the LPS distractor condition (red) and HPS distractor condition (blue). Positive values indicate that the reaching movement deviated toward the distractor. All error bars reflect between-subjects *SEM*

distractor interacted with the influence of the physical salience of the distractor on reach curvature (see Fig. 3). On the individual participant level, we performed a median-split based on reach latency (short vs. long) for each combination of target and distractor location, separately. Next, we grouped the combinations of target and distractor position based on the distance between them (one, two, or three). A three-way repeated-measures ANOVA was performed with the factors reach latency (short vs. long), distractor distance (one vs. two vs. three), and distractor color (LPS vs. HPS). The reported *p*-values were Greenhouse–Geisser corrected for sphericity where applicable; noncorrected degrees of freedom are reported. Apart from the main effect of distractor color, $F(1, 17) = 6.973$, $p = .017$, $\eta_p^2 = 0.291$, a two-way and a three-way interaction effect were significant: distractor distance, and distractor color, $F(2, 34) = 4.328$, $p = .021$, $\eta_p^2 = 0.203$, and distractor distance, distractor color, and reach latency, $F(2, 34) = 3.951$, $p = .029$, $\eta_p^2 = 0.189$. The two-way interaction effect seems related to a larger difference in curvature between the LPS and HPS distractor when the distractor was two positions away from the target (see Fig. 3). Post hoc *t* tests revealed that the difference between the LPS and HPS distractor was only significant when the distractor was two positions away from the target, LPS vs. HPS for distractor distance one, $t(17) = 0.169$, $p_{holm} = 0.868$, $d_z = 0.040$; distance two: $t(17) = 3.300$, $p_{holm} = 0.012$, $d_z = 0.778$; distance three: $t(17) = 1.037$, $p_{holm} = 0.628$, $d_z = 0.244$. Moreover, the three-way interaction effect seems to be driven by a larger difference in curvature between the LPS and HPS distractor on short compared with long reach latency trials when the distractor was two positions away from the target (see Fig. 3). Post hoc *t* test revealed that the difference between LPS and HPS distractor was only significant on short latency saccades when the distractor was two positions away from the target, LPS vs. HPS for short latency and distractor distance one: $t(17) = 0.461$, $p_{holm} = 1.000$, $d_z = 0.109$; distance two: $t(17) = 3.937$, $p_{holm} = 0.006$, $d_z = 0.928$; distance three: $t(17) = 0.746$, $p_{holm} = 1.000$, $d_z = 0.176$; long latency and distractor distance one: $t(17) = 0.405$, $p_{holm} = 1.000$, $d_z = 0.096$; distance two: $t(17) = 0.799$, $p_{holm} = 1.000$, $d_z = 0.188$; distance three: $t(17) = 0.649$, $p_{holm} = 1.000$, $d_z = 0.153$. All other main and interaction effects were nonsignificant, distractor distance: $F(2, 34) = 1.335$, $p = .277$, $\eta_p^2 = 0.073$; reach latency: $F(1, 17) = 1.364$, $p = .259$, $\eta_p^2 = 0.074$; Distractor Distance × Reach Latency: $F(2, 34) = 0.686$, $p = .466$, $\eta_p^2 = 0.039$;

Table 1 Descriptive statistics for reach movement data from Experiments 1–3

	Latency (ms)	Movement time (ms)
Experiment 1		
Baseline	294 ± 24	338 ± 46
LPS	295 ± 26	339 ± 45
HPS	296 ± 27	342 ± 44
Experiment 2		
Baseline	291 ± 48	318 ± 51
LPS	291 ± 48	317 ± 50
HPS	290 ± 49	319 ± 50
Experiment 3		
Search baseline	301 ± 30	298 ± 32
Search HPS	303 ± 31	304 ± 32
Cue baseline	284 ± 86	301 ± 35
Cue HPS	285 ± 36	301 ± 36

Note. Error terms reflect standard deviation. LPS = low physically salient; HPS = high physically salient

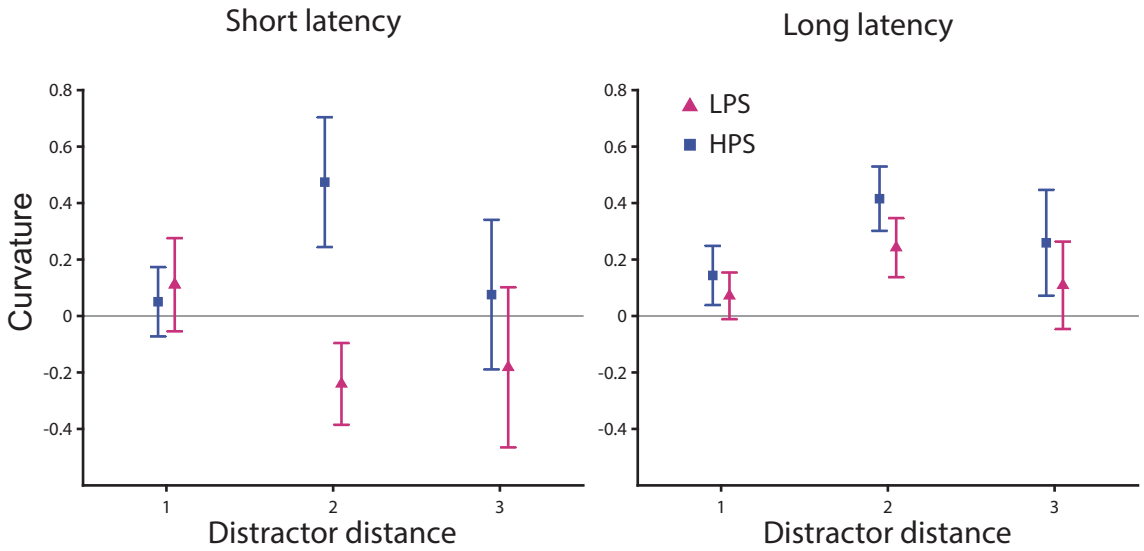

Fig. 3 Exploratory results of Experiment 1: search-to-reach task. Curvature for the low physical salience (LPS) distractor (red) and high physical salience (HPS) distractor (blue) condition depending on the distance between the position of the target and the distractor for short latency (left) and long latency (right) reaching movements. All error bars reflect between-subjects *SEM*

Distractor Color × Reach Latency: $F(2, 34) = 1.181$, $p = .292$, $\eta_p^2 = 0.065$.

Experiment 2: Cued reach task

Experiment 2 aimed to investigate the effect a low and high physically salient distractor have on reaching movements when the target is cued upon stimulus display presentation.

Materials and methods

Participants

Twenty-two volunteers with reported normal or corrected-to-normal vision participated in the experiment. Four participants were excluded due to less than 50% of trials meeting the inclusion criteria in at least one of the conditions of interest, resulting in a final sample of 18 participants (10 females, mean age 24 years). All participants were right-handed according to the Edinburgh Handedness Inventory ($M = 81$, $SD = 18.4$; Oldfield, 1971). All participants performed an Ishihara test (Ishihara, 2004) to ensure normal color vision. Participants gave written informed consent prior to the experiment and received course credits or financial compensation. The study was approved ethics committee of the Justus Liebig University Giessen and was in accordance with the 2008 Declaration of Helsinki.

Experimental setup

The setup was the same as in the first experiment.

Stimuli

The stimuli were the same as in Experiment 1, except from one difference: To transform the search-to-reach task into a cued reach task, a black line (0.39 vd; LAB: 0, 0, 0) was added to the task display pointing out from the eye fixation circle towards the target location. Please note that the cue appeared simultaneously with the shapes. The cue was presented together with, and not before the onset of, the shapes to avoid preplanning of the reaching movement (i.e., to be sure the shapes were present when the movement was planned).

Procedure

The procedure was the same as in the first experiment, with the only difference that participants were now told to reach towards the shape indicated by the centrally presented cue (see Fig. 1a).

Analysis

The analysis was the same as in Experiment 1. We used the same exclusion criteria, resulting in an overall trial exclusion rate of 7.79%.

Results

Main results

A one-way repeated-measures ANOVA with the factor distractor color (LPS vs. HPS vs. baseline) revealed that reaching movement curvature was not influenced by the

distractor color, $F(2, 34) = 0.642$, $p = .533$, $\eta_p^2 = 0.036$. Also, the attraction score was not significantly different between any of the conditions along the normalized reach amplitude (see Fig. 4a).

The reach latency did not differ significantly between the distractor color conditions, $F(2, 34) = 0.527$, $p = .595$, $\eta_p^2 = 0.030$. The movement time was significantly different between the distractor color conditions, $F(2, 34) = 4.241$, $p = .023$, $\eta_p^2 = 0.20$. However, none of the post hoc t tests were significant after Holm correction, HPS vs. LPS: $t(17) = 2.530$, $p_{holm} = 0.066$, $d_z = 0.596$; HPS vs. Baseline: $t(17) = 1.755$, $p_{holm} = 0.194$, $d_z = 0.414$; LPS vs. Baseline: $t(17) = 1.407$, $p_{holm} = 0.194$, $d_z = 0.332$ (see Table 1 for descriptive statistics).

Exploratory results

As in Experiment 1, we tested whether the effect of distractor saliency on reach curvature depends on the reach latency and the distance between the target and the distractor (see Fig. 5). We performed a three-way ANOVA with the factors reach latency (short vs. long), distractor distance (one vs. two vs. three), and distractor color (LPS vs. HPS). The interaction effect between reach latency and distractor color was not significant, $F(1, 17) = 0.986$, $p = .335$, $\eta_p^2 = 0.055$. None of the main or other interaction effects were significant, distractor distance: $F(2, 34) = 0.123$, $p = .720$, $\eta_p^2 = 0.018$; reach latency: $F(1, 17) = 0.005$, $p = .943$, $\eta_p^2 = 0.000$; distractor color: $F(1, 17) = 0.137$, $p = .716$, $\eta_p^2 = 0.008$; Distractor Distance × Reach Latency: $F(2, 34) = 0.544$, $p = .528$, $\eta_p^2 = 0.031$; Distractor Distance × Distractor Color: $F(2, 34) = 0.150$, $p = .783$, $\eta_p^2 = 0.009$; Distractor Distance × Distractor Color × Reach Latency: $F(2, 34) = 0.745$, $p = .434$, $\eta_p^2 = 0.042$. Thus, the influence of distractor salience does not significantly depend on the reach latency.

Experiment 3: Cued reach versus search-to-reach tasks

Experiment 3 aimed to directly compare the effect of a highly physically salient distractor on reaching movements in a search-to-reach task and a cued reach task by conducting a within-subjects experiment.

Materials and methods

Participants

Thirty-nine volunteers with reported normal or corrected-to-normal vision participated in the experiment. Eleven participants were excluded due to less than 50% of trials meeting the inclusion criteria in at least one of the conditions of interest, resulting in a final sample of 28 participants (21 females, mean age 25 years). The sample size was estimated using G*Power (Faul, Erdfelder, Lang, & Buchner, 2007) based on the effect size of the between subject effect of experimental task (Experiment 1 vs. Experiment 2) on reach curvature during HPS trials, $d_z = 0.609$, with α error probability = 0.05, and power = 0.85. This resulted in a sample size estimate of 27 participants. Twenty-eight participants were tested to counterbalance the order of the task between participants. All participants were right-handed according to the Edinburgh Handedness Inventory ($M = 82$, $SD = 16.3$; Oldfield, 1971). All participants performed an Ishihara test (Ishihara, 2004) to

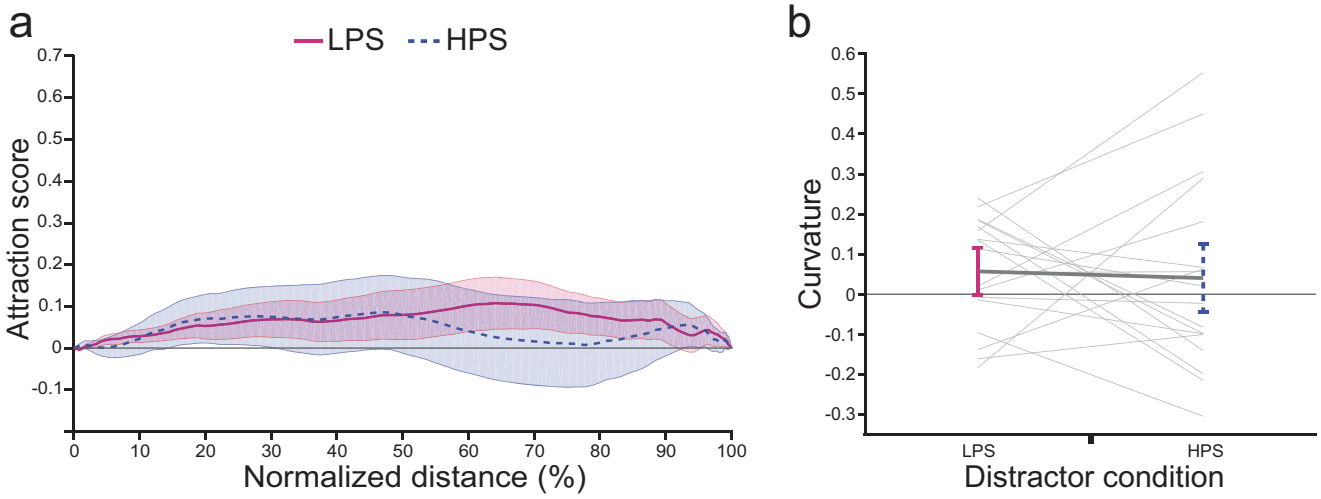

Fig. 4 Results of Experiment 2: cued reach task. **a** Distractor attraction scores along the normalized movement amplitude. The blue line shows the attraction score for the high physical salience (HPS) distractor condition. The red line shows the attraction score for the low physical salience (LPS) distractor condition. Positive values indicate finger position deviated toward the distractor compared with baseline. **b** Curvature for the LPS distractor condition (red) and HPS distractor condition (blue). Positive values indicate that the reaching movement deviated towards the distractor. All error bars reflect between-subjects *SEM*

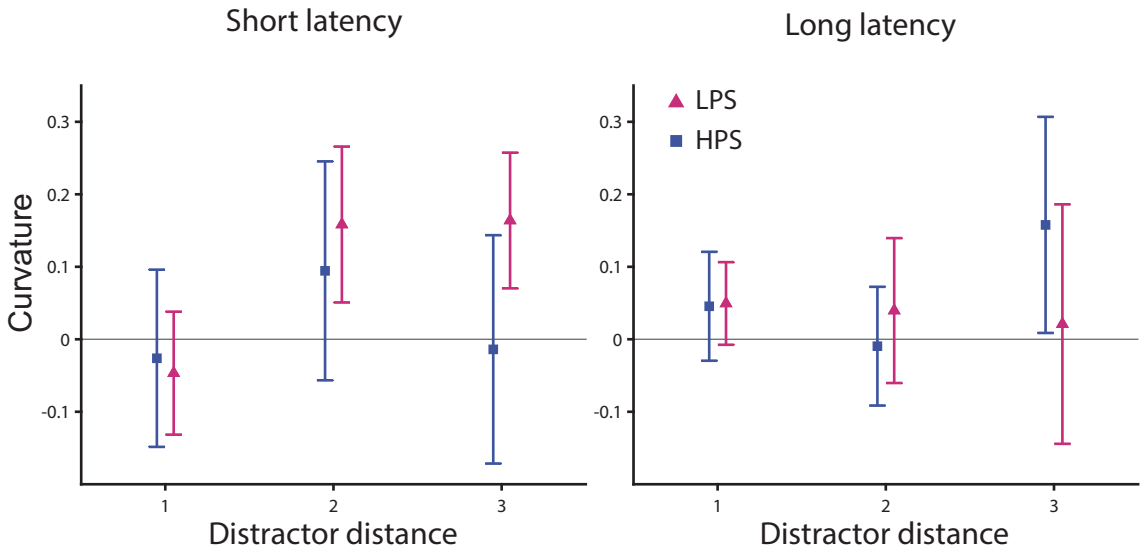

Fig. 5 Exploratory results Experiment 2: cued reach task. Curvature for the low physical salience (LPS) distractor (red) and high physical salience (HPS) distractor (blue) condition depending on the distance between the position of the target and the distractor for short latency (left) and long latency (right) reaching movements. All error bars reflect between-subjects *SEM*

ensure normal color vision. Participants gave written informed consent prior to the experiment and received course credits or financial compensation. The study was approved by the ethics committee of the Justus Liebig University Giessen and was in accordance with the 2008 Declaration of Helsinki.

Experimental setup

The setup was the same as in Experiments 1 and 2.

Stimuli

The stimuli were the same as in Experiments 1 and 2. However, only the baseline and HPS distractor conditions were included.

Procedure

The procedure was largely the same as in Experiments 1 and 2, with some important differences (see Fig. 1a): (i) Participants performed two sessions on two separate days. In one session they performed the cued reach task and on the other the search-to-reach task. The order was counterbalanced between participants. (ii) During the practice blocks, participants received written feedback about their performance presented at fixation level for 750 ms on every trial (correct, too slow, eyes moved, wrong shape, or correct but too slow). (iii) In one third of the trials, the HPS distractor was presented, in the other two thirds of trials, no salient distractor was presented (i.e., baseline trials). Each session consisted of 720 trials divided into six blocks. (iv) Participants were encouraged to perform their reach as quickly as possible by introducing a variable deadline of movement duration. If participants reached the target after this deadline the trial would be marked as too slow and they would receive negative feedback. The variable deadline was based on the 80th percentile of the time it took to reach the target for every participant and target location separately. Based on the average performance in Experiments 1 and 2, the variable deadline was set to 650 ms until participants performed 10 correct trials to each target location.

Analysis

The analysis was the same as in Experiments 1 and 2. We used the same exclusion criteria resulting in an overall trial exclusion rate of 2.45%.

Results

Main results

The two-way ANOVA with factors distractor color (baseline vs. cue) and task (search-to-reach vs. cued reach) revealed a significant main effect of distractor color, $F(1, 27) = 12.91$, $p = .001$, $\eta_p^2 = 0.323$, and task, $F(1, 27) = 12.86$, $p = .001$, $\eta_p^2 = 0.323$, and a significant interaction effect between distractor color and task, $F(1, 27) = 24.89$, $p < .001$, $\eta_p^2 = 0.48$. Post hoc t tests revealed that reaching curvature towards the HPS distractor was larger during the search-to-reach task compared with the cued reach task (see Fig. 6b), $t(27) = 4.989$, $p_{holm} < .001$, $d_z = 0.943$. The curvature on HPS trials compared to baseline was larger in the search-to-reach task, $t(27) = 4.497$, $p_{holm} < .001$, $d_z = 0.850$, but not different in the cued reach

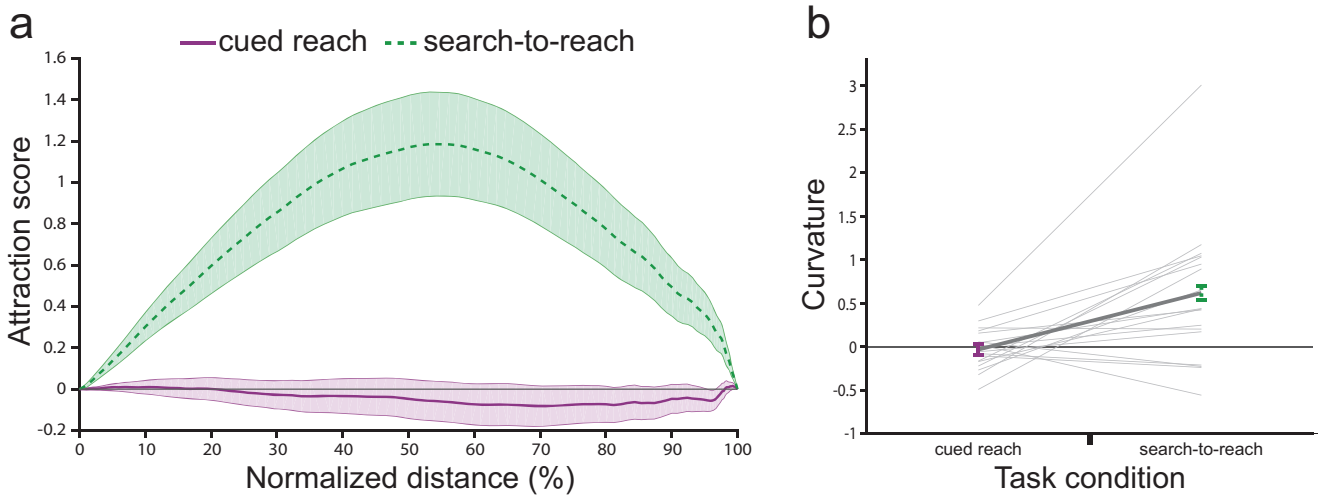

Fig. 6 Results of Experiment 3. **a** Distractor attraction scores along the normalized movement amplitude. The green line shows the attraction score for the high physical salience (HPS) distractor in the search-to-reach task. The purple line shows the attraction score for the HPS distractor in the cued reach task. Positive values indicate that the finger position deviated toward the distractor compared with baseline. **b** Curvature for the cued reach task (purple) and search-to-reach task (green). Positive values indicate that the reaching movement deviated towards the HPS distractor. All error bars reflect between-subjects *SEM*

task, $t(27) = 0.612$, $p_{holm} = 0.546$, $d_z = 0.116$. The attraction score (see Fig. 6a) revealed that in the search-to-reach task the reaching movement was attracted towards the HPS distractor from 3% to 97% along the normalized amplitude compared with the cued reach task and from 3% to 99% compared with baseline.

To investigate whether the reach latency differed between the two tasks and the distractor conditions, a two-way ANOVA with factors task (search vs. cue) and distractor condition (HPS vs. baseline) was performed which revealed a main effect of task, $F(1, 27) = 8.652$, $p = .007$, $\eta_p^2 = 0.243$, and a main effect of distractor condition, $F(1, 27) = 6.088$, $p = .020$, $\eta_p^2 = 0.184$. The interaction effect was not significant, $F(1, 27) = 0.339$, $p = .565$, $\eta_p^2 = 0.012$. Post hoc *t* tests revealed that the latency was higher in the search-to-reach task (302 ms) compared with the cued reach task, 285 ms, $t(27) = 4.183$, $p_{holm} < .001$, $d_z = 0.791$. Reaching movements were initiated later when an HPS distractor was present (294 ms) compared with baseline, 293 ms, $t(27) = 2.798$, $p_{holm} = .007$, $d_z = 0.529$.

Moreover, a two-way ANOVA was performed to investigate whether the movement time differed between task (search vs. cue) and distractor conditions (HPS vs. baseline). A main effect of distractor condition, $F(1, 27) = 18.120$, $p < .001$, $\eta_p^2 = 0.402$, and interaction between task and distractor condition, $F(1, 27) = 20.015$, $p < .001$, $\eta_p^2 = 0.426$, was observed. However, there was no main effect of task, $F(1, 27) = 0.0001$, $p = .98$, $\eta_p^2 = 0.000$. Post hoc *t* tests revealed that the movement duration was longer on HPS (294 ms) compared to baseline, 293 ms trials, $t(27) = 4.001$, $p_{holm} < .001$, $d_z = 0.756$. Regarding the interaction effect, the difference between HPS and baseline condition was significant for the search-to-reach task, $t(27) = 5.03$, $p_{holm} < 0.001$, $d_z = 0.951$, with longer movement times when the HPS distractor was present (304 ms) compared with baseline (298 ms); but not for the cued reach task, $t(27) = 0.407$, $p_{holm} = 0.687$, $d_z = 0.077$.

Exploratory results

Similarly, as in Experiments 1 and 2, we tested whether the effect of saliency on reaching movements depended on the distance between the target and distractor, the latency of the movement or any interaction of those factors with the effect of task (see Fig. 7). Therefore, we performed a three-way ANOVA with factors reach latency (short vs. long), distractor distance (one vs. two vs. three), and task (cue vs. search). We found a main effect of task, $F(1, 27) = 16.969$, $p < .001$, $\eta_p^2 = 0.386$, and distractor distance, $F(2, 54) = 4.960$, $p = .013$, $\eta_p^2 = 0.155$; but no main effect of latency, $F(1, 27) = 1.472$, $p = .24$, $\eta_p^2 = 0.052$. Furthermore, the interaction effect between task and distractor distance was trending, $F(2, 54) = 3.138$, $p = .068$, $\eta_p^2 = 0.104$. All other interaction effects were nonsignificant, Task × Reach Latency: $F(1,27) = 1.919$, $p = .177$, $\eta_p^2 = 0.066$; Distractor Distance × Reach Latency: $F(2,54) = 0.347$, $p = .682$, $\eta_p^2 = 0.013$; Task × Distractor Distance × Reach Latency: $F(2,54) = 0.324$, $p = .705$, $\eta_p^2 = 0.012$. The post hoc *t* tests for the effect of distractor distance revealed a difference between distractor distance two and one (0.54 vs. 0.17), $t(27) = 3.399$, $p_{holm} = 0.003$, $d_z = 0.642$, and distractor distance two and three (0.54 vs. 0.21), $t(27) = 2.413$, $p_{holm} = 0.035$, $d_z = 0.456$, but not between distractor distance one and three (0.17 vs. 0.21), $t(27) = 0.313$, $p_{holm} = 0.757$, $d_z = 0.059$. Hence, the HPS distractor attracted the reaching movements more when the distractor was two positions away from the target. This is similar to the finding in Experiment 1, where we observed a larger difference in curvature between the LPS

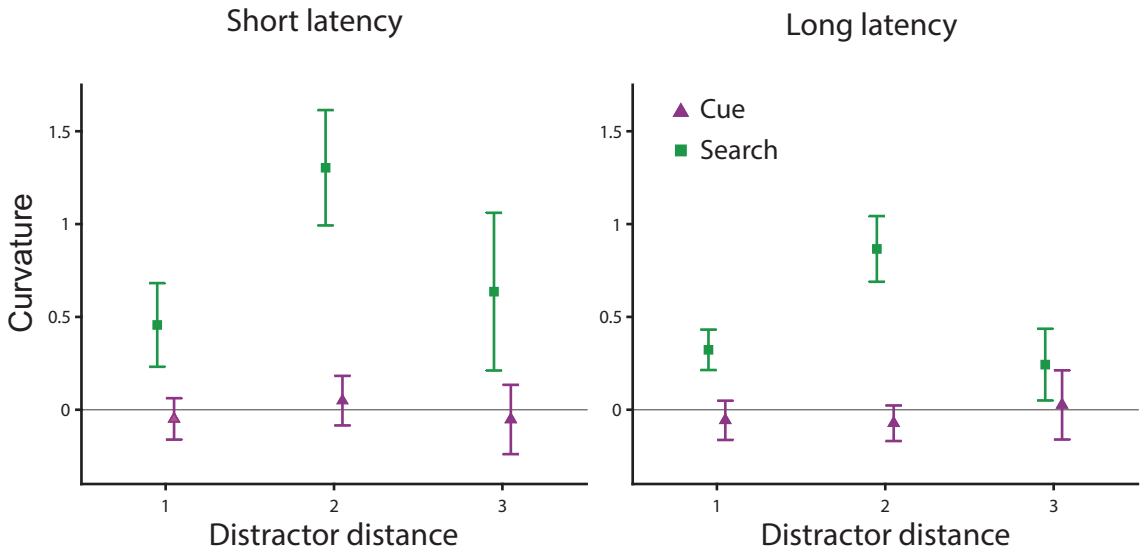

Fig. 7 Exploratory results of Experiment 3. Curvature for the cued reach task (purple) and search-to-reach task (green) over the distance between the position of the target and the distractor for short latency (left) and long latency (right) reaching movements. All error bars reflect between-subjects *SEM*

and HPS condition when the distractor was two positions away from the target.

General discussion

The present study investigated how the top-down task set (i.e., the certainty of the target location) influences the direction and magnitude of the effect that a physically salient distractor has on reaching trajectories. In the search-to-reach task (Experiment 1), when certainty about the target location was low, reaches curved more towards the high physically salient (HPS) distractor than to the low physically salient (LPS) distractor relative to when there was no physically salient distractor present (baseline). Moreover, the trajectory deviated more towards the HPS distractor compared with the LPS distractor from 6% to 69% of the reaching movement. However, in the cued reach task (Experiment 2), when certainty about the target location was high, there was no difference in reach trajectory when there was an HPS distractor or an LPS distractor present compared with baseline. In a direct comparison (Experiment 3), the differences between the search-to-reach task and cued reach task were confirmed. Hence, we showed that a physically salient distractor attracts reach trajectories when the certainty of the target location is low, but not when the certainty of the target location is high.

Our findings suggest that the effect of distractors on reaching movement trajectories is influenced by the level of certainty of the target location during movement planning. In line with previous studies (Moher et al., 2015; Moher & Song, 2013; Song & Nakayama, 2006, 2008; Welsh, 2011; Welsh & Elliott, 2004; Welsh et al., 1999) and with the first part of our hypothesis, we found attraction towards the distractor when certainty was low (Experiments 1 and 3, search-to-reach task). In Welsh et al. (1999), for example, participants had to reach towards a red target that was presented at a random location on a 3 × 3 grid. Note that the certainty of the target location was low. On some trials a yellow distractor was presented at another location on the grid. They found that the reaching movements curved towards the distractor. Our results add to the evidence by showing that reaching trajectories are attracted to an HPS distractor in a search-to-reach task. The results from Experiment 1 can be explained by competition between multiple movement plans (Cisek & Kalaska, 2005; McSorley et al., 2004; Tipper et al., 1998, 2000; see also Cisek & Kalaska, 2010; Gallivan et al., 2015; Gallivan et al., 2018; Herwig, 2015; Schneider et al., 2013; Song, 2017). During movement preparation, a movement plan towards the HPS distractor is activated along with a movement plan towards the target. When a reaching movement is executed, the activation of the movement plan towards the distractor is not fully inhibited, which leads to a reaching movement in which the initial direction is shifted towards the distractor location.

We did not corroborate the second part of our hypothesis, as we did not observe deviation away from the distractor when certainty of the target's location was high (Experiments 2 and 3, cued reach task). We expected that the cue would lead to an active inhibition of the movement plan towards the HPS distractor that would cause the reaching movement to curve away from the distractor. However, this is not what we observed. Based on our results, it is more likely that the suppression occurs on the level of visual attention. The HPS distractor might trigger an "attend-to-me" signal, which, given the top-down task set of high target certainty, leads to active suppression of the distractor (Sawaki & Luck, 2010). We argue that the attentional map, with an already suppressed distractor, is then transferred to the motor

map. There, the movement plan to the distractor is not activated and does not lead to competition with the movement plan. Hence, no curvature away or towards the distractor is observed. However, alternative explanations are warranted: (i) The cue could have activated the movement plan towards the target in a strong fashion relative to the saliency driven activation of the movement plan towards the distractor. However, during the cued reach task, the cue driven movement plan activation might be stronger than the saliency driven movement plan activation, and therefore the movement plan towards the distractor is too weak to affect competition. Consequently, no influence of the distractor on curvature is observed. (ii) Possibly, participants learned to produce a motor command from memory following the cue without engaging in visually guided motor planning. Hence, no influence of the distractor on curvature is observed. We want to point out that all three explanations (distractor suppression, strong target activation, and motor command from memory) predict the movement latency to be shorter in the cued reach task compared with the search-to-reach task, as we did observe. All explanations assume less or no competition for movement selection, which would assume a shorter duration of target selection.

In the study by Welsh and Elliott (2005) a cue presented 1–1.5 seconds prior to target/distractor onset was valid in 75% of trials. On half of the invalid cue trials the distractor was presented at the precued location. They found that the reach was influenced by the distractor when the distractor was at the precued location, but not when the target was validly precued. They argue that the precue leads to a preactivation of the movement plan towards the cued location during movement selection. Therefore, when the target is validly cued, the movement plan to the distractor is activated too late or too weak to influence competition. When the distractor is cued, the activation of the movement plan towards the distractor is increased and does compete with the movement plan towards the target. Similarly, as in our study, the distractor did not influence reaching when the target was cued. However, in their study the cue was presented 1–1.5 seconds before target/distractor was presented. Already before target presentation, a movement plan towards the cued location could have been activated. This was not possible in our study since the cue was presented together with the onset of the target and distractor shapes. Even though our results can be explained by a strong activation of the movement plan towards the target, this could not have been in a preplanned fashion. Alternatively, by cueing the target, the salient distractor could have been suppressed on the attentional priority map which then also affects the motor map. As a consequence, the movement plan towards the distractor would not be activated and thus would not compete with the movement plan towards the target.

Our findings show similarities with the findings in Yantis and Jonides (1990). In their second experiment (reaction time task), a valid cue was either presented before, together, or shortly after the onset of the search display. They showed that an onset distractor slowed down response times when the cue was presented together with or after the search display, but not when the cue was presented earlier. Hence, they show that whether a distractor captures attention depends on the level of certainty about the target location. It has been argued that distractors produce an automatic attend-to-me signal that can be actively suppressed in a top-down fashion to prevent actual capture of attention (Sawaki & Luck, 2010). Whether the distractor is actively suppressed, avoiding capture, depends on the top-down control settings which are task-dependent (Geyer et al., 2008; Lamy & Egeth, 2003; Lamy et al., 2004; Theeuwes & Burger, 1998). An important factor is the certainty of where the target is or, in other words, the certainty that the distractor location is different from the target location. If the certainty of the target location is high the attend-me-signal triggered by the distractor is more likely to be followed by an active suppression of the distractor to avoid attentional capture than when the certainty of the target location is low. The present study shows the consequence of active attentional suppression on the planning of reaching movements. The presentation of the HPS distractor leads to an attend-to-me signal. In the search-to-reach task, this leads to attentional capture and an attraction of the reaching movement to the HPS distractor. However, in the cued reach task, the attend-to-me signal, given the high target certainty, is followed by an active attentional suppression of the HPS distractor. The attentional suppression prevents the attraction of the reaching movements to the HPS distractor.

Our results show that the top-down task set influences the effect a salient distractor has on reaching trajectories. A suggestion for future research to delve into task properties is to vary the level of certainty of the distractor location This suggestion taps into the idea of anticipatory distractor suppression, which has been shown in visual search (e.g., Wang, van Driel, Ort, & Theeuwes, 2019). In case the anticipatory distractor suppression would transfer to reaching movements, we would expect reaching movements to curve less towards distractors presented at an expected location during a search-to-reach task.

In light of a recent paper (Hommel et al., 2019) phrasing valid concerns about the use of the term “attention” and the confusion that comes with it, we would like to clarify how we define attention. In general, throughout this paper, attention refers to the processes influencing the selection of stimuli or locations within the visual domain, which is seen as the consequence of activation and competition in a visual priority map. Correlates of visual priority maps have been found in the intermediate layers of the superior colliculus, the intraparietal cortex and the frontal eye fields (Bisley & Goldberg, 2010; Thompson & Bichot, 2005; White et al., 2017). Moreover, attentional capture and suppression is seen as a consequence of, respectively, the prioritization and inhibition of, for example, a stimulus feature or spatial location within the visual priority map. Priority signals can come from

different sources that are assumed to be initiated in different brain regions. Stimulus salience might originate from early visual cortex and saliency maps in the superficial layers of the superior colliculus (Itti & Koch, 2001). The neural origin of top-down influences is not well understood and might not necessarily be traced back to one neural substrate. However, some evidence has suggested that the anterior cingulate and orbitofrontal cortex play a role in top-down instruction-related value sets (Kennerley, Behrens, & Wallis, 2011).

In this study we show that task-dependent factors do influence the effect a physically salient distractor has on reaching movements. We argue that the top-down task set determines whether the distractor captures visual attention or not, which in turn defines the initial level of activation of movement plans towards the target and distractor and the subsequent amount of competition between them.

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III Appendix

Reaching movements are attracted by stimuli that signal reward

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Abstract

When presented with a set of possible reach targets, the movement trajectory can reveal aspects of the underlying competition for action selection. Current goals and physical salience can affect the trajectory of reaching movements to be attracted towards a distractor. Some studies demonstrated that stimuli associated with reward can also cause an attraction when reaching towards the reward stimulus was previously rewarded and the reward stimulus was physically salient. Here we demonstrate that a non-salient stimulus that signals the availability of reward attracts reaching movements even when moving towards it was never necessary nor rewarded. Moreover, the attraction by reward is particularly evident with short latency movements. We conclude that neither physical salience nor reinforcing the movement towards a stimulus is necessary for reward to gain priority in the selection for action.

Introduction

Movements towards a target can be influenced by the current goals of the observer (Chapman et al., 2014; Nissens & Fiehler, 2018; Moehler & Fiehler, 2017) and the physical salience of the stimuli (Moher, Anderson & Song, 2015; Cisek & Kalaska, 2010; Gallivan, Chapman, Wolpert, & Flanagan, 2018; Herwig, 2015; Schneider, Einhauser, & Horstmann, 2013; Song, 2017). For example, the movement trajectory is often attracted towards a physically salient distractor. This has been explained by competing movement plans during target selection. The movement plan towards the distractor competes with the plan towards the target for action selection. When the competition is not resolved when the reach is initiated, the initial direction of the movement deviates towards the distractor. Consequently, the plan towards the distractor is further suppressed and the movement direction is adjusted so that the reach ends at the target.

Apart from the current goals and physical salience, stimuli associated with reward can influence movement trajectories (Chapman, Gallivan, Wong, Wispinski, & Enns, 2015; Moher, Anderson & Song, 2015; Wirth, Dignath, Pfister, Kunde & Eder, 2016). In previous studies, participants received reward after reaching to a target in a certain color which established an association between that color and reward. On subsequent trials in the same (Chapman et al., 2015; Wirth et al., 2016) or different (Moher et al., 2015) blocks the rewarded color functioned as a distractor. They found that the reaching trajectory was attracted towards the reward-associated distractor. Two points are left open: (i) As reaching towards the reward color was reinforced, it is unknown if the attraction by the reward distractor is due to a learned association between the color and reward or the action of reaching towards the color and reward. This raises the question whether the color itself or the reaching act towards the color gains priority. (ii) As the reward-associated distractor was physically salient (Moher et al., 2015) or presented with only one alternative shape (Chapman et al., 2015; Wirth et al., 2016), it is unknown if a reward distractor would attract reaching movements if it was not physically salient, i.e. presented among multiple differently colored shapes.

There is a growing body of literature showing that stimuli associated with reward attract visual attention and eye movements (Anderson, 2016; Chelazzi, Perlato, Santandrea, & Della Libera, 2013; Failing & Theeuwes, 2018). For example, Failing and colleagues (2015) showed that when participants had to fixate a shape singleton, a non-salient distractor captured the eyes more often when it signaled high compared to low reward. Moreover, this effect was more pronounced in very early saccades. In the current study, we use a similar design to uncover the influence of a reward signaling distractor on reaching movements.

Here, we investigated whether a reward signaling stimulus that was never the target and not physically salient can influence reaching movements towards a target. We expected the reaching movement to be attracted towards the non-physically salient reward signaling distractor driven by an association between color and reward. Since reaching towards the reward signaling color was never

rewarded nor necessary, we can rule out an attraction due to an action-reward association. Furthermore, given that the reward signaling distractor is not physically salient, we can also rule out an initial attraction by saliency that is magnified by reward.

Method

Participants

Twenty-seven volunteers with reported normal or corrected-to-normal vision participated in the experiment. Four participants were excluded due to less than 50% of trials meeting the inclusion criteria in one of the conditions (see Analyses), two participants due to data corruption and one participant for misunderstanding the instructions. This resulted in a final sample of 20 participants (11 males, mean age 25 years). The sample size was estimated using GPower (Faul, Erdfelder, Lang, & Buchner, 2007) based on the effect size of reach curvature observed in a pilot study, n = 4, d_z = 0.87, with α error probability = 0.05, and power = 0.95. This resulted in a sample size estimate of 20 participants. All participants were right-handed according to the Edinburgh Handedness Inventory (M = 78.8, SD = 18.0; Oldfield, 1971). Participants gave written informed consent prior to the experiment and received course credits or financial compensation. In addition, collected reward points were paid out in money (M = 5.25€, SD = 0.47€). The study was approved by the Giessen University ethics committee and was in accordance with the Declaration of Helsinki (2008).

Apparatus

Stimuli were created with the Psychophysics Toolbox (Kleiner et al., 2007) in Matlab and presented on a VIEWPixx monitor (1920x1200 pixels, 120Hz). Reach movements were recorded with an optoelectronic motion tracking system (Optotrak Certus) which registered an infrared marker placed on the fingernail of the right index finger with a sampling rate of 250Hz. Monocular movements of participants' right eye were recorded via a head-mounted video-based EyeLink II with a sampling rate of 500Hz. Participants' head was positioned on a chin rest at a distance of 48 cm from the screen. The experiment was performed in the dark.

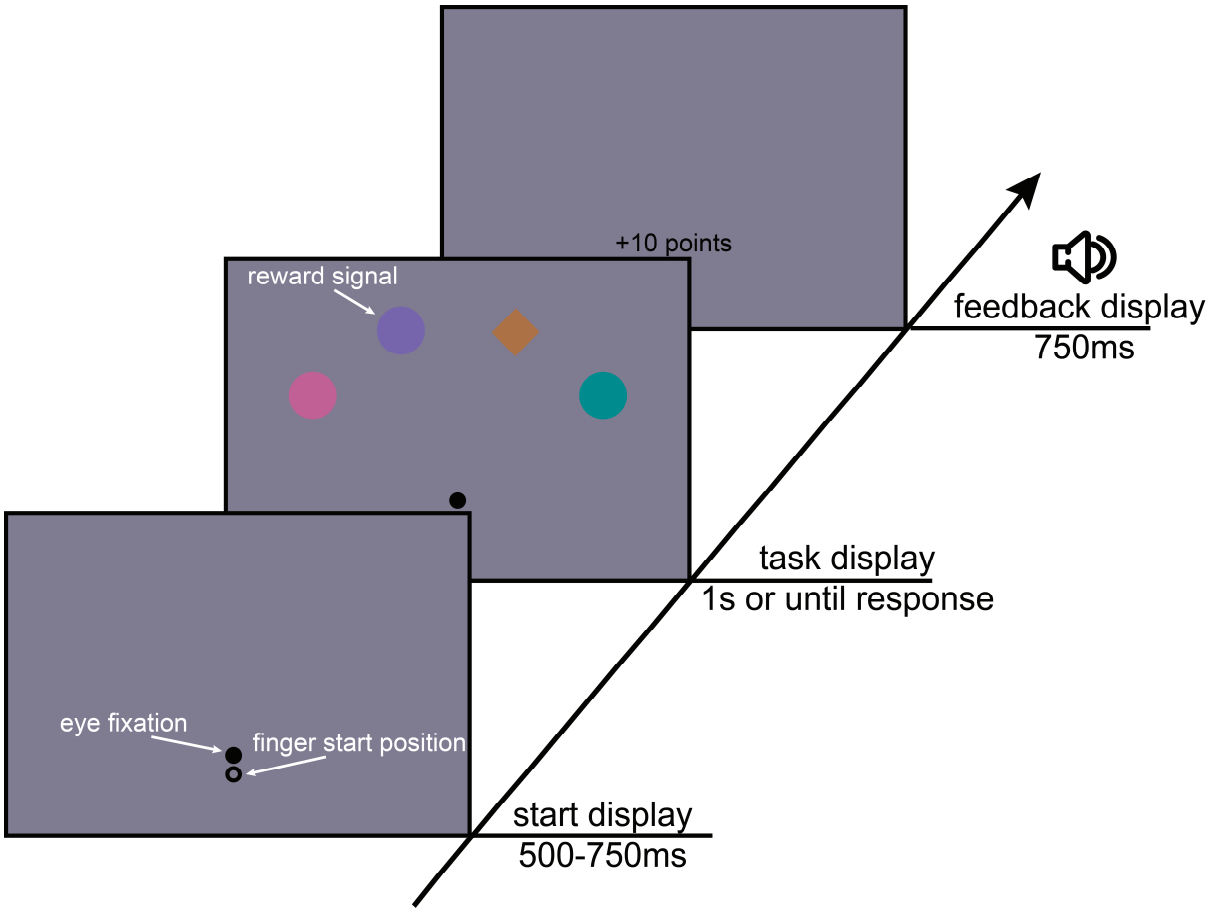

Figure 1. Sequence of trial events. Participants had to reach to a diamond shape presented among circles. In some trials one of the distractor circles was in a color that signaled the possibility of earning either high or low reward on that trial.

Stimuli

The start display consisted of two black circles (0.42vd = visual degrees radius) on a grey background. An eye fixation circle presented 2.5vd below screen center and a finger start circle presented 1.5vd below the eye fixation circle (Figure 1). In the task display, the finger start circle was removed and four shapes (1.25vd, 11mm radius), comprising one target diamond and three distractor circles, were positioned on an imaginary arc (10vd, 88mm radius) around eye fixation with 36 angular degrees between neighboring shapes. All shapes were uniquely colored. During the feedback display, written feedback was presented at the location of the eye fixation circle, together with the presentation of a high or low auditory beep denoting correct or incorrect performance, respectively.

All stimulus colors were defined in LAB color space (CIE, 1967) consisting of three coordinates: Lightness (≈luminance), A (green-red axis), and B (blue-yellow axis). The background (LAB: 50,0,0) and the shapes were isoluminant. The six shape colors had equal

chroma, and were equally spaced around the LAB color space (LAB coordinates of the six shape colors: 50,23.5,40.7; 50,-23.5,40.7; 50,47,0; 50,-23.5,-40.7; 50,23.5,-40.7; 50,47,0). For each participant, one of these colors was randomly chosen as the high reward signaling color and another one as the low reward signaling color. On high and low reward trials one of the distractors was in the high and low reward signaling color, respectively. The colors of the other shapes were randomly sampled from the remaining set of colors without replacement. On baseline trials the colors of all shapes were sampled from the remaining set of colors.

Procedure

The fixation/start screen was presented for a randomized minimum time of 500ms or 750ms, or until gaze and finger position were evaluated positively (finger within 5mm in the x, y dimension and within 3 mm in z dimension from the center of the start circle). Next, the search display was presented for 1000ms or when a reach end was detected (finger velocity dropped below 20 mm/s after moving more than 40mm from the start position). Only when the reach ended before a variable deadline and within 28mm from the center of the target shape, the trial was evaluated as correct. The variable deadline was based on the 80^{th} percentile of the response times (reach latency + movement time) of the last 100 trials in which participants reached the target before the offset of the search display, i.e. within 1000ms. Before 100 trials were gathered, the variable deadline was set to 700ms based on another study from our group with a similar design. Next, the feedback display was presented for 750ms, indicating how much reward was earned on that trial (+10, +1, or 0 points) together with an auditory beep (high pitch for correct; low pitch for incorrect). Participants earned 10 points for correct responses on high reward trials, 1 point for correct responses on low reward trials, and 0 points for correct responses on baseline trials and incorrect responses on any trial type. During practice blocks, the feedback display denoted information about the performance on that trial (correct, too slow, eyes moved, wrong shape, or correct but too slow).

Participants were asked to reach as quickly and accurately as possible to the diamond shape while remaining fixation. During practice, only baseline trials were presented, i.e. the reward signaling colors were not presented. After practice, participants were informed that they could now earn reward depending on their performance and that there are high and low reward signaling colors associated with 10 or 1 points, respectively. It was explicitly stated that the target would never be in one of these colors, thus, had to be ignored. Also, participants were informed that they would only earn reward if they reached the target before a deadline and did not make an eye movement.

Each participant performed 40 practice trials and 792 experimental trials divided into 8 blocks. All possible combinations (36) of target position (4), distractor position relative to the target (3) and distractor condition (3) were counterbalanced; resulting in 22 repetitions of each combination.

Analyses

Small sections (M = 4 samples, SD = 5 samples) of missing reach data due to the temporarily blocked view of the marker were interpolated for each dimension separately. In the offline analysis, the starting point of a reach was defined as the first sample of four consecutive vector velocity readings greater than 25 mm/s where there was a total acceleration of 20 mm/s2 across the four points. The endpoint of a reach was defined as the point in time when the velocity dropped below 20 mm/s (Chapman & Goodale, 2010). Saccades startpoint and endpoint were detected online using minimum velocity and acceleration criteria of 30vd/s and 8000vd/s2, respectively.

Trials were excluded when at least one of the following criteria was reached: a saccade of >2.5vd was detected; the reach end was more than 28mm away from the target center; the reach start was more than 10mm from the finger start circle; the maximum reach velocity was >5000mm/s; the reach latency was <200ms or >600ms. Over all criteria and all participants 9.72% of trials were excluded.

To determine whether reaching movements deviated towards or away from the reward signaling distractor, we calculated the attraction score (Moher et al., 2015). The attraction score denotes the distance at a certain point along the trajectory between the baseline condition and one of the reward signaling distractor conditions relative to the reward signaling distractor's location, with positive values indicating deviation towards, i.e. attraction, and negative values indicating deviation away. Reach curvature is the average of the attraction score values.

To determine when the distractor attracted the reaching movement, we performed a cluster-based analysis (Maris & Oostenveld, 2007; Moher et al., 2015). The *t*-statistics for the distractor attraction score was calculated for each point along the normalized space, then the largest cluster of consecutive t-values for which $p < 0.05$ was detected, and the sum of the *t*-values in that cluster were calculated. If the observed cluster size was significant with $p < 0.05$ under the estimated probability density function, the portion of the reaching movement related to this cluster is reported to be affected by the distractor.

To further investigate the time course of the effect of reward on reaching movements, the attraction score and reach curvature was calculated for movements with short and long latencies, separately. Moreover, a median split based on reach latency was performed for each participant, each distractor condition and each combination of target and distractor location, separately.

Results

Reaching movement curvature

To investigate whether a high reward signaling stimulus, that is physically non-salient and never a target, influences the curvature of reaching movements to a searched target (Figure 2A), we performed a within-subjects analysis of variance (ANOVA) with the factors reward (low vs. high) and reach latency (short vs. long). There was a main effect of reward, $F(1,19) = 8.461$, $p = 0.009$, $\eta_p^2 = 0.308$, which showed that reaching movements curved more towards the high compared to low reward signaling distractor; an interaction effect between reward and reach latency, $F(1,19) = 10.455$, $p = 0.004$, $\eta_p^2 = 0.355$; and no main effect of reach latency, $F(1,19) = 2.252$, $p = 0.15$, $\eta_p^2 = 0.106$. A paired-samples t-test showed that the effect of reward on reach curvature was more pronounced for short compared to long reach latencies, $t(19) = 3.233$, $p = 0.004$, $d = 0.723$.

Reaching movement trajectory and attraction score

To investigate where along the trajectory the reaching movement curved more towards the high compared to low reward signaling distractor, we performed a cluster based analysis on the attraction scores (see analyses). The results show that the high reward signaling distractor attracted the reaching movement more from movement onset until 71% along the trajectory than the low reward signaling distractor. For short latency movements (Figure 2B), the reach was more attracted by the high compared to the low reward signaling distractor from movement onset until 81% along the trajectory. However, for long latency movements (Figure 2C) there was no difference between the attraction scores for trials with a high or low reward signaling distractor.

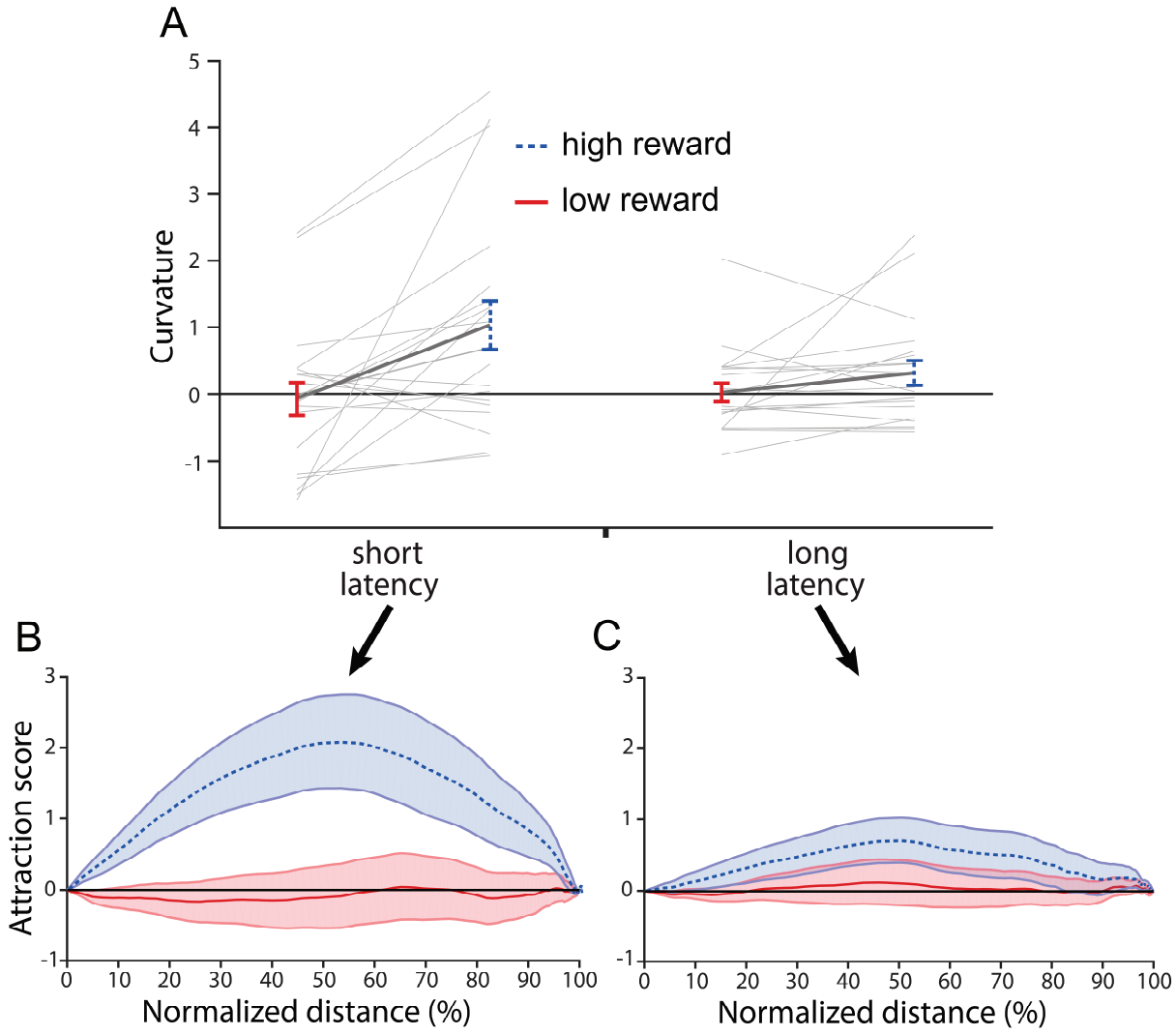

Figure 2. (A) The magnitude of reach curvature by reward signaling value of the distractor separately for short latency trials (left) and long latency trials (right). Positive values denote curvature towards the distractor. Distractor attraction scores along the normalized movement amplitude by reward signaling value of the distractor for short latency trials (B) and long latency trials (C). Positive values denote attraction towards the distractor. All error bars reflect SEM.

Discussion

The current study shows that a physically non-salient stimulus signaling high in contrast to low reward attracts reaching movements. Reaching movements clearly deviated towards the high reward signaling distractor even though it was never the reach target and reaching towards it was never rewarded. Conversely, reaching towards the distractor would have led to the omission of reward. The attraction by the high reward signaling distractor was present in short but not in long latency movements. The attraction of the reaching movement can be attributed to the reward signaling stimuli obtaining an increased selection priority for action independently of physical salience. The priority for selection increases the likelihood of the activation of a movement plan towards the high reward signaling distractor. The activation of the movement plan causes the subsequent reaching movement to be deviated

towards the high reward signaling distractor if the competition with the movement plan is not resolved. The competition is then resolved by suppressing the movement plan to the distractor. As this suppression increases gradually, attraction by the reward signaling distractor is more pronounced for short than long latency movements.

The current findings advance our understanding of how reward association can shape the selection for action. In previous studies (Chapman et al., 2015; Moher et al., 2015; Wirth et al., 2016) reaching to the stimulus associated to reward was previously rewarded, and thus reinforced. Therefore, it was unclear whether reinforcement learning of moving towards a reward associated stimulus is necessary to observe consequent attraction when that stimulus is presented as a distractor. Moreover, the reward associated distractor was always physically salient or presented with only one alternative shape, hence, it was unclear whether reward can gain priority in the selection for action when it is not physically salient. The current results can close these research gaps by showing that a non-salient stimulus associated with reward can gain priority in the selection for action, even when reaching to the reward associated stimulus was neither necessary nor rewarded.

The current findings show similarities with studies on the influence of reward associated stimuli on visual selection. Failing and colleagues (2015) found that saccades are more often directed towards a non-salient reward signaling distractor. Similarly, we found that the direction of reaching movements deviates towards a non-salient reward signaling distractor. Also, the attraction by the reward signaling distractor was mainly pronounced for short latency reaching movements, as was found for short latency eye movements (Failing et al., 2015). Hence, reward associated stimuli seem to affect visual selection and selection for action in a similar fashion.

All together, the present experiment shows that reward signaling stimuli attract reaching movements, even when the reward signaling stimulus is not physically salient, is never a target and reaching towards it is never rewarded. Our findings show that a reward associated stimulus (i) does not have to be physical salient nor (ii) is it necessary to reinforce reaching towards it for the reward associated stimulus to gain priority in the action selection process.

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List of publications

Tom Nissens

Nissens, T., & Fiehler, K. (2020). The attractiveness of salient distractors to reaching movements is task-dependent. *Attention, Perception, & Psychophysics*. https://doi.org/10.3758/s13414-020-01984-6

Nissens, T., & Fiehler, K. (2018). Saccades and reaches curve away from the other effector's target in simultaneous eye and hand movements. *Journal of Neurophysiology, 119*(1), 118-123. http://dx.doi.org/10.1152/jn.00618.2017

Nissens, T., Failing, M., & Theeuwes, J. (2017). People look at the object they fear: oculomotor capture by stimuli that signal threat. *Cognition & Emotion, 31*(8), 1707-1714. http://dx.doi.org/10.1080/02699931.2016.1248905

Failing, M., **Nissens, T.**, Pearson, D., Le Pelley, M., & Theeuwes, J. (2015). Oculomotor capture by stimuli that signal the availability of reward. *Journal of Neurophysiology, 114*(4), 2316-2327. http://dx.doi.org/10.1152/jn.00441.2015

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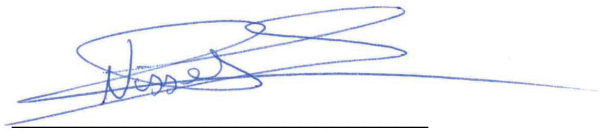

Tom Nissens, 26.02.2020