

Can't Touch This:
Understanding Information Processing for Obstacle Avoidance
Behavior

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**Can't Touch This:
Understanding Information Processing for Obstacle Avoidance
Behavior**

Niet aanraken! Inzichten in de informatieverwerking voor het vermijden van obstakels
(met een samenvatting in het Nederlands)

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Chapter 1 – General Introduction

We all have that *particular* relative or friend who at formal dinner parties manages to knock over his glass of red wine. Although frowned upon, such accidents occur relatively infrequently in everyday life. Thus, we can conclude that colliding with obstacles is most frequently successfully avoided. Obstacle avoidance is a basic yet complex skill that humans have. 'Basic' because it both underlies many other more complex behaviors and it is achieved with different end-effectors. Indeed, moving toward a target object while avoiding non-target objects is something that humans can achieve in cars, on foot, or with their hands. Furthermore, obstacle avoidance is 'complex' in that it occurs frequently and successfully in cluttered and dynamic environments.

To understand how humans manage to perform successful avoidance behavior it is necessary to take a closer look at how the brain processes information in order to plan an action. As mentioned above, humans do not act in a vacuum: we are surrounded by many different objects and surfaces with which we can interact. These objects and surfaces reflect light from the sun that is then captured by the eyes. Our brain's visual cortex then processes the patterns of light along two different pathways: the so-called dorsal stream and the ventral stream. The dorsal stream projects from the back of the brain, i.e. the occipital cortex, to the top of the brain, toward posterior parietal areas. The dorsal circuit processes the incoming stimuli in order to guide action; this means that the information that is gathered is geared toward establishing *where* objects are. The ventral circuit, on the other hand, which runs from the visual cortex to the inferior temporal cortex, processes incoming stimuli in order to identify objects. That is, the information that is gathered is aimed at pinpointing *what* objects are. In bold strokes, therefore, the dorsal stream can be termed vision-for-action, whereas the ventral stream can be described as vision-for-perception. In order to successfully act in our environment we rely on both types of 'vision'; i.e. we need to identify *what* objects are as well as *where* they are.

However, visual information does not just terminate at the end of both streams; it serves as input for actions that need to be prepared and controlled by the brain. This happens in the pre-motor and motor cortex. Here, action is planned and controlled, respectively. The planning of action consists of two main aspects: action selection and action specification. Action selection is the selection of the proper object to move toward and is linked to the goal of the movement. To clarify, if you want to drink a sip of water, then you would move to pick up a glass of water and not a glass of wine next to it. Action specification, on the other hand, deals with how all the elements of an action are executed. In this regard, one can think of how precisely the arm and hand are transported through space (i.e. the trajectory), how the fingers are organized in order to grasp the target object (e.g. precision vs. power grip), whether the movement is executed

quickly or carefully, or which effectors are used (e.g. whether or not the trunk was used to assist the movement toward a glass of water).

The control of action is thought to occur mainly through feed-forward control. This means that a plan for action is prepared --based on previous experience with similar situations-- and executed without the use of feedback from the environment. This is because the central nervous system's processing speed is too slow to update a speeded movement once the movement has started (i.e. the movement will be finished before the correction signal arrives). However, the motor system does make use of feedback information; any discrepancies between the predicted and actual states of the motor system are used to update motor plans for the future. Simply put, if a hand is incorrectly guided toward a water cup around a wine glass, then the fact that the wine glass was knocked over is used to determine that similar future movements should veer away more from wine glasses.

As stated in the above, our environment is cluttered and dynamic; this means that we have to deal with a veritable cornucopia of available information. We are not just passive receivers of all that information; we actively seek out information and block out other irrelevant information. That is, attentional processes are utilized by our brain in order to make sense of the environment relative to our immediate goal(s). In terms of obstacle avoidance, attention can have an effect on the gathering of information (perception) and processing of that information. Therefore, actions are measurably affected, as they are the behavioral end-state towards which information processing is geared. This is because the discussed vision-for-action (and vision-for-perception) feed action specification and action selection, because they share -or have intimately linked- neural substrates. One way of understanding how vision and action are linked and how attention can affect that link is to envision a landscape of peaks and valleys. This landscape is a landscape of neuronal activity that represents a retinotopic map of the environment. So, objects that are present in the environment that are relevant for action are represented in the landscape by a peak of activity. On the other hand, objects that are to-be-avoided are represented by valleys in the same landscape. Peaks, therefore, attract movements, whereas valleys repulse movements. The role for attention here is to modulate the strength of the activity of a particular peak or valley.

To reiterate, information from our environment is processed in order to program a movement through that environment and this process can be modulated by attention. Researchers can manipulate this entire process and see how the behavior of people changes. The manipulations can occur in one of three ways: the perception by an actor can be manipulated, his or her attention can be modulated, or motor aspects can be changed for the

actor. Obstacle avoidance therefore offers a window into understanding visual information processing for goal-directed movements.

This dissertation is not the first research into obstacle avoidance. Indeed, many studies have already been done on the subject. **Chapter 2** is a review of the currently available research on the topic of obstacle avoidance. Next to showing what we currently know about obstacle avoidance, this chapter also describes the obstacle avoidance paradigm in more detail, with special attention for its ecological experimental setting, its strengths, typical results, used tools, and measures. The measures are about which parameters (of action specification) are collected from movement trajectories in order to draw conclusions about the processing of visual information for goal-directed movements.

Generally speaking, prior research has shown that we can learn a lot from hand trajectories about visual information processing for goal-directed movements. One of the main conclusions about obstacle avoidance in prior research has been that avoidance responses are subtle and precise. In essence, this means that each avoidance response is a unique, or tailored, response to its environmental situation: we do not have a stereotypical response to different environmental situations. Under the same conditions however, we do produce stereotypical avoidance movements. This notwithstanding, previous studies have provided only a coarse overall picture of the effect of e.g. obstacle location. In **Chapter 3** an experiment with the aim to map the relation between obstacle position and the avoidance response is considered. The results provide evidence for a fine-grained spatial resolution of obstacle motor representation. In addition, the predictability of the avoidance responses is also discussed. That is, a quantified relation between environmental parameters and behavioral output is described. This represents an attempt to discern a behavioral law that governs obstacle avoidance.

Furthermore, the prior body of knowledge displays some interesting effects that warrant further explanation. For instance, obstacle avoidance responses generally are greater when the obstacle is located to the front and on the right side of a participant (compared the left side). Moreover, in some experiments on obstacle avoidance the avoidance behavior exhibited by participants is much more pronounced. This raises some interesting questions about whether these effects are driven by either motor, attentional, or perceptual aspects. In chapter 4 and 5 two possible explanations for results are pursued.

In **Chapter 4** the contribution of motor lateralization is discussed. It was hypothesized that motor lateralization (i.e. handedness) might be able to account for the left-right hemispheric differences in avoidance responses. The alternative hypothesis was that the relative positioning of the objects with reference to the acting limb accounts for the differences.

The results indicated that a participant's handedness and whether or not a participant uses his or her preferred or non-preferred hand do not influence reaching behavior during obstacle avoidance. Instead, effects for the relative positioning of obstacles were observed, indicating that the more an obstacle obstructed movement, the larger the avoidance movements that were evoked.

In **Chapter 5** the effect of different starting postures on obstacle avoidance behavior is investigated. In this experiment, participants were seated in one of two starting postures, viz. with the forearm placed in front or to the side of the body. The results indicated that the movement trajectories were different when participants had to use different starting postures. In itself, this is not surprising, since movement trajectory planning is thought to be based on calculating the most efficient transformation from a starting posture to an end posture. So, if the start posture is changed, then there is also a change in what constitutes the most efficient transformation. Of more interest is that the results suggest that motor constraints offered by the obstacle contribute (much) more to avoidance responses than attentional effects that stem from interference during action selection (i.e. which object to pick up).

Having established an understanding of constraints offered by motor aspects on avoidance behavior and having determined a quantifiable relation between obstacle position and avoidance responses, the stage is set for a discussion of the possible crosstalk between the ventral and dorsal stream. That is, now that it is possible to control more aspects of the avoidance behavior, we can investigate the interaction between ventral and dorsal stream information. Unique patient studies have elucidated that obstacle avoidance *can* occur with an ablated dorsal stream, yet that effective and smooth obstacle avoidance is hardly possible without the dorsal stream. These findings have led to a narrow focus of investigation on purely dorsal stream features of obstacles, i.e. location, size, orientation etc. Although highly informative, this avenue of investigation neglects the influence the ventral stream may have on avoidance behavior. In **Chapter 6** two experiments are discussed where non-spatial features of obstacles were manipulated. These are features that are normally irrelevant for the execution of movement, at least, according to a strict interpretation of vision-for-action. The aim was to show an effect of a non-spatial obstacle feature on avoidance movements in order to show crosstalk, or at least convergence, between ventral and dorsal streams occurs in healthy participants. To that end, 2 experiments were performed with an obstacle avoidance task where the similarity in color between the to-be-grasped target object and the to-be-avoided obstacle was manipulated; these objects had either the same or a different color. The findings indicated that the non-spatial feature color-similarity did have an effect on avoidance movements. In fact, a dissimilar set of target object and obstacle led to stronger avoidance responses. Here, it was not possible to

disentangle two possible causes of the observed avoidance behavior; either there was an increased capture of attention in this case, or the ‘different identity’-processed via the ventral stream- was responsible for the stronger avoidance response.

The effect of attention on obstacle avoidance movements is explored in **Chapter 7**. Experiments are discussed that were geared toward capturing the participants’ attention prior to movement execution so that the exclusive effect of a purely attentional intervention could be investigated. A ‘low-level’ attentional manipulation was achieved by keeping all features of the obstacle –including identity- the same, while either providing spatial cues, non-spatial cues or no cues at all. The results showed definite effects of spatial cues on obstacle avoidance movement trajectories. Hypothetically, these effects were driven by a stronger weighting in the attentional landscape of the valley of activity associated with the obstacles.

The underlying mechanism for predicting the consequences of action is theorized to be the peripersonal space. Peripersonal space (PpS) is a region around the body that is represented in the brain by bimodal neurons that fire both in response to tactile and visual stimuli. The PpS neurons have also been shown to respond to approaching objects. This is in line with the proposed defensive function of the PpS. There have also been recent demonstrations of the involvement of the PpS in voluntary action: the PpS guides action, because the PpS network shows anticipatory activity prior to contact with a to-be-grasped object. In **Chapter 8** these findings are extended to obstacle avoidance, because we found a continuous remapping of the multisensory PpS as a function of on-line sensorimotor requirements. These results indicate that the anticipation of a collision with a to-be-avoided object may also be represented by the PpS network in the brain.

So, what can avoidance movement trajectories teach us? A lot! As can be concluded from the previous sections the trajectory of the hand through the workspace can reveal much about the interplay between information processing, attentional effects, and motor programming. **Chapter 9** gives an overview of the conclusions.

Chapter 2 – Obstacle Avoidance Movement Trajectories and What They Tell Us

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2016). Obstacle Avoidance movement trajectories and what they tell us. *Manuscript submitted for publication.*

Abstract

Manual avoidance trajectories can be modulated by situational determinants: movement trajectories can either deviate away from obstacles in the workspace or remain unaffected. We review conditions under which these responses are produced and mechanisms underlying avoidance responses. In most cases the avoidance movement is specifically tuned to produce a response that is subtle and precise. This means that although avoidance responses are stereotypical under repeated conditions, avoidance responses are also unique for those conditions. This, in turn, seems to point to determinable laws that allow for prediction and therefore enhanced understanding of (avoidance) behavior. This review attempts to inventory those laws that have been researched at this point. Furthermore, we will show that the obstacle avoidance paradigm allows researchers to investigate what features of obstacles are integrated into the motor plan for movements in a cluttered and natural workspace. Moreover, this paradigm provides a way of testing the interaction between the visual dorsal and ventral stream. We consider obstacle avoidance an experimental framework suited for studying complex visuomotor control.

Every day humans perform a multitude as well as a variety of different obstacle avoidance movements. Conceivably, a researcher may drive to work in his car, while braking and steering to avoid other cars, and then proceed to walk to his or her office while avoiding puddles from that morning's rainfall, all to sit down behind a desk to mouse over emails, while attempting to not knock over a well-deserved cup of coffee. Beyond human obstacle avoidance in driving, locomotion and reaching, there is also robot obstacle avoidance (i.e. how robots avoid obstacles) and simulated obstacle avoidance (how obstacle avoidance is achieved in a simulated flock of i.e. birds).

Search commands for 'review' in combination with 'obstacle avoidance' over the last ten years in scientific literature databases yields many results for reviews of obstacle avoidance in robot and human locomotion. However, there is no dedicated review for manual obstacle avoidance behavior. This is odd as there have been a considerable number of studies that use this paradigm. In fact, over 25 studies have been done in the last ten years of which more than half were done in the last five years. The current review will provide an overview of the manual obstacle avoidance literature that will hopefully stimulate not only the field of manual obstacle avoidance, but also its modeling and robotic counterparts (similarly to Lukic, Santos-Victor, & Billard, 2014). We consider as obstacles any object that physically obstructs any part¹ of the effector system normally involved in a movement to a target object or area.

The studies we review do not all use the same paradigm or method of analysis. There are common denominators qua paradigm however: in a typical obstacle avoidance experiment, a human participant reaches for a target location while moving his or her arm around an obstacle (see figure 1). The location of an obstacle should be determined during the design phase of the experiment and be based on earlier work on natural movement trajectories through a workspace towards a target object. The location for an obstacle should be picked in such a way that it interferes with a normally smooth movement to the target object. Between repetitions of avoidance movements, features of the obstacle, the availability of information, the allocation of attention, expectancy, memory, the context of the act or the actor itself is manipulated. Afterwards, trajectories are compared between conditions and within subjects to infer if (and possibly how) the visuomotor control of the avoidance movement was modulated. For example, a reach is performed toward a target with an obstacle present in the workspace in 1 of 2 locations: one close to the hand and one far away from the hand. The movement data should then reflect the increased avoidance around the closer obstacle relative to the further obstacle and/or a no-obstacle baseline, either in spatial and/or temporal measures. The exact nature of the measures taken from kinematic data and their analyses can vary between experiments but they are often related (see Appendix 1).

¹ or rather: encroaches on the flexible safety margin around parts of the effector system

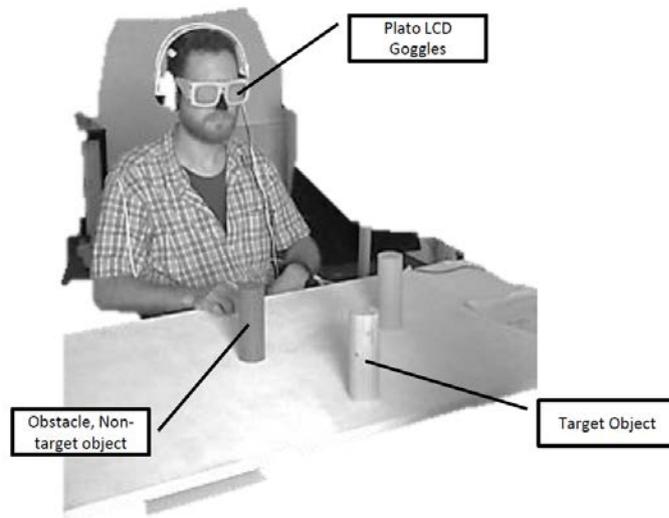


Fig 1. The dimensions of a typical obstacle avoidance setup. A participant is seated behind a table, with objects present in his or her workspace (reachable space without trunk-movements). Vision (and sometimes hearing) is masked.

In this review we have limited the scope to reviewing the findings of empirical studies that report effects of obstacles on reaching trajectories. This has several consequences: first, we will not consider the effect of obstacles on grasping. We refer to the following papers on the effects of obstacles on grasping: Eloka, & Franz, 2011; Hesse, & Deubel, 2010; Verheij, Brenner, & Smeets, 2012; Voudouris, Smeets, & Brenner, 2012. Interestingly, there are contrary effects of illusions on grasping that either have or have not been attributed to obstacle avoidance (Franz, Bühlhoff, & Fahle, 2003; Haffenden & Goodale, 2000). Second, for the details regarding designs and materials of empirical studies we refer to the original documents we cite. Third, we will not wax theoretical and speculate about theoretical mechanisms exclusively underlying obstacle avoidance. The reason for this choice is two-fold: there are general theories available that, in our view, accurately describe obstacle avoidance, and there is little-to-no evidence to warrant an exclusive theory on obstacle avoidance. Hence, we will not speculate on the neural mechanisms behind obstacle avoidance beyond those that are known to affect ‘normal’ motor behavior.

When talking about obstacle avoidance in the proposed scope, there is an elephant in the room. That elephant is distractor interference. That is, there is a large body of evidence on a related topic to obstacle avoidance that has shown that the capture of attention by a non-target can change the motor response to target objects (Castiello, 1999; Chang & Abrams, 2004; Gangitano, Daprati, & Gentilucci, 1998; Howard & Tipper, 1997; Tipper, Howard, & Jackson,

1997; Welsh, Elliott, & Weeks, 1999; Welsh & Elliott, 2004; Welsh, 2011). However, these non-target objects were not obstructing or sometimes not even physical objects at all. Although Tipper et al. (1997) acknowledged that distractor interference occur when there is no physical obstruction, we still cannot completely exclude the effects of distractor interference during typical obstacle avoidance. However, we can keep its effects to a minimum by keeping our focus strictly on empirical studies where obstacle avoidance occurs. So, although distractor interference studies may shed light on the effect of distracting stimuli on motor behavior, we cannot be certain that the results for obstacle avoidance are the same. Indeed, the changes in motor responses evoked by salient distractors and visual cues are thought to be due to the biased resolution of competition between target and distractor during action selection (i.e. which object to reach for), whereas obstacle features (e.g. location, size) must be incorporated in the motor plan that brings the hand and arm around the obstacle and toward the target. After all, in obstacle avoidance, the goal is to *not* interact with the obstacle. This means that a separate motor plan to interact with an obstacle is redundant (once the target is identified). Instead, the detected obstacle information should be incorporated into the motor plan toward the target. This means that an obstacle does not act as a distinct attractor of motor activity, but rather as a repeller of motor activity.

Given this, obstacle avoidance is a clear and simple method that can elucidate the workings of visual processing for the guidance of action in its own right. To be more specific, obstacle avoidance can shed light on the information the brain processes in order to program complex movements and how that can affect movements. Studying such a natural movement gives us ecologically valid insights into how the brain operates at a behavioral level. In addition, the lessons we can learn from obstacle avoidance may allow for a more accurate conceptual understanding of visuomotor control.

In this review, studies are interpreted according to the 'two visual streams' (TVS) hypothesis (Milner & Goodale, 1995, 2008). This model holds that the processing of visual information goes along two functionally separate streams: the dorsal stream and the ventral stream. In bold strokes, the function of the dorsal stream is processing visual input for the real-time and automatic control of action, i.e. vision-for-action, whereas the function of the ventral stream is mediating visual perception and recognition, i.e. vision-for-perception. The information in the ventral stream is processed in scene-based frame-of-reference and uses relational metric. The information in the dorsal stream is processed in an ego-centric frame-of-reference and uses absolute metrics. The dorsal stream is therefore associated with the processing of size, distance, and orientation information of the obstacles. The ventral stream, on the other hand, is associated with processing color, material, and identity information. Both streams receive input from striate cortex and while the ventral stream projects to

Inferotemporal cortex, the dorsal stream projects to posterior parietal areas. Although the ventral and dorsal streams appear distinct, there must be much cross-talk between the circuits or at least the networks that are fed by these circuits (Rossetti & Pisella, 2002). Obstacle avoidance provides an interesting paradigm to study the interactions between dorsal and ventral stream, because it is a complex movement that relies on multiple sources of visual information that are relevant for action. That is, object identity as well as object size are important factors to consider when trying avoiding collisions.

A framework that succinctly describes how obstacle avoidance related information is processed in the brain is offered by Cisek (2007) and Cisek & Kalaska (2010) and is termed the affordance competition hypothesis. It focuses on two problems that are presented to an actor's brain: deciding what to do (action selection) and how to do it (action specification). According to Cisek (2007), multiple potential actions are simultaneously represented as continuous regions of activity within populations of cells in the Frontoparietal cortex. This happens through the transformation of visual information along the dorsal stream into peaks of activity in parietal and premotor areas. These response codes engage in a competition for overt execution that is biased by modulatory influences. The competition between potential actions happens through mutual inhibition until a quenching threshold is reached, i.e. one peak beats the other. Biasing influences from recurrent connections mediate this competition through 'votes' in favor of one of the peaks. These influences can also come from areas in the frontal cortex and basal ganglia, casting possible light on the influence of top-down attention and reward on simple motor behavior. The model exhibits activity patterns that closely correlate with measured neural activity in macaque parietal, prefrontal and premotor cortex (Cisek 2007). Because defining potential actions and deciding between them is viewed as an integrated process, then when one activity hill beats another and a target object is selected for action, a motor plan is also (being) fully specified and executed.

The competition between response codes may be better understood in terms of the 'attention landscapes' described by Baldauf & Deubel (2010). According to these authors, the planning of a complex movement entails the creation of a so-called 'attentional landscape' which weights the attentional distribution across all action-relevant locations in the visual lay-out of the workspace (Baldauf & Deubel, 2010). In addition to locations, the weighting is also sensitive to other motor-related aspects of the task, such as the required accuracy, with more weight being attributed to a location that requires more accuracy. Movements are then executed toward the (highest) peak in the landscape and away from low(er) activity regions or valleys. In the case of obstacle avoidance, it could be that the target object is the peak in the landscape and the non-target object or obstacle a valley in the attentional landscape. The 'activation' in the valleys is initially determined by dorsal stream input, but can be modulated by ventral stream

input (either directly or indirectly), top-down and bottom-up attentional processes, and further executive and reward inputs from frontal and midbrain areas, before it crystallizes into an observable motor plan.

To summarize, the previous theories link together in the following way: visual information is processed along the ventral and dorsal stream (TVS). This information is used in order to select 'where' to do action and 'how' to do an action (Affordance competition) and is represented in an attentional landscape (Baldauf & Deubel, 2010). These representations of prepared motor activity then compete in order to draw prepared actions towards them.

In this review we will first discuss obstacle features that prompt changes in avoidance movements, followed by a review of the effects of the availability and processing of information on avoidance movements: i.e. manipulations of the context of acting and the actor itself. Next, we will look at the motor control background of obstacle avoidance. Lastly, the neurological background of obstacle avoidance and the patient studies that inspired explanations of the workings of obstacle avoidance will be discussed.

Obstacle features

Obstacle Position (Dorsal stream feature)

There are a large number of studies that show an effect of obstacle position on the spatiotemporal characteristics of avoidance movements (Biegstraaten, Smeets, & Brenner, 2003; Chapman & Goodale, 2008, 2010a, 2010b; de Haan, Van der Stigchel, Nijens, & Dijkerman, 2014; Dean & Bruwer, 1994; Grimme, Lipinski, & Schöner, 2012; Menger, Dijkerman, & Stigchel, 2014; R. Menger, Van der Stigchel, & Dijkerman, 2012; Rudmer Menger, Dijkerman, & Van der Stigchel, 2013; Menger, Van der Stigchel, & Dijkerman, 2013; Mon-Williams & McIntosh, 2000; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Rice et al., 2006; Saling, Alberts, Stelmach, & Bloedel, 1998; Tresilian, Mon-Williams, Coppard, & Carson, 2005; Tresilian, 1998). Indeed, it is known that the lateral (left to right) and saggital position (near to far in depth) of obstacles affects movements differentially, with near obstacles giving rise to larger avoidance movements than far obstacles. Additionally, obstacles that are on the right side of the workspace during right-handed avoidance movements also give rise to larger veering movements than obstacles located on the left side of the workspace. The response to obstacle locations has been described as subtle and precise (Mon-Williams et al., 2001), meaning that each individual obstacle location gives rise to a unique avoidance response. The important role of the dorsal stream in obstacle avoidance implies that the processing of ego-centric information of the obstacle plays an important role in programming the avoidance response. That is, it is not the allocentric location of the obstacle in space that is used in programming a

response, but rather the egocentric location of the obstacles. The egocentric location of obstacles is determined by the distance between the hand and the obstacle and also the direction of the obstacle with respect to the hand. To elucidate, the direction of the obstacle can be thought of as a particular heading of the hand that would lead it from its starting position toward the obstacle. The obstacle heading direction is then represented as an angle with respect to a reference heading 'straight ahead' along the saggital reference axis (see also Figure 2).

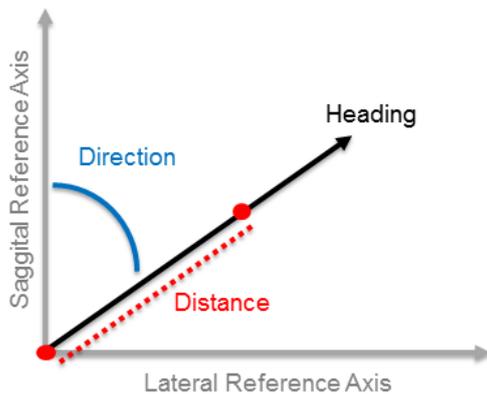


Fig. 2. Schematic for defining Direction, Distance, and Heading. The grey arrows represent the saggital (near to far) and lateral (left to right) reference axes. The black arrow represents a heading towards a non-target object. Please note that this particular heading is simplified to a linear heading, since actual human movements always occur as curves. The red circles indicate two different positions along the given heading. The space between two positions dictates the distance. The angle between the saggital reference axis and the heading is defined as the direction (in blue).

The sign and magnitude of this angle can be used to predict the strength avoidance response; Menger et al. (2014) do indeed show that the direction and distance of obstacles can be used to predict avoidance responses. Moreover, in this experiment, the direction of the obstacle seemed to play a larger role than the distance. In general however, the location of obstacles relative to the actor seems to determine the level of obstruction offered by the obstacle. The more obstructing the obstacle the more pronounced the avoidance movement around it. Interestingly, the results reported by Menger et al. (2014) bear a fair resemblance to the data reported by Fajen & Warren (2003) for obstacle avoidance during locomotion.

Obstacle Size and Orientation (Dorsal stream features)

Several studies have shown either an effect of obstacle size on avoidance movements (Alberts, Saling, & Stelmach, 2002; Saling et al., 1998) or have reported a null result of object size (Mon-Williams et al., 2001), though the latter may have been due to methodological limitations

(Chapman & Goodale, 2008). As Chapman & Goodale (2008) discuss, Mon-Williams et al. (2001) placed their obstacles very close to the target in terms of depth. This means that the obstacles in the Mon-Williams study possibly constrained the reaching movement too little to allow for a detection of a modulation of avoidance responses due to size. An effect of size may therefore more readily detectable when obstacles are placed in such a way as to evoke a medium to large avoidance response.

Another study by Verheij, Brenner, and Smeets (2014) showed no effects of obstacle size on movement trajectories. In this study the diameter of obstacles was manipulated while the obstacles were located below the hand's path. The manipulation of size was therefore performed in the same plane as the movements: the hand passed *over* obstacles and obstacle *height* was manipulated. This is analogous to the studies by Mon-Williams (2001) and Chapman and Goodale (2008), where the hand passed *around* obstacles and the *diameter* of obstacles was manipulated. So, researchers can keep and have kept the manipulation of size in the same plane as the movement in order to study the effects of size increments on avoidance movements. This allows us to generalize the results. To reiterate, size effects are dependent on picking obstacle locations that constrain the movement. For future research, it would be interesting to look at how size increments along the different planes interact, as in the normal world a bigger size normally implies along bigger size in both the horizontal and vertical planes.

Although not classified as obstacle avoidance studies by the authors themselves, we mention two studies here because they do feature manipulations of dorsal stream features of objects and physical obstruction is considered as a partial explanation of observed effects (in addition to the greater role attributed to distractor interference). As such, they can shed light on how these factors can influence obstacle avoidance. Kritikos, Dunai, and Castiello (2001) and Kritikos, Bennett, Dunai, and Castiello (2000) performed two experiments into distractor interference effects where they demonstrated effects of distractor size on movement kinematics. Kritikos and colleagues (2000) also investigated the effect of the orientation of distractors on movement kinematics. In this experiment distractor objects were slanted at 45 degree angles to the saggital plane. The data revealed that this intervention did not influence results systematically, in that the forward-slanted objects interfered more with the hand movements than backward-slanted objects only under very specific other experimental conditions. Obviously, when objects are slanted inward they obstruct movement more, so this could actually be demonstration of (i) obstacle avoidance and (ii) the sensitivity of obstacle avoidance to object orientation. Further study is needed to determine if and how the slant of obstructing objects affects avoidance movements. Nevertheless, we can –tentatively- state that avoidance movements are indeed affected by obstacle size and that obstacle orientation is likely to have a role in evoking avoidance responses. Moreover, more work is needed to determine

how different dorsal stream functions interact, i.e. the evidence seems to point toward a leading effect for obstacle location, followed by other effects such as obstacle size and orientation, but a precise experiment utilizing and testing all three manipulations has not yet been performed and is called-for as it may enhance the predictability of the behavior.

Obstacle identity (Ventral stream feature)

Evidence from Kritikos, Dunai, and Castiello (2001) points towards the likely primacy of dorsal stream features over ventral stream features. That is, Kritikos et al. (2001) compared the effects of semantic category, i.e. living vs. non-living objects, with the effect of object size. These researchers found that what we have identified as a dorsal stream feature, affects the programming and control of hand movements more than what we consider as ventral stream features. Indeed, these researchers were unable to pinpoint a systematic and reliable effect of semantic category. Again, this study fits more with the distractor interference paradigm, but is interesting because it shines a light on the interaction between dorsal and ventral stream information during movement programming of complex hand movements.

The results by Kritikos et al. (2001) were confirmed for actual obstacle avoidance in a recent study by de Haan, Van der Stigchel, and Dijkerman (2014) who showed a differential avoidance response to empty glasses and glasses filled with water. de Haan et al. (2014) placed these objects halfway the reaching distance from the starting position of the hand and a target button and varied the identity of the obstacles by filling them with and draining them of water. When the obstacle (a glass) was filled with water then participants responded to it by veering more away from it than from empty glasses, but only if the obstacle was obstructing, i.e. on the right side of the workspace. This study showed that the identity of potential obstacles, which is important for predicting the consequences of a collision, is registered during obstacle avoidance. In fact, this ventral stream feature, i.e. object identity, further modifies the movement trajectory which is supposedly primarily governed by dorsal stream –or spatial- features such as obstacle size, direction and distance.

Along a similar vein, Menger et al. (2013) demonstrated an effect of non-spatial object features on avoidance movements. In this study participants reached towards and grasped a target object while obstacles were placed to the left and right of the transport of the reaching arm. The obstacles and target were either similar in color or dissimilar in color. No effect of color an sich was observed. However, there was an effect of target-obstacle similarity when obstacles were on the right side of the workspace. The data showed that participants had a stronger avoidance response to dissimilar target-obstacle sets than to similar sets. Two possible interpretations of these data are possible: either the processing of higher level information in the ventral stream influenced the processing of dorsal stream information and/or the

dissimilarity influenced attentional capture thereby upsetting the competition between target and obstacle for attention.

To conclude, ventral stream features of obstacles appear to affect avoidance movements, but they only modulate effects of dorsal stream features.

Availability of information/context/actor

Handedness

Generally speaking, there are asymmetries in performance between the preferred and non-preferred hand: the preferred hand is often faster, stronger, more consistent than the non-preferred hand (for a review, see Goble & Brown, 2008). In addition, a typical observation in obstacle avoidance studies has been that non-targets positioned ipsilaterally to the acting limb interfere more with the trajectory of the hand than contralateral non-targets (Chapman and Goodale 2008; Dean and Bruwer 1994; Meegan and Tipper 1999, 1998; Mon-Williams et al. 2001; Pratt and Abrams 1994; Tipper et al. 1992). A possible explanation for these findings could be that avoidances movements in experiments are performed by the actor's preferred hand. As such, the avoidance responses may be attenuated by increased attention -enhanced spatial processing- for objects near the preferred limb. Menger et al. (2013) investigated whether obstacle avoidance is mediated by motor lateralization. Participants were asked to perform reaches towards physical target objects with their preferred or non-preferred hands while physical non-targets were present in different possible positions in the workspace. Both left-handers and right-handers were tested. The data revealed that participant's handedness did not influence reaching behavior in an obstacle avoidance paradigm. Furthermore, no statistically significant differences between the use of the preferred and non-preferred hand were observed on the kinematic parameters of the reaches. We found evidence that non-targets positioned on the outside of the reaching limb influenced the reaching behavior more strongly than non-targets on the inside. Moreover, the type of movement also appeared to play a role, as reaches that crossed the workspace had a stronger effect on avoidance behavior than reaches that were 'uncrossed'. We interpret these results as support for the hypothesis that the avoidance response is determined by keeping a preferred distance between the acting limb and the non-target position in all stages of its reach toward the target. This process is not biased by hand dominance or the hand preference of the actor.

Starting position

We have highlighted the overlap between obstacle avoidance and distractor interference. Tentatively, we can move a step further: obstacle avoidance and distractor interference form the extremes of single spectrum: if an obstacle is far away it can operate as a distractor, and conversely, if a distractor is (too) close it can operate as an obstacle. We considered that we could change the way participants dealt with objects in the workspace by not altering the workspace itself (moving the objects closer, thereby creating obstacles, or further away, thereby creating distractors), but rather by changing the participant. Specifically, we opted for using the posture of the participant at the beginning of the movement in order to evoke different avoidance responses. Menger, Van der Stigchel, and Dijkerman (2012) thus investigated whether avoidance responses were mediated by the starting posture of participants. Participants performed reaches from one of two starting postures: a frontal posture, where the hand was in resting front of the participant and a lateral posture, where the hand was resting next to the participant. In both cases the participants reached toward and grasped a target object while avoiding obstacles that were placed in the workspace. Each participant performed the avoidance movements under both conditions according to an ABBA-design. Menger et al. (2012) further manipulated the location of the object. Menger et al. (2012) also computed measures that were specific for the start of the movement, because in those measures distraction effects are more easily detectable (because the motor system has not had 'time' yet to correct the movement). The results indicated that a frontal posture increased the amount of required avoidance and replicated that obstacles closer to the reaching arm evoked stronger avoidance responses. The data showed that it is important to control the starting posture of the movement, as it affects the entire movement. Researchers should therefore take care to stereotype the posture of participants within and between experiments.

Reward

The aforementioned affordance competition hypothesis (Cisek, 2007) holds that multiple potential actions compete with each other during decision-making. It is further stated that this competition can be influenced by a variety of biases. One of those biases could be reward. Possibly, the reward associated with a potential action might affect the competition between that action and another action. In terms of motor programming, two possible motor plans could compete for execution in the pre-motor cortex and the response code that 'wins out' could have received input from reward areas in the brain (e.g. basal ganglia). For obstacle avoidance it is often clear as to what the target and what the obstacle is. Therefore, the bias reward can offer might not influence action selection, but rather action specification. That means that reward

might influence the avoidance responses by not forcing a decision about what to avoid, but more about how much to avoid it. In bold strokes, an obstacle that has a particular reward associated with it may evoke a smaller avoidance response. So far, not much has been done with regards to obstacle avoidance and reward.

More generally, Trömmershauser, Maloney, & Landy (2003a, 2003b) have looked at the relation between reward and motor behavior in light of optimal movement planning. Nevertheless, there are some implications of note from these experiments that might be useful for a much-needed study on obstacle avoidance and reward. To wit, Trömmershauser et al. (2003a, 2003b) showed participants three overlapping stimuli on a computer screen. The stimuli were color-coded disks which were associated with rewards and penalties. The participants had to reach-to-point toward reward areas to earn money while avoiding penalty areas. As there was overlap between stimuli, the difficulty of accurately pointing only 'on' reward areas was quite high. The experimenters varied, among other things, the cost of hitting the penalty area. They found that movement planning was sensitive to changes in the cost of hitting the penalty area. Hudson, Wolfe, and Maloney (2012) found corroborating evidence that humans move in a way that maximizes the expected gain on an obstacle avoidance task, where touching the target yielded rewards and touching (virtual) obstacles yielded monetary losses. That is, other possible movement objectives (i.e. speed, noise reduction) were passed over in favor of maximizing the possible gain of the action. The implications for obstacle avoidance are clear; if the cost of collision could somehow be increased than we hypothesize that avoidance responses will be more pronounced. Please note that the cost of collision may also be strongly related to the identity of the obstacle, e.g. de Haan et al. (2014) or --more colloquially speaking-- grandmother Maria's porcelain coffee set. In addition, from the work by Trömmershauser and colleagues that is discussed here, it also becomes clear that, interestingly, the obstruction does not need to be mechanical in order for participants to move around it. Indeed, a penalty region may be treated as an obstacle in terms of movement control. The need to maintain eye-contact with this region is a probable cause for the hand to move around the region.

Priming

From a methodological perspective it is important to take the work by Jax & Rosenbaum (2007; 2009) into account, as it demonstrates important aspects to consider when designing an experiment that features repetitive hand movements and is aimed at understanding the processing of information. In bold strokes, these experiments point toward temporal effects of repeated obstacle avoidance. Jax & Rosenbaum (2007; 2009) looked at the retention of visual information in circuits of the brain involved with feeding information to avoidance behavior producing circuits. They did this by having participants perform a visually guided obstacle

avoidance task with varying times between trials. The results first showed an effect of the presence or absence of an obstacle on the previous trial on the current trial. That is, when an obstacle was present on the current trial while it was absent on the previous trial, then the avoidance response on the current trial was initially less curved which increased the chances of collision. Conversely, when no obstacle was present on the current trial and the previous trial did have an obstacle present, then the avoidance response was unnecessarily curved which indicated increased energy expenditure. These drawbacks, i.e. increased collision risk and energy expenditure, occurred because movement planning efficiency was optimized. Simply put, programming upcoming movements may be accomplished more efficiently by keeping the old movement in memory and change those features that distinguish it from the recent movement, rather than programming an entirely new movement. Second, the results of Jax & Rosenbaum (2007; 2009) further showed that the priming effect became less as time between trials increased. To wit, after 1000 ms inter trial interval the priming effect of the previous trial was nearly but not entirely eliminated. Effects flowing from the retention of previous trial information can be minimized from obstacle avoidance experiments by either using a invariant obstacle setup (where the obstacle does not change place) or having inter trial intervals longer than 1000 ms.

Attention

During earlier obstacle avoidance studies it was impossible to disentangle effects of attention from effects caused by changed physical features of the obstacle (e.g. identity, size or orientation). Relatedly, any effect caused by a manipulation of the features of an object could always also be an attentional effect. Menger and colleagues (Menger, Dijkerman, & Van der Stigchel, 2015) investigated the exclusive contribution of attention on obstacle avoidance movements. More specifically, Menger et al. (2015) tested the possible tuning of the avoidance response by providing a spatial cue in an obstacle avoidance paradigm as a go cue for movement. In two experiments, spatial and non-spatial cues were given as go cues for an obstacle avoidance movement: participants' avoidance trajectories veered more away from obstacles that were cued spatially than from obstacles that were not or non-spatially cued. These responses were observed regardless of the presence or absence of another obstacle. Menger et al. (2015) conclude that the tuning of avoidance responses can be influenced by spatial attentional cues.

Of course, there is a whole body of literature that is concerned with the effect that distracting stimuli have on hand movements (for the theoretical model on the mechanism that governs this see Tipper et al. 1997). Such studies, e.g. Welsh (2011), show that hand movement trajectories can be influenced by a non-obstructing stimulus, because it attracts attention to it,

which leads to competition between response codes for the target object and non-target object. The competition between response codes is then resolved via mutual and often asymmetrical inhibition in such a way as to create a bias away from or towards the non-target object, depending on the specific parameters of the task. Most often, however, deviation away from the non-target stimulus or distractor stimulus is observed. In addition, a level of uncertainty about the identity of the target object is required for this effect; that is, the period during which it remains unclear as to which of two objects is the target determines a) the type of deviation (towards to away) and b) the level of deviation (large to small). That is, deviation behavior migrates from deviation towards to deviation away to energetically economic deviation (i.e. obstacle avoidance) the more time passes between go and target identification cues (Chapman, personal communication). Naturally, the study by Menger and colleagues could cover movement behavior evoked solely by distractor interference. That is, the non-target object could compete for attention with the target object during action selection and require subsequent inhibition to be quenched, which results in a functional --but affected- movement path, because the inhibition occurs through biased mechanism (see Tipper et al. 1997). However, the Menger et al. (2015) study features certainty about what the target is in combination with sufficient preparation time for obstacle avoidance ‘to emerge’ and a very obstructive nature of the non-target objects in addition to spatial attention cueing manipulations, which shows the merit of a unique blend of classic distractor interference and obstacle avoidance studies. That is, we know that objects evoked avoidance responses, but we also know that distractor interference effects interfered with those responses, though those effects were of a much smaller magnitude with regards to the hand movements. Speaking in terms of the attentional landscape (Baldauf & Deubel, 2010) and for this particular experimental paradigm, the peaks in the attentional landscape associated with the obstacles that were evoked by the obstacles’ size, position, etc. were further modified by the distracting effects of the flash; i.e. a higher peak in the attentional landscape when an object was cued.

Motor planning

The goal of motor planning is the composition of a movement plan, which is an algorithm that, when executed, starts and controls movement. The outcome of running the algorithm is a motor trajectory, which is partly stochastic. This means that the choice in plan does not completely determine the trajectory: each trajectory is unique and the result it may have on the world is determined by running the algorithm not the plan itself. A case in point would be playing darts; players want to be able to throw the dart at the high-scoring ‘triple twenty’ location and compose a motor plan to accomplish that. However, in the execution of that plan, the running of

the algorithm, a movement is executed that is unique and results in a unique final location of the dart on the board. If you are a novice, if you throw 3 darts with the same motor plan, noise will ensure the darts end up in quite different locations (as a function of the movement trajectory of the arm and hand). If you are an expert, then the three darts are likely to end up closer together but still at unique locations as a result of unique trajectories. In the case of obstacle avoidance, this is true as well.

According to Rosenbaum, Meulenbroek, Vaughan, and Jansen (2001) developing a movement plan for reaching and grasping an object requires the actor to satisfy several constraints. Simply put, if you want to drink coffee, then you should grasp the cup with your thumb and index finger facing each other at the widest possible distance. This satisfies the constraints of using an appropriate effector and selecting the correct position for a grasp. Perhaps other constraints that need to be satisfied are high speed and collision avoidance or high accuracy and end-state-comfort. Yet other constraints can be minimizing motor noise, ease of control, biomechanical costs, and taking visual uncertainty into account (Cohen, Biddle, & Rosenbaum, 2010) and so on; the number of possible constraints is very high. To specify a movement to a target object the motor system is thought to first select an appropriate goal or end-posture (from memory) and then compute the transformation from the current or start-posture to that end-posture while satisfying constraints such as –but not limited to- minimal energy expenditure (Cohen et al., 2010).

Motor control of obstacle avoidance movements requires an additional in-between-posture of the acting limbs during movement to prevent a collision with the non-target (Rosenbaum et al. 2009; Vaughan, Rosenbaum, & Meulenbroek, 2001; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 1999). The specification of an avoidance movement is therefore governed by the extra constraint of the ‘via posture’, which is also a stored posture and is generated similarly as the end posture. The use of via postures satisfies the key constraint during obstacle avoidance: to avoid collisions with objects. Empirical evidence shows that humans move in such a way as to reduce the likelihood of such a collision (Liu & Todorov, 2007; Sabes, Jordan, & Wolpert, 1998; Sabes & Jordan, 1997).

Although no single constraint can explain all movements, one of the constraints in the constraint hierarchy for obstacle avoidance that deserves attention is reduction of (end-state) variability. Indeed, Hamilton and Wolpert (2002) predicted empirical avoidance trajectories with a model that minimized the probability of collision near the non-target object as well as mean-squared error of position at the target location. This implies that both probability of collision and position accuracy are important in planning obstacle avoidance movements.

Hamilton & Wolpert (2002) posited that variability in motor neuronal firing and variability in the motor unit recruitment pattern are sources of signal dependent noise in muscle force output (Hamilton & Wolpert, 2002) and that it is critical to minimize them. This means that when force output is increased, the size of the motor units recruited is also increased which leads to larger variability in movement. The size of the motor unit is related to how many muscle fibers are present in the motor unit; a large motor unit has many muscle fibers within it while a small motor unit has few muscle fibers within it. Therefore, when stronger avoidance responses are required (the arm needs to be moved further sideways), then a larger muscle force output is required which leads to more variability. This in turn needs to be minimized at certain points in the movement, which leads to constraints on the movement that reduce variability coming from this source, i.e. slowing down near obstacles or positioning the arm in such a way as to minimize rotations and translations.

Please note that not all movement constraints can be satisfied at the same time and that at times satisfying one constraint goes to the detriment of another. For example, consider Fitts' Law (Fitts, 1954; Fitts & Peterson, 1964): movement time is affected by both the distance to be traveled and the accuracy required. Therefore, movements cannot be more accurate and faster and the same time. This is also true for obstacle avoidance: Vaughan, Barany, Sali, Jax, and Rosenbaum (2010) showed that Fitts' Law also applies to three-dimensional obstacle avoidance movements confirming earlier 2D work by Jax, Rosenbaum, & Vaughan (2007). Furthermore, these authors found that movement time increased with an increase of degree of obstruction by the obstacle. Vaughan et al. (2010) concluded that this result was congruent with Fitts' Law, which states that longer movement paths (around more obstructing obstacles) should lead to longer movement times.

Classic results from Scott Kelso, Putnam, & Goodman (1983) already pointed out that the constraints on movements are not strictly hierarchical; that is, energy efficiency is not always prioritized above other constraints. As Scott Kelso and colleagues (1983) show, by moving two limbs in a unitary fashion humans do not move efficiently in terms of energy expenditure, but instead prioritize ease of control through interlimb coordination. This was shown by placing an obstacle in the path of one hand and finding that the other hand's trajectory was similarly affected by the obstacle.

Moreover, Hughes & Franz (2008) showed that the constraint hierarchy is never entirely strict, but flexible. These authors investigated the interplay between spatial, temporal, and end-state-comfort constraints and found that these constraints are not enforced in strict manner. Particular constraints appear to become dominant based on the task demands and the

context of the task. Anecdotally, the end-state comfort of an action geared toward catching a falling bottle is much less relevant as movement speed, compared to an inverse situation where one wants to leisurely take a sip (where end-state comfort overrules movement speed). So, fortunately the motor system can flexibly satisfy different constraints.

The generation of movement trajectories itself is likely to occur through simple mechanisms (Grimme et al., 2012). That is, these authors discovered that naturalistic arm movements during obstacle avoidance follow certain regularities under a myriad of conditions. These regularities include isochrony and planarity: isochrony refers to the tendency for humans to move with a roughly constant movement speed independent of distance traveled (global isochrony), having bell-shaped velocity profiles for straight hand paths (local isochrony) and valleys in the speed profile during curving movements (double-peak velocity profile). Planarity is a more complex principle that reflects that humans move along a single and preselected plane toward a target object and thereby reduce torsion. Torsion is a measure of how much a curve twists out of the plane of curvature. Grimme et al. further found that avoidance movements can be decomposed into so-called primitives, which are invariant components of the movement. For obstacle avoidance a lift/descend primitive and a transport primitive were identified. These primitive apparently vary independently when situational determinants like obstacle position are varied: for obstacles close to the start position the transport primitive is initially stymied while the lift primitive remains unaffected. This leads to a combined trajectory that is dominated early on by the lift component and later on determined by the transport component. As should be clear from the example, the two primitives are scaled according to the lay-out of the workspace. By using such building blocks, i.e. movement primitives, and following governing principles like isochrony and planarity, the central nervous system is able to generate a complex and well-timed avoidance movement.

One characteristic of avoidance movements (once generated) is that they are curved. There are many theories as to why this curvature is present in movements. We will discuss one theory here that explains curvature of movements and which also –on the face of it- resonates well with obstacle avoidance behavior in terms of a control strategy. To wit, Petreska and Billard (2009) argue that movement curvature is deliberately planned by the central nervous system (CNS) in order to take the actor's own body, viz. the body's geometry, joint angles, and inertial properties, into account. These authors describe this idea as the encapsulation of embodiment in the control system and that embodiment should be regarded as the main reason for curved movement trajectories. They have developed a mathematical model that accurately describes real human movements and which is, importantly, not only limited to self-oriented movements (their original focus of study), but which can also applied to any point-to-point

reaching movement such as for example reaching to targets in the workspace. Building on the postulation by Petreska and Billard (2009) that their model can be constrained by to-be-avoided objects in the environment, we would like to apply this model here to obstacle avoidance.

However, first the particulars of the model need to be discussed: Petreska & Billard (2009) showed that a naturally curved movement could be replicated through a simple yet useful dynamic systems equation which was modulated by a virtual force-field. These authors found that both spatial and temporal features of normal human movement could be reproduced by the model. The trajectories the model generated were the result of the interaction between the attraction of a target object and the virtual repulsive forces generated for extreme joint angles, inertial properties of the limb, and bodily geometry. Specifically, the dynamic systems equation contained terms for the aforementioned factors which all contributed to a sum vector gradient for each position in the workspace. This gradient, described as a force field, then repulsed the hand away from undesired locations. This means that certain positions in the workspace, based on its particular layout – a target here and an obstacle there- and the initial posture of the body – e.g. hand in front with the elbow bent- will not likely be traversed, because there is a strong gradient ‘carrying’ the hand away from it (see Figure 3 for a schematic representation).

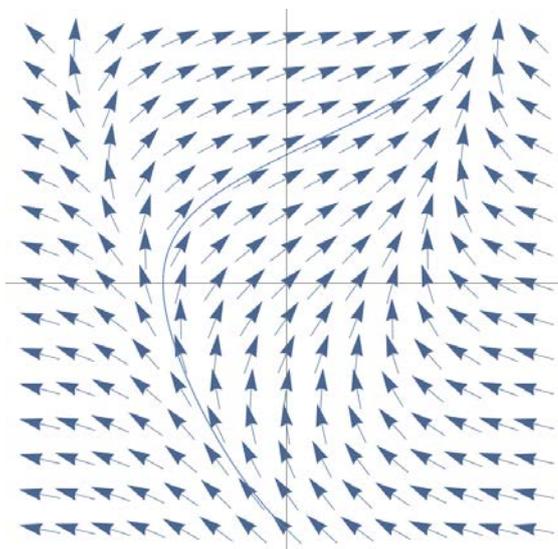


Fig. 3. Schematic of a hypothetical vector gradient field. This is a top-down overview of a workspace, where for several positions vectors have been drawn. Each vector (dark blue arrows) is the result of a dynamic systems equation with attracting terms for the target and repulsing terms for e.g. obstacles. Together these vectors form a gradient along which trajectories are executed. The blue line indicates such a trajectory through space that conforms to the vector gradient. As such, this is a representation of an implementation of the force field hypothesis for obstacle avoidance.

Petreska and Billard (2009) assume the existence of neural populations in humans that code the workspace in this fashion. These authors propose that Area 5 might be involved in computing the force field, as it receives the required visual and somatosensory information. In the next chapter, we will discuss another area, viz. the IPS, which appears to be involved in obstacle avoidance. The precise connectivity of the control mechanism notwithstanding, this force field model provides us with an intriguing theoretical model, because just as the hand may be repulsed away from other limbs, it may also be repulsed from obstacles near the body. That is, the positions in the workspace that are occupied by obstacles may generate strong vector gradients away from it, resulting in a virtual force field which repulses the hand, similarly to the force field that is created for area occupied by the actor's own body. Because the force field model accurately describes why natural human movements are curved, it is therefore likely that the neural control mechanism for movement generation is similarly organized. After accepting the likelihood that such a control mechanism exists, it is not a giant leap to posit that obstacle avoidance is governed by the same control mechanism.

Neurological background & patient studies

There has been extensive research into the neural substrates required for obstacle avoidance (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; McIntosh, McClements, Schindler, et al., 2004; Rice et al., 2006, 2008; Schenk, Schindler, McIntosh, & Milner, 2005; Schindler et al., 2004; Striemer, Chapman, & Goodale, 2009). Schindler et al. (2004) tested 2 patients with optic ataxia (damage dorsal stream projections, ventral stream intact) on their avoidance behavior. The participants' reaches remained invariant with changing obstacle position, while showing retained line-bisection performance (pointing to the midpoint between 2 obstacles) with changing 'obstacle' locations. Therefore, the authors concluded that the dorsal stream ordinarily provides the necessary visual guidance to avoid obstacles. Interestingly, Rice et al. (2008) showed that an individual optic ataxia patient responded to the obstacles present in his workspace after a 5-s delay before reach onset. These authors account for this performance improvement by positing that the delayed action was partly mediated via the ventral stream. In patients with visual form agnosia (ventral stream damaged, dorsal stream intact) the opposite pattern of results of optic ataxia patients has been demonstrated: Rice et al. (2006) found that 2 patients with visual form agnosia responded to changes in obstacle location with different avoidance movements, while showing poor bisection performance.

Along similar lines, McIntosh et al. (2004a) show preserved obstacle avoidance in patients with left visual neglect while patients had impaired line-bisection. In a related study, McIntosh et al. (2004b) showed that in a patient with visual extinction after right Temporoparietal damage the degree of avoidance was unrelated to whether the patient was able to report the obstacles presence. This prompted the conclusion that visual awareness, i.e. a ventral stream function, was not necessary for obstacle avoidance. Furthermore, Striemer et al. (2009) demonstrated that an individual with dense left field visual hemianopia remained sensitive to obstacles placed in his blind field. This sensitivity disappeared in a second experiment with a 2-s delay before reach onset. This sensitivity to visually unconscious objects shows that primitive subcortical visual pathways are hooked up to the dorsal stream and can influence avoidance behavior (Weiskrantz 1996).

The dissociation between visuomotor guidance and perceptual performance observed in these studies prompted the conclusion that the dorsal stream is necessary but not sufficient for obstacle avoidance. That is, the dependence of proper obstacle avoidance on the dorsal stream does not restrict the role of the ventral stream, as the ventral stream may influence avoidance behavior based on semantic properties of the obstacle (Milner & Goodale, 2008). Furthermore, in a recent paper, evidence was brought forward that indicated that conscious processing of visual information influenced obstacle avoidance (Hesse, Lane, Aimola, Schenk, 2012). This casts doubt on the presumed automatic and subconscious nature of the obstacle avoidance ability. Generally speaking, however, and caveats notwithstanding, visual processing of information about the obstacle in the dorsal stream is very important for obstacle avoidance behavior. However, the dorsal stream does not operate in isolation, that is, processing of information does not end there; it is further projected into peaks of activity in premotor areas.

One dorsal stream area that appears to play a vital role in obstacle avoidance is the posterior Intraparietal sulcus (IPS) (Chapman, Gallivan, Culham, & Goodale, 2011). These authors have shown that when obstacles interfere with grasp planning there is a top-down modulation of the early visual cortex by this area. Indeed, these authors demonstrated that objects that physically interfere with to-be-performed actions are detected by the contralateral (with respect to the reaching hand) IPS which then suppresses the neural representation in the early visual cortex areas which is associated with these objects. In addition, Chapman and colleagues showed that the modulation of visuomotor planning areas by the IPS was dependent on the degree of interference or obstruction afforded by the object. This means that the more the object obstructed movements the more activity was registered in IPS.

In bold strokes, Chapman and colleagues (2011) define obstacle avoidance along the following lines: positive neural activity is evoked by physical objects in the visual cortex and this activity represents a retinotopic map of the workspace. This map can be pictured as an attentional landscape with hills and valleys of activity, both noting locations relevant for actions. Movements are drawn toward high activity regions (hills) in this landscape and are repulsed from low activity regions (valleys). So, obstacles will first give rise to activity in the landscape and will attract attention. Only when obstacles are tagged by the IPS as interfering with a movement to the target, will the activity (hill) be suppressed to a relatively low level (valley). The function of the IPS in this case appears to be to reduce the activity of peaks in a visual attentional landscape to ultimately have the hand move away from certain objects while it travels toward the goal object. This process can be further understood when we look at the force field model as postulated by Petreska and Billard (2009); when the obstacle has not yet been tagged, it may attract movements toward it, i.e. the positions around the object are represented by vectors pointing toward the object; simply put, the object functions as attractor. However, once the IPS has tagged the object position as obstructing, these vectors will now point away and beyond the object position so that a virtual force field is created that repels movement away from that part of space: the object now functions as a repeller. Here, the attentional landscape model and the force field model converge, offering an account for obstacle avoidance that is based on visual information processing and motor control, using similar mechanisms.

Summary and conclusions

The obstacle avoidance paradigm can yield information about visual processing prior to motor plan execution for more complex movements. As such, this paradigm allows us to investigate what features of obstacles are integrated into the motor plan for a cluttered and more natural workspace. Moreover, the obstacle avoidance paradigm provides an interesting way of testing the interaction between the dorsal and ventral stream. That is, the ventral stream features (i.e. its identity) of an object are likely to affect obstacle avoidance behavior in addition to its dorsal stream features (i.e. its size). As Chapman & Goodale (2008) pointed out: “one would expect participants to be sensitive to the harmful nature of an object (like a cactus) and give these objects a wider berth when making reaches” (p. 96). As the cactus-identity is not a feature traditionally thought to be processed by the dorsal stream, obstacle avoidance can therefore provide a window into the confluence of the dorsal and ventral stream.

If we interpret the experiments discussed above along the lines of the attentional landscape model by Baldauf & Deubel (2010) and the Cisek affordance competition model (2007) the potential mechanisms underlying the observed responses are as follows: obstacles are valleys in the attentional landscape, and as such, their features, such as position and identity determine the depth of the valley in the attentional landscape and the avoidance response resultant from the co-occurring motor plan. Logically speaking, we can assume that the deeper the valley in the attentional landscape, the larger the avoidance response will be (veering more away from the obstacle). In experiments where the manipulation of dorsal stream features led to behavioral changes, i.e. different avoidance responses (see 2.1 and 2.2), we can speculate that the processing along the dorsal stream influenced the emergent attentional landscape and that the resultant motor behavior is a unadulterated reflection of the competition between the attentional hill of the target and the attentional valley of the obstacle. Moreover, we can theorize that when ventral stream features are manipulated in an experiment (see 2.3), then the information processing along the ventral stream affects the attentional landscape through direct input on the competition by adding votes to an obstacle-related valley (making it deeper). A similar result, i.e. a deepened valley of activation related to an obstacle, could be obtained if low-level attention were to be focused on the obstacle in an experiment (see 3.5). In experiments where reward is coupled to motor behavior there is a role for the reward centers of the brain (frontal nuclei and basal ganglia) in upvoting or downvoting attentional valleys and hills. Unfortunately, this avenue is left unexplored for obstacle avoidance, but experiments on pointing accuracy were discussed (see 3.3). Once the competition between response codes is resolved, the 'winning' motor plan needs to be executed and results in unique emergent behavior. Several empirical and theoretical factors that influence action specification for obstacle avoidance were discussed (see 3.1, 3.2 and 4). Of special note is the force field model that offers an account of motor control that succinctly describes how obstacle avoidance movements could also be programmed.

Here we reviewed the obstacle avoidance paradigm and we have discussed features that prompt changes to normal avoidance behavior as well as contextual factors that can influence obstacle avoidance behavior. We have also looked at the theoretical and neural underpinnings of the avoidance behavior. What can be concluded from all this is that obstacle avoidance behavior is a complex and automatic skill that relies heavily on visual information processing along both the ventral and the dorsal stream. At this point, the exact mechanisms remain unclear; however, there is room for speculation: all effects on avoidance movements can be thought to flow through the attentional landscape. The dorsal and ventral stream feed information into this landscape, where factors such as obstacle location (dorsal) and obstacle

identity (ventral) may cause modulations of the activation level for a given object. That is, Grandma Maria's porcelain coffee cup that is on the outside of your right wrist may prompt a larger activation in the attentional landscape than the plastic plant on the left side of your hand. Next the IPS tags both object-representations in the attentional landscape as obstacles (you're going for the chocolates of course). The behavioral that then results seems to hinge on the incorporation of the activation codes for obstacles in the attentional landscape with its specific own 'identity' or activation level into the motor plan.

An aspect of obstacle avoidance left to explore is multisensory interactions near obstacles as that may shed further light on the representation of obstacles in the brain; because obstacles are -almost by definition- near to the body and, as such, within the peripersonal space (Rizzolatti, Fadiga, Fogassi, Gallese, 1997) of individuals, it is likely that obstacles will activate multisensory networks in the brain. It would be interesting to see whether the predicted consequences of collisions, which are a natural cause for obstacle avoidance, are actually in play via the peripersonal space mechanism during obstacle avoidance. Indeed, the force field model for motor control seems to resonate well with the idea of an area around the body's geometry that deals with actions: that is, the representation used by the force field model (Petreska & Billard, 2009) of the body does not need to stop at the skin, but may, instead extend into the space around it. Furthermore, the effects of attention on obstacle avoidance need further exploration; what are likely effects of, among others, IOR and the strength of visuospatial cues (i.e. very salient versus more subtle cues) on obstacle avoidance behavior. In addition, avoiding moving obstacles or self-movement relative to stationary obstacles is a very relevant avenue for research with regards to real-world applicability and the integration of hand-related obstacle avoidance with locomotor and robot avoidance behavior. Lastly, the neural substrates underlying obstacle avoidance can only be pointed broadly to. It would aid understanding of this fascinating behavior if a more dedicated network could be uncovered through imaging techniques.

Appendix 1: How to measure avoidance responses?

Unlike eye movements, where the trajectory from A to B is almost irrelevant (eye movements hardly ever knock something over), hand movements, especially obstacle avoidance movements, can have very constrained trajectories. During hand movements speed is also sometimes sacrificed to satisfy other constraints (e.g. accuracy). Although particular trajectories are idiosyncratic, repetitions of trials can point to a movement plan via a mean trajectory. Analysis of mean trajectories can be performed in one of two ways: some measures include all the points on the trajectory, such as the FDA-analysis technique performed by e.g. Chapman et al. (2010), while others, e.g. Menger et al. (2012), look at a specific reference-sample of the trajectory, such as deviation at passing. The former method may be preferable because it is less sensitive to sample noise. However, there might be valid reasons to focus on some aspect of trajectories over others. Please note, that many consecutive points in a trajectory are not statistically independent (each point in a trajectory depends on the previous point) and that as a result some measures correlate highly with each other as well. That is, if the deviation at the start of the movement is high, then it is bound to be high during the middle part of the movement as well. Nevertheless, conclusions should be based on corroboratory evidence from multiple measures. Other relevant sources to consider are not just measures of space, like grip aperture, but also those of time, like movement and reaction time, space-time, like measures of speed or acceleration (given a high enough sampling rate). Table 1 gives a short description of each measure, while figure 4 and 5 depict ways of establishing each measure.

Table 1. Frequently used possible measures of obstacle avoidance trajectories. Font color is used to link measures to figure 2 and 3.

Name	Definition	Sample Reference
Reaction Time (ms)	Time from the start of the trial to the first frame used as the beginning of the reach movement	Chapman & Goodale, 2008
Movement Time (ms)	Time from the beginning of the reach movement until termination of the reach movement	Chapman & Goodale, 2008
Peak Velocity (mm/s)	Highest Velocity obtained during movement time	Mon-Williams et al., 2001
Time to peak Velocity (ms)	Time from the beginning of movement until peak velocity is reached	Chapman & Goodale, 2008
Grip Aperture (mm)	The distance between thumb and index finger	Tresilian, 1998
Maximum Grip Aperture (mm)	The maximum observed grip aperture during movement	Mon-Williams et al., 2001
Deviation at Location (mm)	The horizontal deviation at a selected depth location, i.e. 50% depth or location of peak velocity.	Menger et al. 2013
Maximum Deviation (mm)	The maximum observed deviation during movement time	Tresilian, 1998
Error at location (mm)	The standard error of deviation scores across repetitions of a condition	Menger et al., 2014
Path Length (mm)	The cumulative distance moved by i.e. the index finger	Tresilian, 1998
Direction (°)	The slant of the movement vector with respect to the midsagittal line	Menger et al., 2013
Area (mm ²)	The area between two trajectories, approximated by a trapezoidal method	Chapman & Goodale, 2008
Maximum height (mm)	Maximum height above surface	Tresilian, 1998

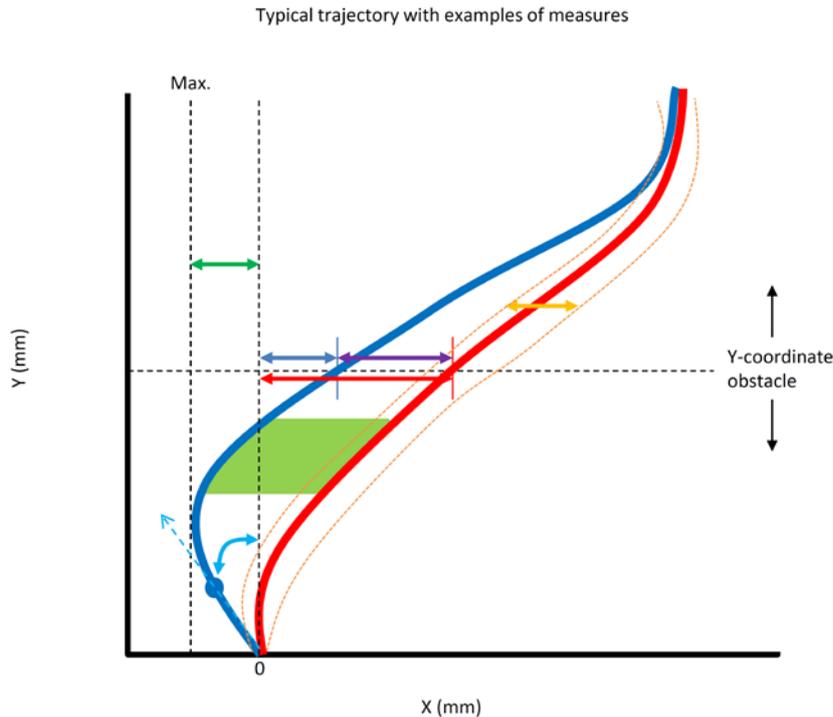


Fig. 4. Typical trajectories with examples of measures. This graph shows two thick lines which show trajectories in red and blue, a control and experimental trajectory, respectively. The length of these trajectories is measured with the path length parameter. Black dashed lines have been used to indicate $x=0$ and $x=\text{max}$ as well as y -coordinate of the obstacle, which serves as a reference for the calculation of Deviation measures. The blue double-headed arrow shows the deviation with reference to $x=0$ for the 'experimental' condition, while the red double-headed arrow shows the deviation with reference to $x=0$ for the 'control' condition. The height measure is obtained in the same way, but in a different cardinal direction (z axis, not depicted). The purple double-headed arrow shows the deviation as a difference score between experimental and control conditions. The grip aperture measure is obtained similarly, but only by calculating the difference between the thumb and index finger trajectories instead. The maximum deviation score is indicated by the difference between the $x=0$ and $x=\text{max}$ lines with the dark green double-headed arrow. The blue dotted line coming from the origin $(0, 0)$ which moves through the center of the big blue dot which represents the n^{th} sample indicates the direction in degrees. The direction measure is taken with reference to the dashed line $x=0$ and is represented with a light blue arc. The area between two curves is shown by the light green prism for a limited amount of samples, but can be extrapolated to the entire curve.

Typical y-component of trajectory with examples of measures

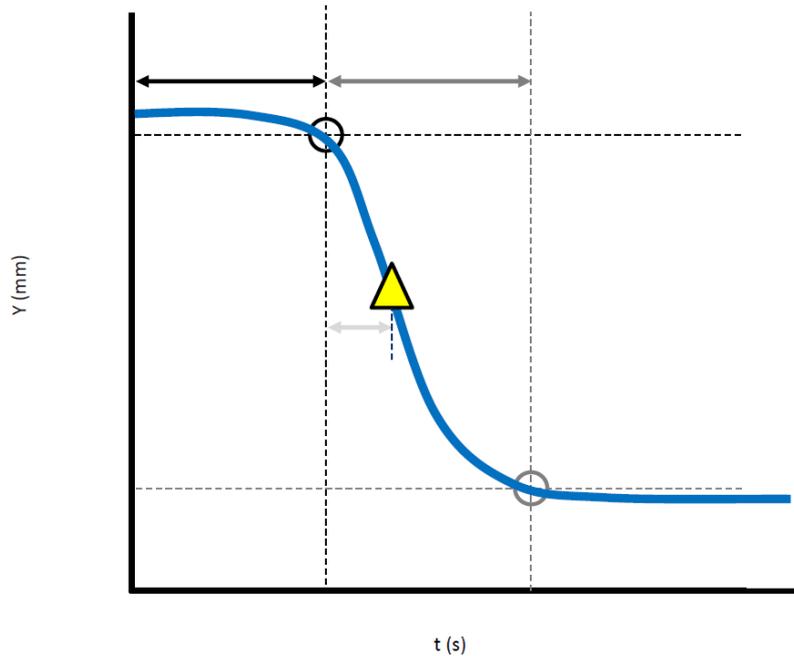


Fig. 5. Typical y-component of a trajectory with examples of measures. This figure shows a simplified example (2 cardinal directions have been removed) of measures that can be taken from position and time data. The thick blue line shows the progress of the hand in the y-direction (towards the target object) over time. The black and grey circle show the beginning and end of movement, respectively (established by using the MSI-method (Schot, Brenner, & Smeets, 2010. Simply put, the position and change in position (and the change in change of position) are used to determine when movement starts. The time between go-cue ($t=0$) and the start of movement is represented by the black double-headed arrow, which represents reaction time. The time between start and end of movement is depicted by the dark grey double-headed arrow and represents movement time. The time of occurrence of the maximum change in position (peak velocity) is identified with a yellow, black bordered, triangle. The difference between the aforementioned position and the start of movement is considered the Time To Peak Velocity which is depicted by the light grey double-headed arrow.

Chapter 3 – On the relation between nontarget object location and avoidance responses

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2014). On the relation between nontarget object location and avoidance responses. *Journal of Vision, 14(9)*: 21-21.

Abstract

The presence of nontarget objects influences kinematic parameters of reaches toward target objects. In previous studies, several different nontarget positions have been used. Taken together, these studies suggest that when the horizontal or vertical distance to nontargets is decreased, avoidance responses are more pronounced. Furthermore, responses to nontarget objects are asymmetrical across workspace, i.e., responses in the presence of equidistant nontargets on the inside and the outside of the reaching arm are different. However, these studies have provided a coarse overall picture of the effect of nontarget location. Therefore, the aim of this experiment was to systematically map the avoidance responses across the workspace in order to determine in detail the relation between nontarget position and the avoidance response. Specifically, we were interested in the contribution of four parameters to the reaching response: the nontarget's horizontal and vertical position, its distance from the starting position, and its angle with the vertical midline of the workspace. Participants were asked to perform reaches towards physical targets while nontargets were present in 1 of 24 different positions. Our results replicate horizontal and vertical effects of the nontarget object on reaching behavior. We also replicate stronger avoidances of nontargets on the outside of the reaching limb compared to nontargets on the inside. Furthermore, our results provide a detailed overview of the interaction between these factors and demonstrate that there is a “hot” region qua nontarget positions that prompt the strongest responses. Lastly, our results provide evidence that support a fine-grained spatial resolution of nontarget motor representation.

Obstacle avoidance is a skill that humans possess in a number of movement domains, which is important for successfully acting in and upon our environment. For hand movements, obstacle avoidance is the ability to steer the hand around objects that obstruct movement toward a target. Research has determined that people are generally well able to perform these movements under a myriad of conditions: whether the nontargets are close to the hand (e.g., Mon-Williams, Tresilian, Coppard, & Carson, 2001) or next to the target (Biegstraaten, Smeets, & Brenner, 2003), large or small (Chapman & Goodale, 2008), oriented vertically or diagonally (Kritikos, Bennett, Dunai, & Castiello, 2000), close or further away in distance (e.g., Chapman & Goodale, 2008; Rice et al., 2006), the avoidance response is ostensibly subtle and precise (Tresilian, 1998). This is reflected by the fact that the hand veers smoothly around or away from a (partially) obstructing object with a minimum distance between hand and object (Dean & Bruwer, 1994). Therefore, kinematic parameters of the movement appear to be altered to reduce the risk of collision (Hamilton & Wolpert, 2002). These parameters include the deviation of the movement (i.e., the change in trajectory of the hand relative to a move in a workspace without an obstacle present), but also movement speed, grip aperture, movement time, and reaction time. The same spatial and temporal adaptations are noticed when nontargets are not necessarily obstructing the movements of the limbs towards the target (e.g., Tipper, Howard, & Jackson, 1997; Welsh, 2011).

It has been suggested that avoidance responses are primarily dependent on dorsal stream information (Rice et al., 2006; Schindler et al., 2004; Striemer, Chapman, & Goodale, 2009), especially the egocentric location of the obstruction (e.g., Chapman & Goodale, 2008). Indeed, it is known that horizontal and depth position affect hand movements and also that ipsilateral nontargets cause larger deviations than contralateral nontargets (Chapman & Goodale, 2008; Dean & Bruwer, 1994; Meegan & Tipper, 1998, 1999; Menger, Van der Stigchel, & Dijkerman, 2012; Mon-Williams et al., 2001; Pratt & Abrams, 1994; Tipper, Lortie, & Baylis, 1992). However, several questions remain as to the nature of those effects: (a) What is the precise relation between horizontal/vertical position of the nontarget and the avoidance responses, i.e., is there a linear decrease or an abrupt shift in avoidance responses with increasing horizontal and vertical distances? (b) How do the horizontal and vertical positions of nontargets interact, i.e., is there a single hotspot or are there multiple hotspots at which avoidance responses are greatest? (c) Can different spatial locations of nontargets be lumped together or is the avoidance system as subtle and precise as suggested by Tresilian (1998) in that it generates a unique response to each layout of the workspace, i.e., is the spatial resolution of nontarget position coarsely or finely grained during visuomotor control?

Therefore, we believe it is worthwhile to systematically manipulate the location of the nontarget across 24 positions to map out the location effect in detail. Because hand trajectories

are our behavioral measure of interference during visuomotor planning by nontarget objects, this setup allows us to investigate the spatial resolution of the nontarget motor representation. By placing the nontarget at many different locations we can determine whether the spatial resolution of the location representation is coarse or fine: Either there are differentiated responses to nontargets at different locations when the objects are close to each other (fine) or not (coarse). In addition, by using many different locations we can disentangle the unique contributions of the horizontal and vertical position of the nontarget, as well as the angle toward the nontarget (with respect to straight ahead) and the distance to the target. Angle and distance are a way to define position in an egocentric reference frame and therefore more likely to drive behavior. Proper identification of the relevant parameters can then lead to a more quantified understanding of obstacle avoidance: Simply put, if distance is a predictor of avoidance response, then how much distance leads to how much avoidance response?

By using many different nontarget locations during this experiment we are also able to observe the transition of nontargets from obstructing to no longer obstructing movement toward the target. In the latter case, participants are possibly only distracted by the presence of nontargets. However, whether the behavioral responses to nontarget objects are better qualified as distractor interference (Tipper et al., 1997) or obstacle avoidance (Tresilian, 1998) is a discussion beyond the scope of this paper. For now, we assume that both can account for deviations to reaching behavior when objects are present. In a recent model by Cisek and Kalaska (2010), biases during target selection (distractor interference) and the specification of the action so as to avoid collision (obstacle avoidance), are postulated to operate in parallel and involve similar neural processes. Therefore, as attentional allocation and movement planning are closely related (see also Deubel & Schneider, 2003; Rolfs, Lawrence, & Carrasco, 2013), reported effects might not be uniquely attributable to either attentional allocation or movement planning. Indeed, if the processes operate in tandem, it is difficult to see where one influence stops and the other begins. With the current experiment we aim to underline this parallel processing by demonstrating that there is a gradual shift in strength of behavioral responses to nontargets that offer different levels of obstruction. On the contrary, if we would find a sudden drop in avoidance responses with increasing nontarget distance, this would suggest that the behavioral response to nontarget is indeed driven by only, or much more strongly, the obstruction the nontargets offer in this experiment. Thus, if indeed nontargets are relevant during action specification as well as bias action selection—processes that run in the same neural substrate—we do not expect an abrupt shift in movement deviation as horizontal or vertical distance of the nontarget increased.

It is important to note that the behavioral response is not a simple response to only the nontarget location. Indeed, movement trajectories are the result of a complex interplay between

different motor control processes. First, properly controlling an avoidance movement may require a certain in-between-posture of the acting limbs during movement to prevent a collision with the nontarget (Rosenbaum et al., 2009; Vaughan, Rosenbaum, & Meulenbroek, 2001). This will prompt a mean curved movement trajectory over trials that deviates from a mean control movement trajectory over trials. Additionally, the requirement to have little positional variance at the location of the nontarget, that is, to be accurate and thereby reduce the chance of collision, may be revealed by characteristics of trajectories over repetitions of trials. For instance, promoting limb stability near nontarget objects may lead to little variance in position in curved movement trajectories. In contrast, there is no need to be accurate when there is no constraint on accuracy as is the case when no or a far-away nontarget is present. In this light, we propose to look at the variance of behavioral measures in addition to the means extracted from hand trajectories as our behavioral measures of interference elicited by nontarget objects during visuomotor planning. This is based on the assumption that humans can minimize limb position variability (or increase accuracy) during movement.

We designed an experiment to systematically map the effect of nontargets on hand trajectories. Right-handed participants were asked to perform reach-to-grasp movements toward a physical object with a physical nontarget present in the workspace. The nontarget could be located at 24 positions that were ipsi- and contralateral to the reaching hand. In other words, the nontargets could be on the inside or outside of the hand when it moved to the target.

Methods

Participants

We determined the sample size using power analysis software, viz. G*Power (Franz Paul, Universität Kiel, Germany). We obtained a partial η^2 from an earlier study (Menger et al., 2012). The effect size, f , was then determined to be 0.29. This related to the difference in hand movements between the different obstacle location conditions (i.e., a main effect of nontarget location on the deviation of the hand). Menger et al. (2012) found an effect in two separate experiments each with a population of 10 participants. The effect size of 0.29 will be detected with a precision $\alpha = 0.05$ (two-sided). With $\beta = 0.05$ (power = 95%), and 24 conditions, 10 participants were included in total. Three men and seven women volunteered for this study in exchange for curricular credit and gave their informed consent. All participants were right handed and had normal or corrected-to-normal vision. The faculty's institutional review board under the Medical Research Act issued a formal written waiver that this research project did not require approval from a Medical Ethics Review Committee.

Apparatus and stimuli

The participants were seated at a white table (610 mm × 1220 mm). The table had a surreptitious workspace of 400 mm × 400 mm in which the experimental task was performed. Two buttons were embedded along the midline of the workspace in the table: one start button, located in front of the participant and one target button that was at a distance of 400 mm from the start-button at a 0° angle. The target button responded to a target being lifted from it. Pine wooden cylinders (150 mm height × 50 mm diameter) were used as target object and as nontarget object.

Nontargets were placed at one of 24 possible locations in the workspace. The locations were defined by grid formed by four horizontal and six vertical dimensions. Figure 1 provides a top-down overview of the spatial locations of possible nontargets. The spatial locations were chosen so as to coincide with earlier work (Chapman & Goodale, 2008, 2010; McIntosh et al., 2004; Meegan & Tipper, 1998; Menger et al., 2012; Rice et al., 2006; Tipper et al., 1997). Egocentric distance and angle from the starting button to the nontargets are given in Table 1, while Figure 1 also gives an example of the angle and distance of a single nontarget.

Participants wore PLATO LCD goggles (Translucent Technologies, Toronto, Canada), and MiniBird magnetic markers (Ascension Technology Corporation, Burlington, USA) that permitted, respectively, manipulation of visual feedback and kinematic tracking with a sampling rate of 100 Hz over 3 s. The tracking markers were placed at the tips of participants' right index finger and thumb to measure their spatial positions with 0.1 mm accuracy. These locations have been reported earlier as sites for markers (see e.g., Mon-Williams & McIntosh, 2000) and are considered to be the focus of prehension research (Ansuini, Tognin, Turella, & Castiello, 2007). Care was taken to avoid situations in which the width of the marker itself interfered with the movement. By fixing the cables to the participants' arms and the table with tape and elastic participants could move their hands and arms without restriction.

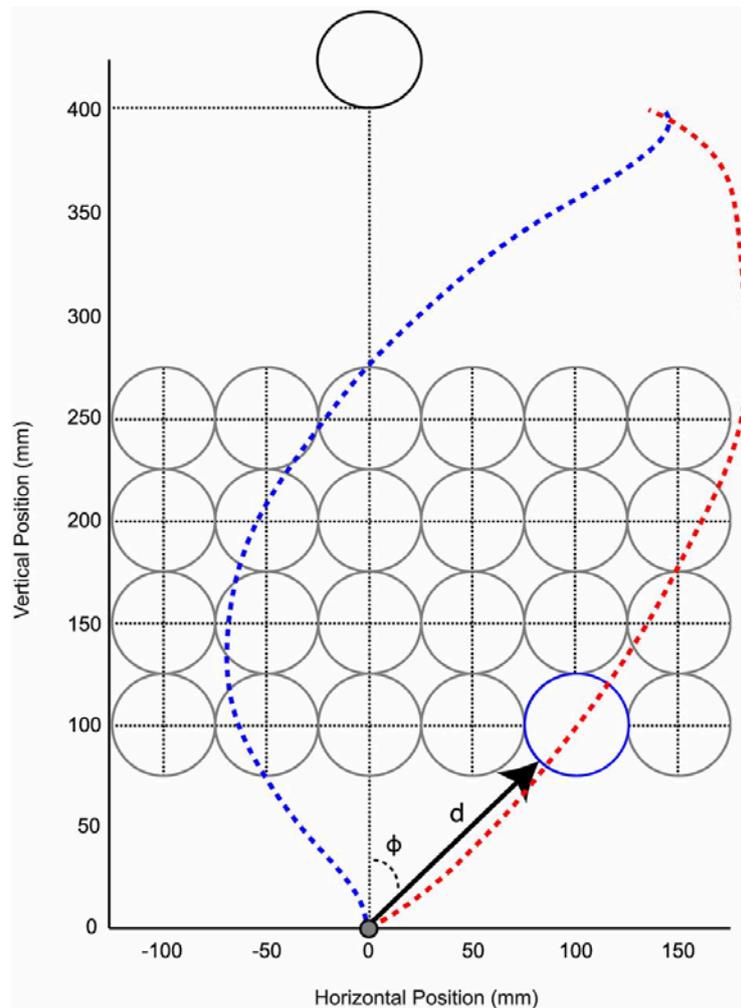


Fig. 1. A top down view of the experimental setup. The x axis shows horizontal position (in mm), while y axis shows vertical position (in mm). The starting (gray-filled circle), target (black-bordered circle), and nontarget locations (crossed circles) are shown. Only the starting button is not to scale. One nontarget location is highlighted (blue bordered circle). The distance (d) and angle (ϕ) toward this example are displayed. The red dashed line is a typical movement of the index finger during control conditions while the blue dashed line is a typical movement of the index finger when the blue nontarget is present. Because most of our analyses pertain to the reach part of the movement and not the grasp component, the movements in this figure have been cut off at the 400-mm depth mark to highlight only the transport phase of the movement.

Table 1. Horizontal and vertical positions of nontargets with associated distances from starting button (in mm) and angular difference (in degrees) with respect to straight ahead (0°).

Nontarget's horizontal position						
Nontarget's vertical position	-100	-50	0	50	100	150
250	269 mm -22°	255 mm -11°	250 mm 0°	255 mm 11°	269 mm 22°	291 mm 31°
200	224 mm -27°	206 mm -14°	200 mm 0°	206 mm 14°	224 mm 27°	250 mm 37°
150	180 mm -34°	158 mm -18°	150 mm 0°	158 mm 18°	180 mm 34°	212 mm 45°
100	141 mm -45°	112 mm -27°	100 mm 0°	112 mm 27°	141 mm 45°	180 mm 56°

Design

All participants performed control trials in which no nontarget was placed in the workspace. The control trials served as a baseline for normal reaching behavior for comparison with the experimental trials. The control trials consisted of reaches toward the target location. During the experimental trials a single nontarget was present in addition to the target. For each experimental trial there were 24 possible nontarget locations, some of which were on the inside of the reaching hand, while others were directly in front or on the outside of the reaching hand. We designed the experiment with the previously found asymmetrical response to equidistant nontargets (see e.g., Chapman & Goodale, 2008; Menger et al., 2012) in mind. Our aim was to create a pyramid, where responses between the outermost, innermost, and in-between conditions would be similar instead of inherently biased by the use of the right arm. There was one control condition and there were 24 experimental conditions that were defined by the XY coordinates of the nontargets center relative to the starting button [vertical position (100, 150, 200, 250 mm), horizontal position (-100, -50, 0, 50, 100, 150 mm)]. All conditions were presented seven times, which makes a grand total of $(24 + 1 \times 7) = 175$ trials excluding 25 practice trials. In addition, the experiment was divided into two blocks to allow for a post-hoc split-half comparison. All trials were presented in a random sequence.

Procedure

Participants were instructed to execute their reach-to-grasp movements with their right hand. The participants were given the instruction to start the movement as fast as possible after hearing an auditory cue, and also to smoothly reach and grasp the target object without touching the possible nontarget. We further told participants to grasp the target with thumb and

index finger halfway along its vertical axis. This particular constraint at the end of the movement combined with both the movement constraints offered by the nontarget and the selected starting posture was used to increase behavioral consistency. This way the most direct trajectory to the target never went over the top of the obstacle or passed the inside of the obstacle when it should have gone passed the outside or vice versa. Nonetheless, sometimes participants would not select a consistent route to the target across conditions by, e.g., going round the outside once and along the inside the other times. Because these switches did not occur frequently during a given experiment (i.e., more than once or twice) the aberrant trajectories were excluded from further analysis (i.e., treated as outliers).

Before each trial the experimenter soundlessly placed the target object and nontarget on the workspace. After trial setup the Plato goggles would open, thereby granting vision of the workspace to the participant. After a short delay (800–1200 ms) an auditory signal cued the participants to perform the task as instructed: the participant had to reach towards, grasp, and lift the target object with their thumb and index finger. Once the target was lifted by the participant movement data collection ceased. Upon task completion the participant put down the target and used their index finger to press the start-button. This closed the PLATO goggles and ended the trial. After pressing of the start button, participants were required to hold their index finger and thumb at that location while awaiting the start of the next trial.

Dependent measures and analysis

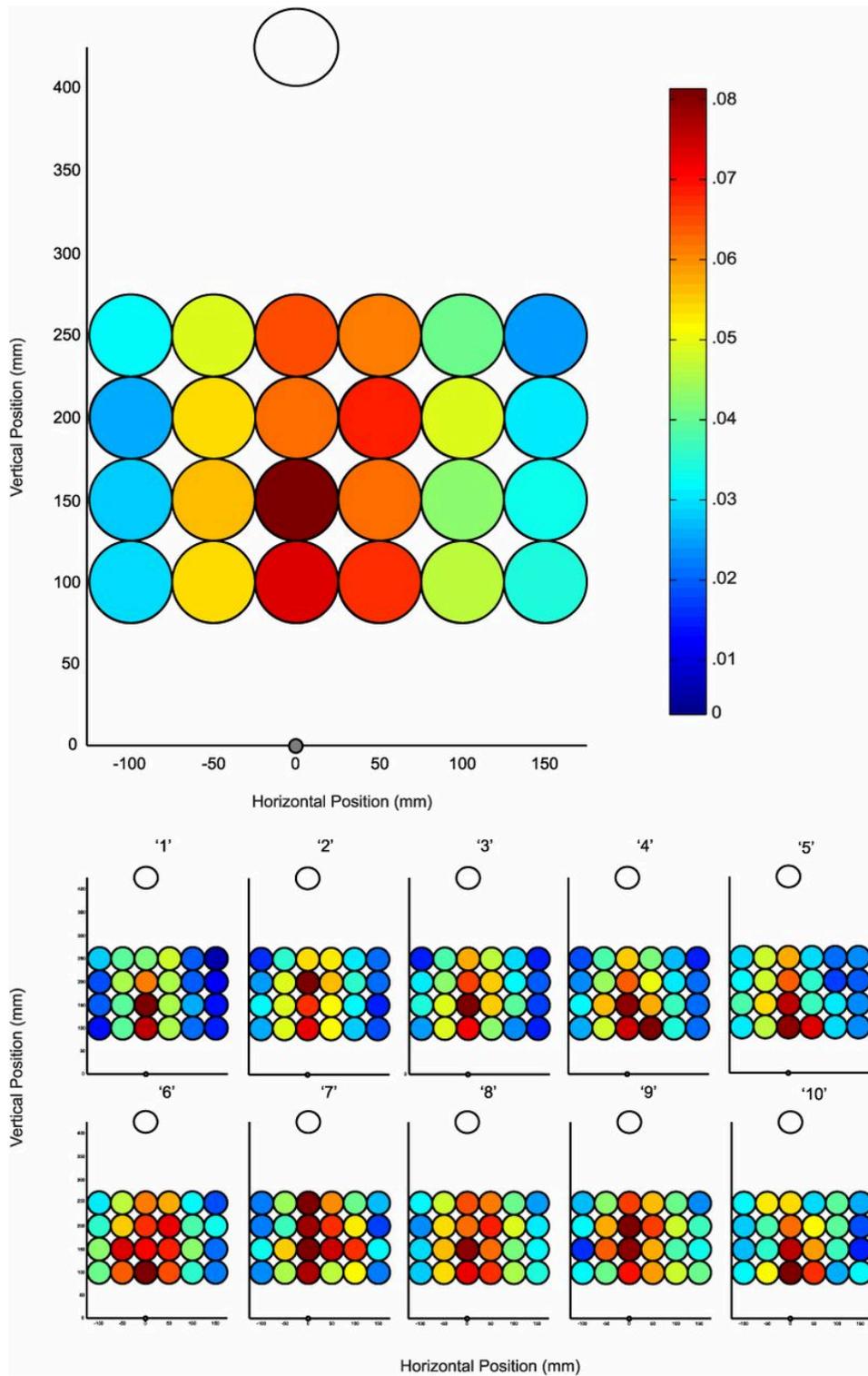
The raw trajectory data of each trial was filtered by using a dual low-pass second-order Butterworth filter with a cut-off frequency of 20 Hz (see also: Mon-Williams et al., 2001; Tresilian, Mon-Williams, Coppard, & Carson, 2005). The filtered trajectory data was then normalized using a cubic spline interpolation into 100 samples (see also: Smeets & Brenner, 1995; Tresilian et al., 2005).

Using the position data and stimulus presentation data the following measures were computed¹: reaction time (the time between the auditory cue and movement onset), movement time (the time from movement onset until the end of the reach-to-grasp movement), grip aperture (the three-dimensional distance between thumb and index finger markers), peak

¹ Unless specifically stated otherwise all spatial measures were computed from index finger marker data. Please also note that temporal measures are partly constrained by the refreshing frequency of the miniBird system (100 Hz), as movement onset was computed from processed position data. We calculated speed in each cardinal dimension (x , y , and z). These were used to define the beginning of the movement (Schot, Brenner, & Smeets, 2010). We determined movement onset by checking whether marker position was sufficiently close to the starting location (within a 3-mm radius), and whether the threshold for marker velocity (5 mm/ms) was exceeded for a sufficient number of samples (50 ms). A continuous function then expressed which of the candidate samples was actually closest to the threshold of e.g., minimal speed: $F_v = 1 - V_{min}$.

velocity (the maximum velocity attained during movement), time to peak velocity (the time from movement onset until peak velocity was reached), deviation at passing (distance between the location of the index finger and the edge of the nontarget at the moment the hand passed the vertical position of the middle of the nontarget), and error at passing (the standard error computed for deviation at passing across repetitions of a condition). For each dependent variable, we computed an individual difference score between the experimental and the control condition. To do this for the deviation at passing score, we specified the deviation in the control condition (in which no nontarget was present) relative to the location of the nontarget in the respective experimental condition. In order to build heat maps of the workspace we further expressed the deviation for a given participant and location as a fraction of the sum of deviations at all locations and then averaged that over participants (henceforth: summed deviation fraction). This way the distribution of the deviations, which is not constant across participants (see also Figure 2), could be compared. Trials were rejected if the reach was initiated before the starting cue was given, the reach did not end within the recording window (3 s), or because of unforeseen recording errors. No participants were rejected because less than 10% of their trials were excluded from further analysis.

Fig. 2. (Next page) Discrete heat maps showing averaged (big panel) and individual (small panels) avoidance responses to nontarget locations. Target and starting location are shown as a white-filled circle and gray-filled circle, respectively. Color denotes the magnitude of the avoidance responses where hot colors (red, orange) are strong responses and cold colors (green, blue) are weak or no responses (blue). In this case avoidance responses are expressed as a fraction of the summed deviation for a given participant, which was then averaged. A strong response is therefore equal to one (dark red) and a weak response is close to zero (dark blue).



Results

We performed an initial Repeated Measures Analysis of Variance (henceforth: RM ANOVA) with an extra factor block (two levels: first and second) and within subject factors horizontal position (six levels: @X-100, @X-50, @X0, @X50, @X100, @X150) and vertical position (four levels: @Y100, @Y150, @Y200, @Y250). Below, these locations may be referred to as “middle, medial, and lateral” and “close and far” (in depth), respectively. In addition, locations to the left of the middle were considered as on the inside of the reaching arm and locations to the right were considered as on the outside of the reaching arm. Our analysis showed no significant difference between reaches performed in the first half of the experiment versus the second half of the experiment for all dependent measures (all p 's > 0.05). Therefore, split half data were collapsed. When descriptive statistics are reported ‘±,’ always refers to ±1 standard error of the mean.

Deviation at passing

A main effect was found for vertical nontarget location, $F(3, 27) = 7.28, p < 0.01$, partial $\eta^2 = 0.35$. The mean deviation at passing for the closest nontargets was 39.7 mm (± 8.7), for the intermediary vertical positions it was 33.5 (± 6.8) and 33.0 (± 7.6), while for the furthest vertical positions, i.e., the furthest in depth, it was 25.7 mm (± 7.1). This indicates that participants more strongly deviated away from nontargets closer in depth than from those further away. The effect of vertical position is further illustrated in Figure 2, which shows the heat map we calculated from deviation data of index finger trajectories. Specifically, positions closer in depth to the starting position are hotter than those further away.

Another main effect was determined for horizontal position, $F(5, 45) = 18.9, p < 0.001$, partial $\eta^2 = 0.87$. The mean deviation at passing for the middle nontargets was 57.0 mm (± 3.4), for the inside medial and outside medial nontargets it was 40.4 (± 2.3) and 53.4 (± 2.3), respectively. The inside lateral nontargets evoked a mean deviation at passing of 5.34 (± 1.85), and for the less lateral nontargets and the extreme lateral nontargets on the outside the deviation at passing was 33.2 (± 1.0), and 8.49 (± 1.3), respectively. This suggests that participants generally deviated more away from the nontargets that were directly in front of their hand than those on the inside or outside of the hand. Again Figure 2 illustrates this effect, as it shows that avoidance responses to nontargets directly in front of the start position are avoided more strongly (noted by the hotter colors), followed closely by responses to the most proximal outside nontargets. We can also see that the more lateral the nontarget was the weaker the avoidance response was. In addition, please note the asymmetry of avoidance responses to nontargets that were equidistant, but were on different sides of the reaching arm,

with larger deviations for nontargets on the outside of the reaching arm. We performed a further statistical analysis of the inside-outside asymmetry by comparing the eight inside conditions with the eight most proximal outside conditions. We collapsed the four vertical conditions and put these data into a repeated-measures ANOVA. The model contained two factors: side (two levels: in and out) and proximity (two levels: near and far). The results showed main effects of side, $F(1, 9) = 36.84, p < 0.001$, partial $\eta^2 = 0.86$ and of proximity, $F(1, 9) = 42.38, p < 0.001$, partial $\eta^2 = 0.88$. This indicates that overall responses to the nontarget on the outside were larger than responses on the inside and that the avoidance responses were more pronounced when the nontarget was closer to the midline of the workspace, i.e., more obstructing. We found a further interaction effect between side and proximity, $F(1, 9) = 8.18, p < 0.001$, partial $\eta^2 = 0.58$. This interaction shows that the asymmetric effect of equidistant nontarget objects, which is determined by the side of the arm they are positioned at, is further modulated by the proximity of nontargets. That is, the avoidance effects decrease in strength from high to low when: the nontarget object is near and on the outside of the arm, near and inside, far and outside, and far and inside.

There was no significant interaction between vertical and horizontal position for deviation at passing. However, we did find an interesting pattern with Bonferroni-corrected paired t tests for the vertical position conditions in the deviation data that is illustrated in Figure 3: roughly speaking we found that the @X0 and @X50 conditions differed from the @X-50 and @X100 conditions, all p 's < 0.0083 , which in turn differed from the @X-100 and @X150 conditions, all p 's < 0.0083 . The vertical position condition data were separated per horizontal condition in Figure 3 in order to be able to present an additional comparison with the control condition in the same figure. Particularly, we further performed one-sample t tests to ascertain whether the experimental conditions differed from the control condition. The control condition was taken as reference of zero for this test, because no deviation implies that the hand path in an experimental condition was identical at the passing mark to the control hand path. As can be seen in Figure 3, we found that all @X-50, @X0, @X50, and @X100 conditions differed from control, all p 's < 0.0021 , while the @X-100 and @X150 conditions did not differ from control. All such departures in experimental conditions from the control condition were deviations away from the nontargets. Indeed, no evidence was found in any condition of deviation towards nontargets.

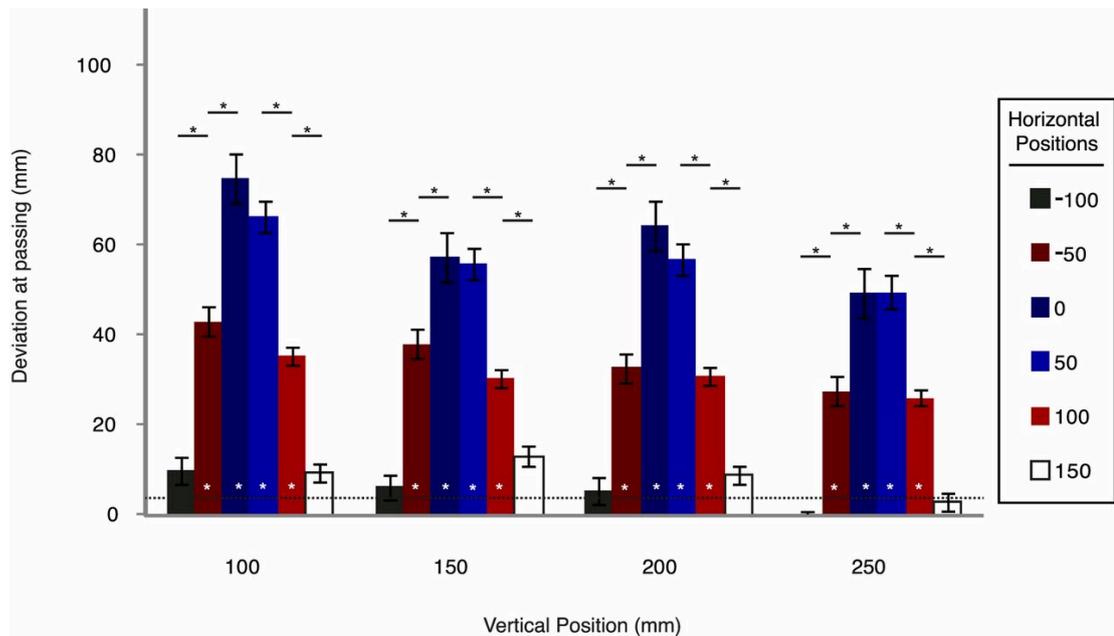


Fig. 3. Mean deviation score for all conditions. Mean deviation scores sorted per vertical position category. Error bars represent standard error of the mean. Lines with asterisks denote significant differences between conditions on Bonferroni-corrected paired t tests. Deviation at passing is relative to the control condition, so a score of zero represents the control condition is this figure. The dotted line represents the upper bound of the between subjects standard error of the control condition. White asterisks indicate p 's < 0.002 for one-sample t tests of experimental condition with the control condition referent (0).

We have provided an additional heat map in Figure 4, which displays error at passing. These data were also analyzed with a RM ANOVA. We found a main effect for horizontal position, $F(5, 45) = 3.97, p < 0.01$, partial $\eta^2 = 0.81$. This indicates that the variability in movement trajectories was different for different horizontal nontarget locations. In addition, a main effect was found for vertical position, $F(3, 27) = 4.31, p < 0.025$, partial $\eta^2 = 0.95$, which suggests that movement trajectories had different levels of variability for different vertical positions. An interaction effect between horizontal position and vertical position for error at passing was not present.

There was a significant correlation between deviation at passing and error at passing scores, $r = 0.591, p < 0.01$, which implies that higher deviation scores were associated with higher error scores, see also Figure 5. The pattern for error at passing closely resembles the pattern described in the above for mean deviation at passing: Generally speaking, more obstructing nontargets elicited more variability over trials than less obstructing nontarget objects.

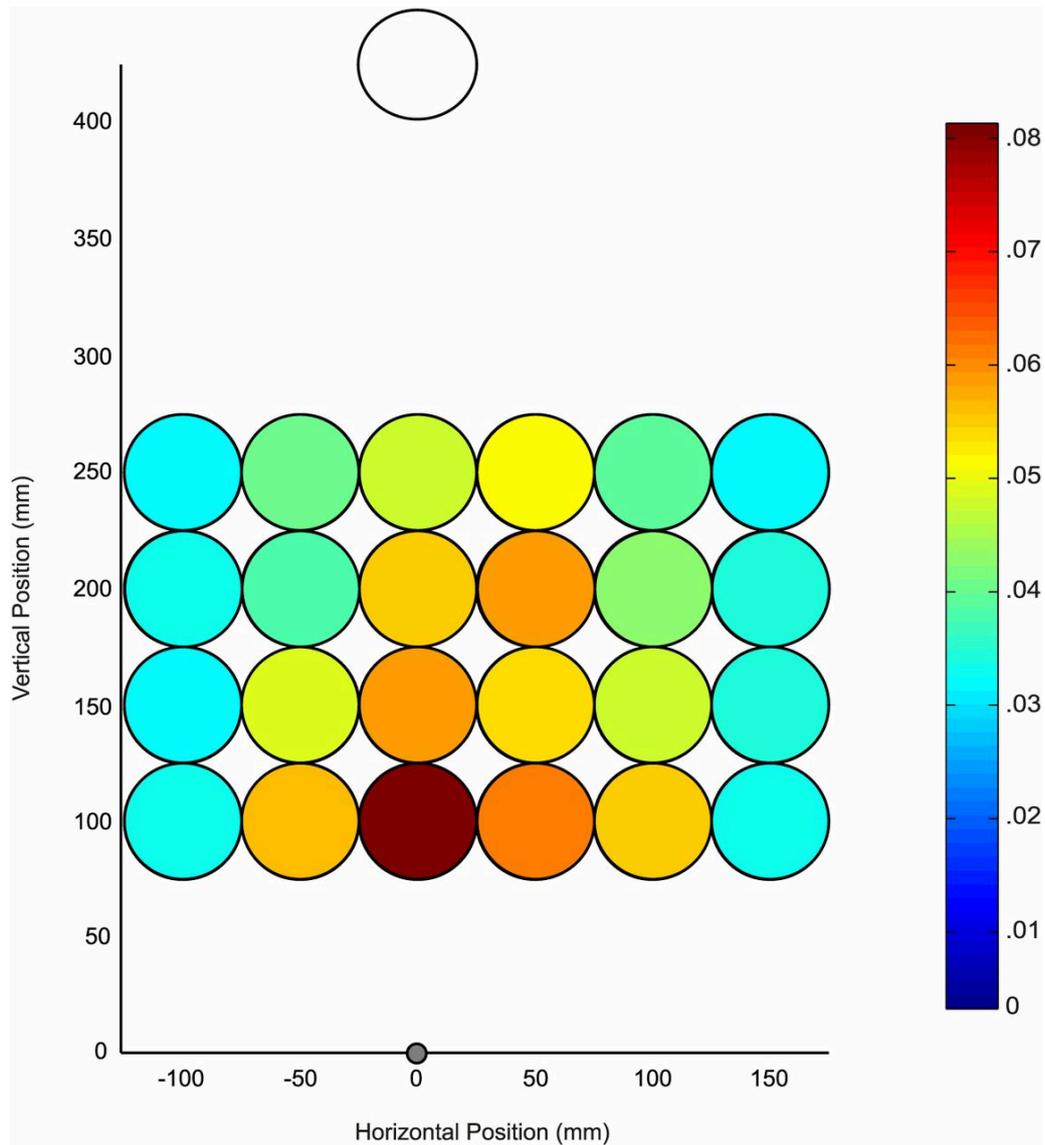


Fig. 4. Discrete heat map of error at passing. Color denotes the mean amount of variability present in conditions across participants: hot colors (red, orange) refer to larger variability and cold colors (green, blue) refer to small amounts of variability.

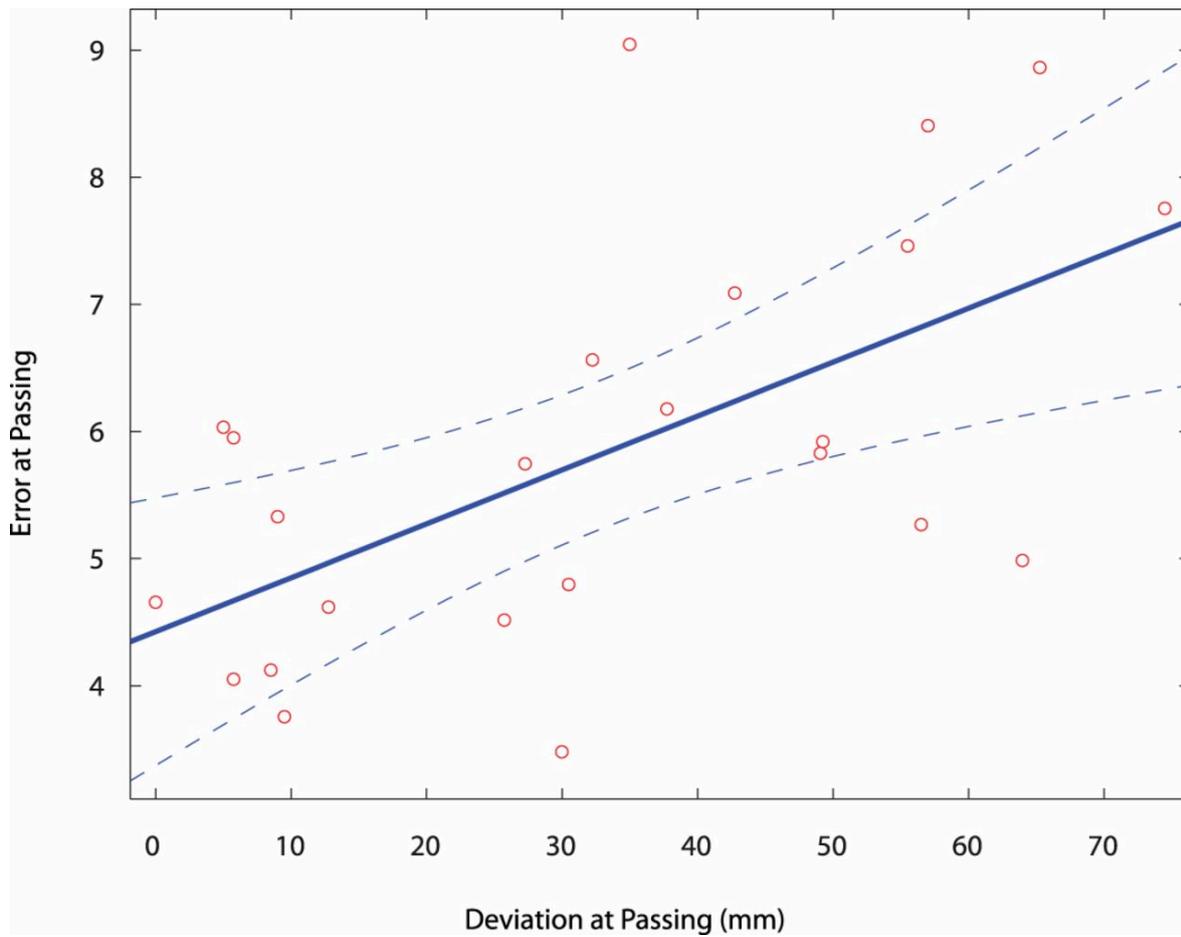


Fig. 5. Scatter plot of deviation at passing versus error at passing. Mean deviation at passing scores are displayed on the x axis. Mean error at passing scores are displayed on the y axis. The solid blue line is the least squares linear fit to the data points of all experimental conditions. The dashed blue lines represent the 95% confidence interval of that fit.

No association was found between the distance from the starting button (see Table 1) and summed deviation fraction (see Dependent measures and analysis section): There was no significant Pearson's correlation, $r = -0.23$, $p > 0.05$. This suggests that closer nontargets were not associated with a stronger avoidance response. However, we found a significant correlation between deviation and the angle (see also Table 1) of the nontarget relative to the starting button, $r = -0.80$, $p < 0.01$. This implies that when the angle toward nontargets (from the starting position) was more closely aligned with the straight ahead heading the associated avoidance response was stronger. Furthermore, we performed a backward stepwise linear regression analysis to test for the contribution of distance and angle parameters ($r_{angle, distance} = -0.06$) to summed deviation fraction. The analysis showed that a model with both angle and distance explained the most variability, with $r^2 = 0.84$. However, the contribution of the distance parameter was relatively small compared to that of angle: The change in r^2 for distance was 0.05 and for angle it was 0.79. The parameters x position and y position could not be included in this

analysis because they were collinear with distance and angle ($r_{y,vector} = 0.93$ and $r_{x,angle} = 0.88$, p 's < 0.01).

Interestingly, the relation between the strength of the avoidance response (y) and the angle toward the nontarget (x) can be described by the following function:

$$y = axe^{-|bx|}e^{-c}$$

This function describes obstacle avoidance as a function of obstacle angle, with $r^2 = 0.96$ see also Figure 6. To obtain this fit we used unconstrained non-linear minimization of the sum of squared residuals with respect to the various parameters (a , b , and c). What follows from this equation is that the avoidance responses are very strong for small angles from starting position toward the target and decrease quickly with larger angles, meaning that the hand is turned away from obstacles at a decreasing rate. The above equation is the obstacle term from Fajen and Warren's dynamical model for obstacle avoidance during locomotion (Fajen & Warren, 2003). The explained variance of the fit function decreases to $R^2 = 0.80$ when the straight ahead angle (0°) conditions are taken into account, as these evoke very strong, or near asymptotic, responses. Taken together, this implies that the angle between the (would be) direction of the hand and the direction towards the obstacle is the main determinant of avoidance behavior and that the obstacle acts as a repeller of the hand. Please note the asymmetry present in this relation, in that positive small angles give larger avoidance responses than negative angles.

Reaction time

We found no significant differences between conditions for reaction time.

Movement time

We found significant differences between horizontal position conditions for movement time, $F(5, 35) = 4.41$, $p < 0.01$, *partial* $\eta^2 = 0.39$. Mean movement time with the nontarget @X-100 was 34 ms (± 2) slower than in the control condition, whereas it was 69 ms (± 3) slower for @X-50, 136 ms (± 4) slower for @X0, 122 ms (± 2) slower for @X50, 56 ms (± 2) slower for @X100, and 37 ms (± 2) slower for @X150. This indicates that longer movement time was needed to perform the reach when the nontarget was in the middle or medial compared to more lateral. We performed additional one-sample t tests to determine whether experimental conditions were different from the control condition. Results indicate that participants moved significantly slower in the experimental conditions than in the control condition, all (Bonferroni-corrected) p 's < 0.05 . Taken together with the absence of a systematic effect on speed-related measures,

this seems to point toward a strategy where participants kept their movement speed constant across trajectories of different length (see below), which means that their movement times varied across conditions as a result. No further main effect or interaction effect was found for movement time.

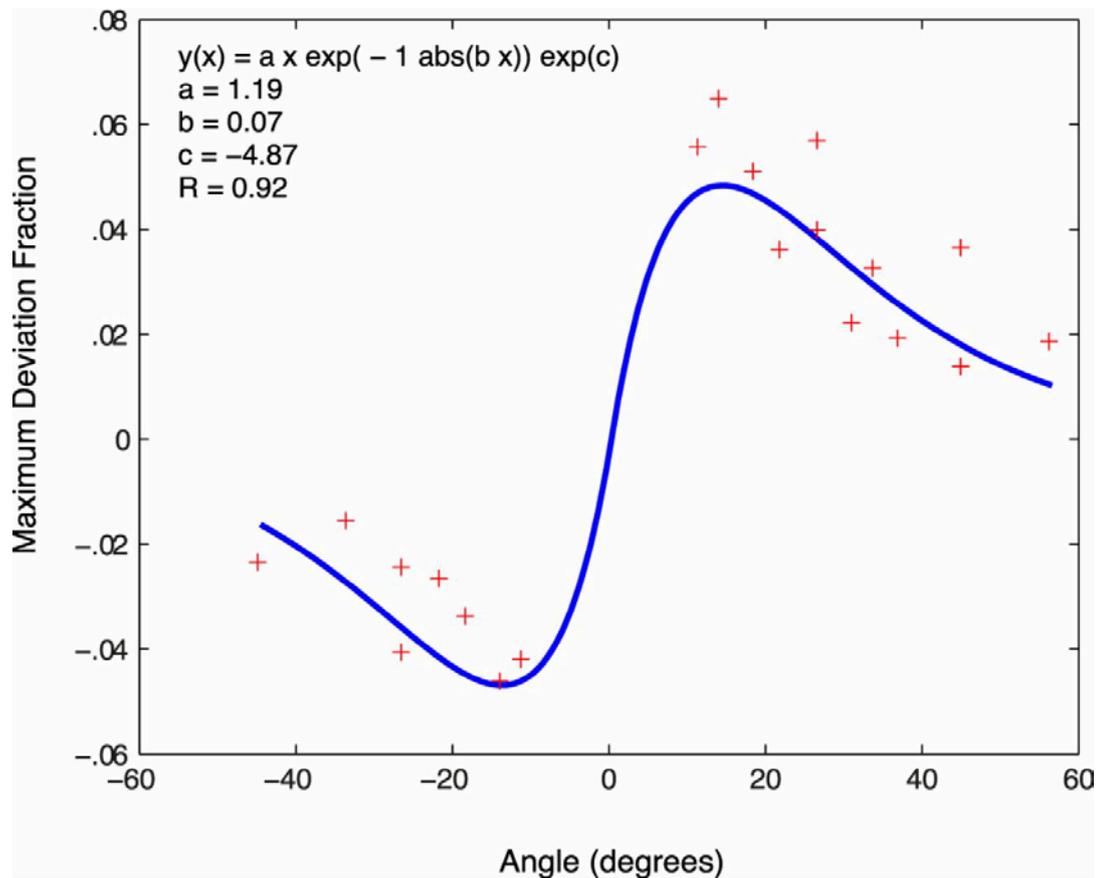


Fig. 6. Scatter plot of deviation fraction versus target-nontarget angle. The deviation as a fraction of summed deviation is on the y axis. Fractions associated with movements to the left were provided with a negative sign. The angle of the nontarget object with respect to the straight ahead is on the x axis (0° is the straight ahead direction, while negative angles are leftward angles, and positive angles are rightward angles). The solid blue line is the fit to the data points. The red pluses represent averaged (across participants) deviation fractions for all nontarget angles.

Grip aperture

We found no significant differences between experimental conditions for grip aperture. This suggests that participants had a consistent grip aperture during the experiment and that they did not vary their grip aperture systematically as part of an avoidance response. This means that the deviation measures reported earlier (and measured using the index finger marker) are not confounded by grip aperture responses.

Peak velocity & Time to peak velocity

We found no significant differences between conditions for peak velocity and time to peak velocity.

Discussion

The current study aimed to systematically map the effect of nontarget position in the workspace on reach to grasp movements. We used 24 different possible locations of the nontargets to determine the spatial consistency of avoidance responses. Our results show that the influence of each nontarget position on movement kinematics is specific. We demonstrated effects of horizontal position and vertical position of the nontarget on hand paths toward a target. The direction of our deviation effects were always away from nontargets and therefore we did not find evidence of any deviation towards nontargets. The avoidance responses to nontargets did not vary with distance from the start position to nontarget positions in the workspace. In addition, the angle toward the nontarget relative to the target seemed to determine the strength of the responses, with objects that are more medial in the workspace causing stronger veering movements. Although distance did not predict avoidance responses by itself, distance still affected avoidance responses in conjunction with angle. The relative contribution of distance, however, was marginal. Furthermore, we have also confirmed that the distribution of responses is not symmetrical across the workspace, that is, in this experiment we showed that right handed participants reacted more strongly to right side nontargets than left-side nontargets. So, although two given nontarget objects may be equidistant, the response to them may differ because of the side (in or out) of the reaching arm the nontarget is on. Taken together, these data imply that there is a fine-grained motor representation of nontarget position in the workspace.

We found interesting shifts in avoidance responses across space, as demonstrated by the absence of a relation between distance and avoidance and the complex relation between angle and avoidance. Accordingly, the obstructiveness of a nontarget is in a large part determined by the angle between the direction of the target and the direction of the nontarget, as this drives the avoidance response. This is in line with an empirically based model on obstacle avoidance in locomotion by Fajen and Warren (2003) where a similar relation (among others) between obstacle influence and angle to the obstacle is used to predict locomotion paths. Although the time scale and the reference frames in this experiment are quite different it is interesting to see that nontargets can function as repellers in a hand movement paradigm as well. Because we have not found an effect of distance on avoidance strength we interpret this as evidence

supporting the representation of both obstructing and nonobstructing objects during motor planning. Otherwise, if only objects that were close to the hand would be represented, then there would have been an obvious shift in avoidance responses for nontargets that were closer to the hand compared to those further away from the hand.

The activity in visuomotor planning areas that is associated with objects present in the workspace may be thought of as an attentional landscape that denotes objects that are relevant for behavior (Baldauf & Deubel, 2010). Movements are then executed toward the (highest) peak in the landscape and away from low(er) activity regions or valleys. Interestingly, Chapman, Gallivan, Culham, and Goodale (2011) have shown that there is top-down modulation of the early visual cortex when obstacles interfere with grasp planning. These authors found that the contralateral (to the reaching hand) posterior Intraparietal Sulcus (henceforth: IPS) is responsible for detecting objects that physically interfere with to-be-performed actions. In addition, it is responsible for suppressing the neural representation of obstructing objects in early visual cortex areas associated with visuomotor planning. Moreover, Chapman and colleagues found that the modulation of the visuomotor planning areas by the IPS was dependent on the degree of interference or obstruction afforded by the object. That is, the more the object obstructed the more activity was registered in IPS. The IPS thus reduces the activity of peaks in an attentional landscape to ultimately have the hand move away from obstructing objects while it travels toward the goal object. This process runs parallel to the top-down action selection process that determines the object that is grasped, which, according to Tipper et al. (1997), explains the deviating reaching behavior when objects are not obstructing. This explanation is based on the nervous' system inability to be completely selective during action planning. Behavioral biases are the result of competition between response codes within a distributed population of direction sensitive neurons. This is because if the response codes for the target and nontarget overlap, then the inhibition of nontarget related activity leads to inhibition of part of the activation for the target as well. The global vector that arises from the activation then points away from the nontarget, which is observed in the deviation of the trajectory of the hand away from the nontarget. According to Tipper et al. (1997) this occurs when the nontarget is not obstructing. However, data from Chapman et al. (2011) suggest that the IPS was only active when the object obstructed the planned movement, which implies that the severe reduction in early visual area activity via IPS is only present when nontargets obstruct movement. Although we have focused more on reaching, the study by Chapman et al. (2011) therefore provides a clear neural background for our findings: First, we see a decline in avoidance responses with increasing angle, which implies that the less obstructing a nontarget object is, the weaker the avoidance response is. This relation may be based on the decrease in

IPS suppression associated with less obstructing nontargets. Moreover, this can also explain the differential response to ipsilateral and contralateral nontargets (relative to the reaching hand), as the ipsilateral objects obstruct the planned movement more: In bold strokes, in this experiment, the increased obstruction by nontargets led to increased IPS activity and in turn to a larger avoidance response away from the nontarget object.

We showed that nontarget objects lead to stronger avoidance responses when they are closer in depth and closer to the direct route to the target, as demonstrated by the vertical and horizontal nontarget position effects, respectively. This effect has been reported earlier by, e.g., Chapman and Goodale (2008) but never with many different locations of a single nontarget. Chapman and Goodale (2010) showed that avoidance responses were greater with one obstacle than with two obstacles. The fact that two obstacles were present in some studies means that the avoidance response in those cases might have been constrained. In bold strokes, the avoidance responses to a primary obstacle may have been smaller in order to properly avoid the secondary obstacle. We consider that although the magnitude of the avoidance response may have been smaller with two obstacles present, the direction of the effect is still quite systematic, i.e., away from the nontarget.

We speculated that movements veer more systematically around nontargets that are more obstructing because the movements around these targets require more stability or accuracy than movements around nontargets that are further away. This, however, does not resonate with our data as we find more stereotypical movements when nontarget objects are further away in horizontal and vertical position. Conversely, we find more variable movement once the nontarget is closer in horizontal and vertical position. The discrepancy between our hypothesis and our results can be explained by assuming that the required accuracy for an avoidance movement was not very high after all: The participants only needed to avoid knocking over the nontarget. In fact, the data suggests that it was not necessary for participants to control accuracy at all. Instead, movement speed was kept constant: We show that participants did not systematically vary speed during the experiment. An explanation may therefore be found in Fitts's law (Fitts, 1954; Fitts & Peterson, 1964): Participants' accuracy suffered in trials with longer (more curved) movement paths around more obstructing nontargets because they controlled the speed at which they moved. This supports findings by Vaughan, Barany, Sali, Jax, and Rosenbaum (2010) who showed earlier that Fitts's law applies to three-dimensional obstacle avoidance movements. These authors also found that movement time increased with an increase of degree of obstruction by the obstacle. Vaughan et al. (2010) concluded that this result was congruent with Fitts's law, which states that longer movement paths (around more obstructing obstacles) should lead to longer movement times.

A further explanation for the increased variability in evoked avoidance responses to nontargets that obstruct more can be found in the theory by Hamilton and Wolpert (2002). These authors predicted empirical avoidance trajectories with a model that minimized the probability of collision near the nontarget object as well as mean-squared error of position at the target location. This implies that probability of collision and position accuracy are important in planning obstacle avoidance movements. Hamilton and Wolpert (2002) also posited that variability in motor neuronal firing and variability in the motor unit recruitment pattern are sources of signal dependent noise in muscle force output (Hamilton & Wolpert, 2002). This means that when force output is increased, the size of the motor units² recruited is also increased, which leads to larger variability in movement. Therefore, when stronger avoidance responses are required (the arm needs to be moved further sideways), then a larger muscle force output is required, which leads to more variability. This seems to be the case in our experiment.

In conclusion, we have mapped avoidance responses to a mesh of nontarget positions and have demonstrated that participants respond differentially across the vertical and horizontal dimension, where the strength of the response seems to be primarily driven by the angle between the target and nontarget. There is a hot region in the workspace where nontarget obstacles evoke the strongest avoidance responses and this region is mainly defined by obstacle positions with a direction that has small differences relative to the target direction. In other conditions where the angle and vertical distance is large, participants react stereotypically, so it seems these conditions can be lumped together with a normal reach-to-grasp movement. In all other instances the avoidance responses seem to follow a pattern that is predicted by a complex function. This finding indicates that there is no lumping together of conditions (other than obstructing vs. not obstructing) if the resolution of our experiment is as coarse as the physical size of the objects we used. That is, the grain in our experiment was the diameter of the nontarget objects. Therefore, the threshold for fine grained responses was 50 mm. We found that the resolution of the avoidance system is at least this size as each obstructing nontarget evoked a unique response. Moreover, the function we fit had a very large explained variance. Taken together, this may indicate that participants use a smooth scaling strategy to respond to obstacles either on foot (Fajen & Warren, 2003) or with their hands (this study). We therefore suggest that the spatial resolution of the nontarget location is fine grained, because responses are specifically tuned.

² The size of the motor unit is related to how many muscle fibers are present in the motor unit; a large motor unit has many muscle fibers within it while a small motor unit has few muscle fibers within it.

Chapter 4 — Outsider interference: no role for motor lateralization in determining the strength of avoidance responses during reaching

Menger, R., Van der Stigchel, S., & Dijkerman, H. C. (2013). Outsider interference: No role for motor lateralization in determining the strength of avoidance responses during reaching. *Experimental Brain Research*, 229(4), 533-543.

Abstract

When reaches are performed toward target objects, the presence of other non-target objects influences kinematic parameters of the reach. A typical observation has been that non-targets positioned ipsilaterally to the acting limb interfere more with the trajectory of the hand than contralateral non-targets. Here, we investigate whether this effect is mediated by motor lateralization or by the relative positioning of the objects with reference to the acting limb. Participants were asked to perform reaches toward physical target objects with their preferred or non-preferred hands while physical non-targets were present in different possible positions in the workspace. We tested both left-handers and right-handers. Our results show that a participant's handedness does not influence reaching behavior in an obstacle avoidance paradigm. Furthermore, no statistically significant differences between the use of the preferred and non-preferred hand were observed on the kinematic parameters of the reaches. We found evidence that non-targets positioned on the outside of the reaching limb influenced the reaching behavior more strongly than non-targets on the inside. Moreover, the type of movement also appeared to play a role, as reaches that crossed the workspace had a stronger effect on avoidance behavior than reaches that were 'uncrossed.' We interpret these results as support for the hypothesis that the avoidance response is determined by keeping a preferred distance between the acting limb in all stages of its reach toward the target and the non-target position. This process is not biased by hand dominance or the hand preference of the actor.

During everyday activities, people often reach for specific objects in cluttered environments in order to manipulate them. Our ability to correctly select a target from many objects to execute a reach-to-grasp movement is one of the key features in human motor planning. We also specify reaches toward objects to occur with a very low probability of colliding with other objects. Research into these skills has shown that non-target objects have an effect on the spatiotemporal characteristics of hand trajectory (Castiello 1996; Chapman and Goodale 2008; Menger et al. 2012; Mon-Williams et al. 2001; Tipper et al. 1997; Tresilian 1998; Welsh 2011) and that these effects are mediated by an intact dorsal stream (Rice et al. 2006; Schindler et al. 2004; Striemer et al. 2009). Whether these effects were caused by biases during target selection or were caused by the specification of the action (so that non-target objects were avoided) has been difficult to determine for a given situation. Recently, however, an account has been put forward that unifies both problems (Cisek and Kalaska 2010). Action specification and action selection were theorized as neural processes that run in parallel and in the same or similar substrates. Therefore, as attentional allocation and movement planning are closely related, effects reported might not be uniquely attributable to either attentional allocation or movement planning.

Keeping this in mind, we would like to point out that in the majority of studies there was a difference in magnitude between the effects observed for movement trajectories with ipsilateral non-target objects compared to contralateral non-target objects. Specifically, ipsilateral non-targets caused more deviation of the reaching trajectory than contralateral non-targets (Chapman and Goodale 2008; Dean and Bruwer 1994; Meegan and Tipper 1999, 1998; Menger et al. 2012; Mon-Williams et al. 2001; Pratt and Abrams 1994; Tipper et al. 1992). Whether this finding was explained better by the claims that contralateral non-targets were either less 'distracting' or 'obstructing' than ipsilateral non-targets is a futile exercise if one assumes the processes to be the same. However, one outstanding point remains: in both the obstacle avoidance and distractor interference literature, a typical experiment reports an asymmetry between ipsilateral and contralateral non-targets. That is, reach-to-point or reach-to-grasp movements that were made with the right hand by right-handers differed when distracting or obstructing objects were ipsilaterally or contralaterally placed between the starting location and the target location¹.

¹ Chapman and Goodale (2010) showed that avoidance responses were greater with one obstacle than with two obstacles. The fact that two obstacles were present in some studies means that the avoidance response in those cases might have been constrained. In bold strokes, the avoidance responses to a primary obstacle may have been smaller in order to properly avoid the secondary obstacle. We consider that although the magnitude of the avoidance response may have been smaller with two obstacles present the direction of the effect is still quite systematic, in that ipsilateral obstacles still evoke a stronger response than contralateral obstacles.

Simply put, when the right hand was used, objects placed on the right side of the workspace were on the *outside* of the reaching hand and gave rise to larger interference effects or avoidance responses, whereas objects placed on the left side were on the inside of the reaching hand and led to smaller or negligible interference effects or avoidance responses.

The aim of the current study was to investigate the observed differences in magnitude of effects associated with ipsilateral and contralateral non-targets (see, e.g., Chapman and Goodale 2008). We propose two possible explanations for these differences: ipsilateral non-targets potentially obstruct the movement of the lower arm, whereas contralateral non-targets cannot (i), or ipsilateral non-targets affected reaching behavior more strongly because right-handers employing their dominant hand were tested, i.e., because of motor lateralization (ii). In previous experiments, participants only used their preferred right hand and arm to execute the task which makes it impossible to disentangle these effects. Our aim was to test both left- and right-handed participants using their preferred and non-preferred hand to reach and grasp a target with non-target present either ipsi- or contralaterally to the reaching hand. In the following sections, the two alternative hypotheses will be discussed in detail:

(i) Contralateral non-targets caused less deviation than ipsilateral ones because, during normal reach-to-grasp movement execution, the lower arm would never occupy the same space as the contralateral non-target, whereas the lower arm could have knocked over the ipsilateral non-target more readily. This was due to the constraint on the movement imposed by the elbow joint, which, although it allowed the extension of the arm to bridge the distance from starting position toward a target object, also automatically brought the lower arm closer to an ipsilateral non-target. The contralateral non-target was never on the outside of the reaching arm and therefore never in the direction the lower arm travelled when the elbow was extended. As such, the contralateral non-targets could never obstruct the movement in the way ipsilateral non-targets did. If, as has been put forward (Tresilian 1998), the avoidance response is a 'subtle' and 'precise' reaction to a particular layout of object and non-target object(s) in a workspace, then responses should be symmetrical across hand preferences and which hand (dominant or non-dominant) was used to perform the task.

(ii) Several studies have shown that there are asymmetries in performance between the dominant and non-dominant hand, where the dominant hand typically performed better in a manual aiming task than the non-dominant arm (Roy et al. 1994; Carson et al. 1993; Elliott et al. 1993; Sainburg and Schaefer 2004). Furthermore, there are numerous studies that have shown a right arm advantage in strength, speed and consistency of movement compared with the left arm in right-handers (for a review see Goble and Brown, 2008). In addition, skill-related

differences between preferred and non-preferred hands have been observed in several domains. These include drawing lines (e.g., Woodworth 1899), finger tapping (e.g., Todor et al. 1982), precision-placing movements (e.g., Annett et al. 1979), reaching-to-point to a visual target (e.g., Elliott et al. 1993) and bimanual coordination (e.g., Buckingham and Carey 2009). The effects of motor lateralization might extend into the obstacle avoidance paradigm. To our knowledge, this has not yet been tested. An asymmetry in avoidance responses between the dominant and non-dominant hand would prohibit the generalization of right-handed avoidance responses by right-handers and place the findings concerning stronger ipsilateral effects in a new light.

We designed an experiment to test whether non-targets presented on the outside of the reaching hand cause more deviation irrespective of where they were located qua absolute position, the hand preference of the actor or which hand was used. Right- and left-handed participants were therefore asked to perform reach-to-grasp movements toward a physical object with a physical non-target present in the workspace. The target could be located ipsi- or contralaterally to the reaching hand. This means that during reaches, the elbow joint could cross the midline of the workspace (e.g., right hand was moved toward left target) or stay on one side of the workspace (e.g., left hand was moved toward left target), leading to crossed and uncrossed reaches, respectively. The non-targets could be on the inside or outside of the hand when it moved to the target. Reaches were performed using either the right or left hand.

Methods

Participants

Twenty participants (6 men and 14 women) volunteered to take part in this study and were all between the ages of 19 and 28 years old ($M = 22.0$, $SD = 2.03$) and had normal or corrected-to-normal vision. Half the participants were right-handed, while the other half were left-handed. All participants volunteered to participate in exchange for a small fee or curricular credit and gave their informed consent. The faculty's institutional review board under the Medical Research Act issued a formal written waiver that this research project did not require approval from a Medical Ethics Review Committee.

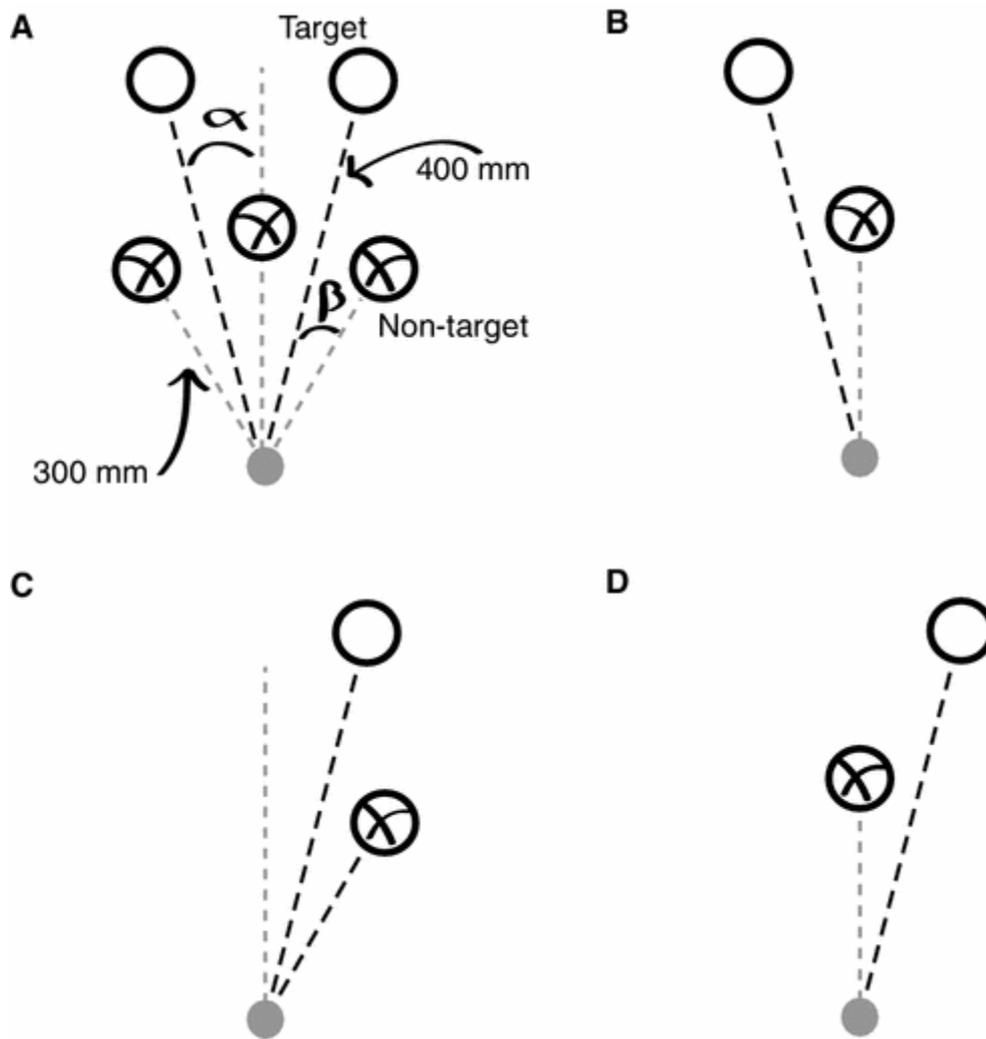


Fig. 1. Top down view of possible layouts of the experimental workspace. (A) The possible target locations and possible non-target locations. The gray filled circle represents the starting location of the hand. The blank circles represent targets. The crossed circles are possible non-targets. The targets were always located at a depth of 400 mm from the starting location, whereas non-targets were positioned at a depth of 300 mm. The angle $\alpha = 15^\circ$ represents the angle between the vertical midline and the direction of the target. This angle (α) could be negative or positive, leading to targets to the left and right of the midline, respectively. The angle $\beta = \alpha = 15^\circ$ is the angle between the direction from the starting position toward the target and the direction from the starting position to the non-target. Once again, the sign of the angle, in this case: β , determined whether a non-target was more to the right (positive β) or to the left (negative β) in the workspace than the target. The angles α and β and the hand that were used determined the type of trial that was performed by the participant. To illustrate, if a right hand was used to perform the reaches to a target, then the above panels show a contralateral target with an outside non-target (B), an ipsilateral target with an outside non-target (C) and an ipsilateral target with a non-target on the inside of the reaching arm (D). If, on the contrary, a left-handed reach was performed with these setups, then these panels would represent an ipsilateral target with a non-target on the inside of the reaching arm, a contralateral target with an inside non-target and a contralateral target with an outside non-target.

Apparatus and stimuli

The participants were seated at a white table (610 mm × 1,220 mm). The table had a workspace of 400 mm × 400 mm in which participants were asked to perform the experimental task. Three buttons were present in the table: one start button, located in front of the participant, along the midline of the workspace and two 'target' buttons that were in fact triggers that responded to a target being lifted from them. The target locations were both at a distance of 400 mm from the start button, one at an angle of 15° with respect to the midline, while the other was at a -15° angle (see Fig. 1). Wooden cylinders (150 mm height × 50 mm diameter) were used as target objects and as non-target objects.

All non-targets were placed at a distance of 300 mm from the start button. The center of the right non-target was placed at an angle of 30° with respect to the midline of the workspace (a further 15° beyond the direction of the right target location). Similarly, the center of the left non-target was placed at an angle of -30° (see Fig. 1). The central non-target was located at an angle of 0° with respect to the midline of the workspace (the center of this non-target was straight ahead of the start button). Note that the non-targets in this experiment were all at the same distance from the start button, viz. 300 mm.

Participants wore PLATO LCD goggles (Translucent Technologies, Toronto, Canada) and MiniBird magnetic markers (Ascension Technology Corporation, Burlington, USA), which permitted, respectively, manipulation of visual feedback and kinematic tracking with a sampling rate of 100 Hz over 3 s. The tracking markers were placed at the tips of participants' right index finger and thumb to measure their positions with .1 mm accuracy. These locations have been reported earlier as sites for markers (e.g. Mon-Williams and McIntosh 2000) and are considered to be the focus of prehension research (Ansuini et al. 2007). Care was taken to avoid situations in which the width of the marker itself interfered with the movement. The cables were fixed to the participants arm as well as to the edge of the table with tape and elastic, so that participants could move their hands and arms without restriction.

Design

Left-handed and right-handed participants performed both control and experimental trials with their preferred and non-preferred hands. The control trials served as a baseline for normal reaching behavior for comparison with the experimental trials. The control trials consisted of reaches toward both target locations with either the left or the right hand, i.e., crossed and an uncrossed reaches dependent on target location and which hand was used. During the control trials, a non-target was never present. During the experimental trials, a single non-target was

present. For each experimental trial, there were 2 possible non-target locations on the inside and outside of the reaching hand. There were 4 control conditions [hand used (left, right) × target location (left, right)] and 8 experimental conditions [hand used (left, right) × target location (left, right) × non-target location (inside, outside)]. All conditions were presented eight times, which makes a grand total of ($12 \times 8 = 96$) trials excluding the practice trials.

The left- and right-handed participants were randomly divided into one of two groups, starting the first block of trials with either their left or their right hand. Each group was counterbalanced so that it contained an equal number of left- and right-handed participants. The experiment was divided into four blocks: two blocks for each hand used. After the second block, the experimenter changed the markers to the other hand. In each block, all conditions for that hand were presented twice ($2 \times 12 = 24$ trials per block). The sequence in which the trials were presented in each block was randomized.

Procedure

At the beginning of a block, the participants were instructed to begin their movements with a particular hand. The chair and the MiniBird markers would be placed accordingly. The participants were then given the instruction to start the movement as fast as possible after hearing an auditory cue and to smoothly reach and grasp the target object without touching the possible non-target. We instructed participants to grasp the target with thumb and index finger halfway along its vertical axis. This particular constraint at the end of the movement combined with both the movement constraints offered by the obstacles and the starting posture was used in order to increase behavioral consistency. This way the most direct trajectory to the target never went over the top of the obstacle or passed the inside of the obstacle when it should have gone passed the outside or vice versa. Before each odd-numbered block, participants first went through six practice trials in which only a target object, either on the left or on the right target location, was presented.

Before each trial, the experimenter prepared the relevant condition by placing the target object and non-target on the workspace. Upon completion of the setup, the experimenter would cause the goggles to open. The participant was then granted vision of the workspace for a short time (800–1,200 ms) before an auditory signal cued them to perform the task. Next, the participant had to reach toward, grasp and lift the target object with their thumb and index finger and then put it back on the target location. Upon task completion, the participant used their index finger to press the start button. This closed the PLATO goggles and ended the trial.

After pressing of the start button, participants were required to hold their fingers at that location while awaiting the next trial.

Dependent measures and analysis

The raw trajectory data of trial were filtered by using a dual low-pass second-order Butterworth filter with a cut-off frequency of 20 Hz (see also: Mon-Williams et al. 2001; Tresilian et al. 2005). The filtered trajectory data were then normalized using a cubic spline interpolation into 100 samples (see also: Smeets and Brenner 1995; Tresilian et al. 2005).

Using the position data and stimulus presentation data, the following measures were computed²: reaction time (response latency after the auditory cue until movement initiation), movement time (the time it took from the start of the movement until the end of the reach-to-grasp movement), grip aperture (three-dimensional distance between thumb and index finger markers), peak velocity (the maximum velocity attained during movement), time to peak velocity (time since the start of the movement until peak velocity was reached) and deviation at passing (horizontal position at the moment the hand passed the vertical position of the middle of the target). For all measures, difference scores were computed between the experimental condition and the relevant control condition (i.e., only movements with the same hand toward the same target were compared thusly) per condition and per participant. Trials were rejected if the reach was initiated before the starting cue was given, the reach did not end within the recording window (3 s), or because of unforeseen recording errors. Three participants were rejected because at least 10 % of their trials were excluded from further analysis.

Results

We performed an initial mixed model repeated-measures ANOVA with a between subjects factor *handedness* (2 levels: left and right) and within-subject factors *hand used* (2 levels: left and right), *target location* (2 levels: crossed and uncrossed), and *non-target location* (2 levels: inside and outside of the reaching arm). Our analysis showed no significant difference between left-handed and right-handed individuals, nor any significant interaction effects which involved the factor handedness, for all dependent measures (all p 's > .05). Therefore, handedness data were collapsed as follows: first, to test for a difference between the use of the preferred and non-preferred hands, it was necessary to 'mirror conditions.' For example, a movement trajectory around a non-target toward a target such as depicted in Panel B of Fig. 1 is quite different when either the right or left hand was used. In this case, a comparison between hands

² Unless specifically stated, otherwise all measures were computed from index finger marker data.

used with the 'same' setup would be a false comparison. To compensate for this, we took reaches that had the same relative setup and took the mirror image of one through horizontal mirroring. To illustrate, a reach with the right hand in a situation as depicted Panel B should be compared with a left-handed reach as in a setup as depicted in Panel D, after mirroring was complete. During this mirroring procedure, all conditions were projected to the right side of the workspace to ease the meaningful comparison. Second, the factors, hand used (left and right) and handedness (left-handed and right-handed), were collapsed into preferred and non-preferred, so that non-preferred and preferred handed reaches could be analyzed per non-target location. Please note, therefore, that in the following analyses, hand used no longer refers to left or right hand as it did in the design section, but now refers to the fact whether participants used their preferred or non-preferred hand to perform the experimental task.

We analyzed all subsequent measures with a within-subject analysis, viz. a repeated-measure ANOVA with the within-subjects factors described in the above. Where descriptive statistics are reported, ' \pm ' always refers to ± 1 standard error of the mean.

Deviation at passing

There was no main effect for hand used, such that mean deviation at passing in the conditions where the dominant hand was used was not significantly different from mean deviation at passing in the conditions where the non-dominant hand was used. Right-handed and left-handed participants did not move their index finger along different trajectories toward the target during similar conditions, e.g., a reach toward an ipsilateral target with an outside non-target. This similarity between right-handers' and left-handers' movements is further illustrated in Fig. 2, which shows the mirrored nature of index finger trajectories made by right-handed and left-handed individuals. A main effect was, however, found for non-target location, $F_{(1, 16)} = 174, p < .001$. The mean deviation at passing for outside non-targets was -29.2 mm (± 2.03), and for inside non-targets, it was 1.54 mm (± 1.04), which indicates that participants strongly deviated away from the outside non-targets but did not do so for inside non-targets (see also Fig. 3). To increase support for this, we statistically tested 'inside' conditions with the reference value of the control condition (0). This showed that 'inside' conditions taken together did not significantly depart from the relevant control condition, $p = .17$, whereas the difference between 'outside' conditions and the relevant control condition reached significance, $t_{(16)} = -14.3, p < .001$. This implies that participants deviated from the 'normal' path to the target when the non-target was on the outside, while in the 'inside' conditions, participants' hand trajectories did not deviate at all from the control condition. Although reported only once here, this is true for all subsequent measures as well. Because we find no significant departures from the control

conditions for any ‘inside’ non-target conditions, we postulated that no deviation toward inside non-targets occurred in this experiment.

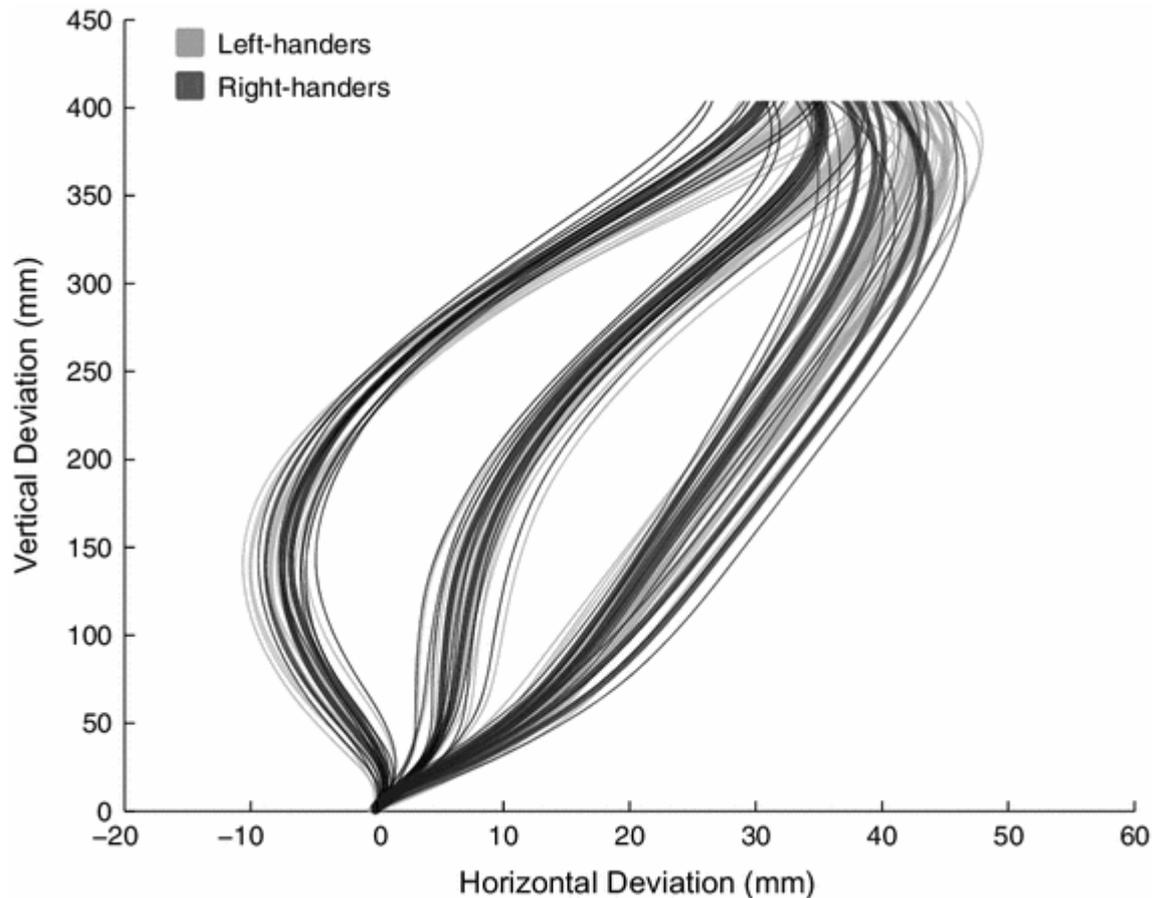


Fig. 2. Trajectories for all conditions of left-handers and right-handers. Mean trajectories for all experimental conditions for left-handers (*thick gray lines*) and right-handers (*thick black lines*). The *thin lines* depict standard error of the mean across subjects per group. All reaches were standardized to a straight reach for a target. Please note that only the index finger data are plotted, which means that the trajectories are skewed because the index finger always ended up on the ‘outside’ of the target (right side for right-handed reaches and left side for left-handed reaches). In addition, to ease comparison between conditions, all trajectories have been rotated and the left-handed trajectories mirrored to resemble a straight reach forwards with the right hand

Another main effect was determined for target location, $F_{(1, 16)} = 43.6, p < .001$. The mean deviation at passing for uncrossed targets was $-10.4 \text{ mm} (\pm 1.21)$, and for crossed targets, it was $-17.3 \text{ mm} (\pm 1.26)$, which indicates that participants generally deviated more away from the non-targets when performing crossed reaches to targets than during uncrossed reaches to target objects. There was an interaction effect for target location with non-target location, $F_{(1, 16)} = 75.6, p < .001$. Further investigation using Bonferroni-corrected t-tests revealed that when

the non-target was on the outside of the reaching arm, it interfered differently with reaches toward the target requiring a crossed reach than the target requiring an uncrossed reach, $t_{(16)} = -12.4, p < .001$, whereas non-targets on the inside of the reaching arm did not differentially interfere with crossed and uncrossed reaches, $t_{(16)} = -.62, p = .54$.

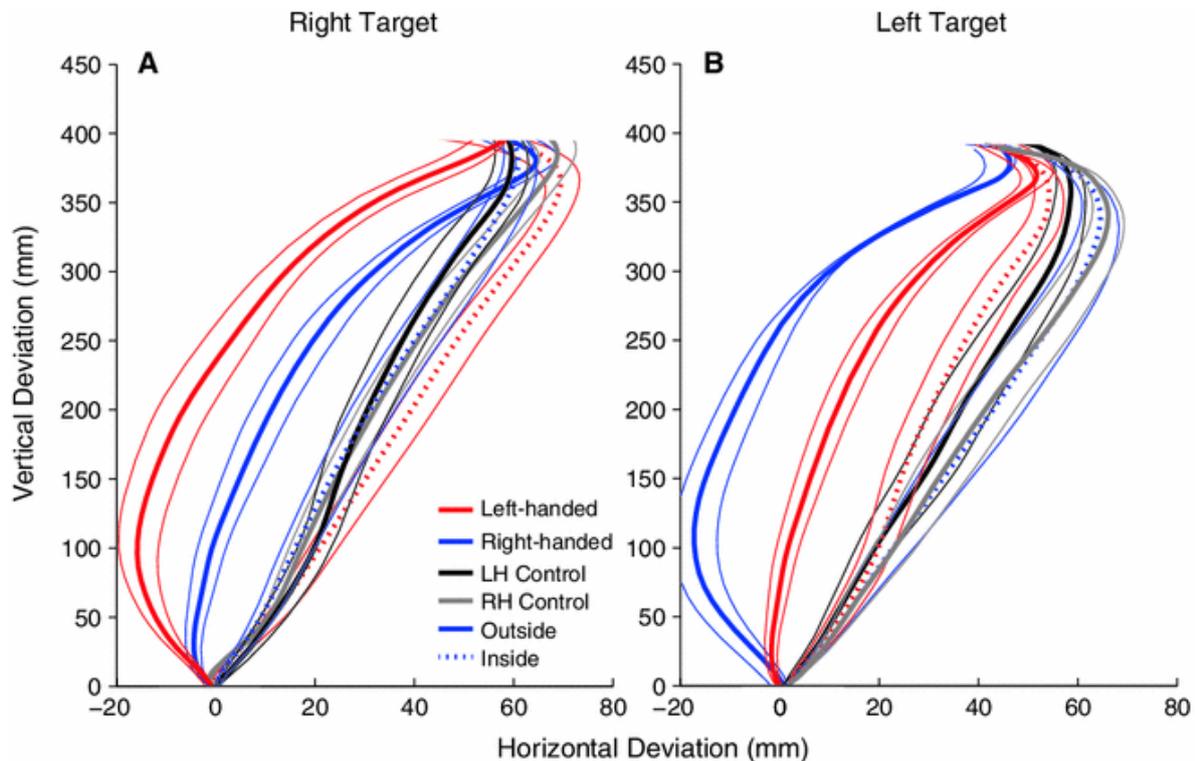


Fig 3. Mean trajectories toward the left and right target. Mean movement trajectories across participants in the x, y plane. The *thick lines* indicate average trajectories in the experimental and control conditions. The *thin lines* represent movement error around those trajectories, specifically: between subjects error using the between subjects error correction for repeated measures as proposed by Cousineau (2005) for use in figures. Please note that only the index finger data are plotted, which means that the trajectories are skewed because the index finger always ended up on the ‘outside’ of the target (right side for right-handed reaches and left side for left-handed reaches). The hand dominance conditions (dominant and non-dominant) were collapsed. *Color* was used to denote whether right-handed (*blue* and *gray*) or left-handed reaches (*red* and *black*) were performed. *Solid lines* represent reaches with outside non-targets present, while *dotted lines* show reaches with non-targets on the inside of the reaching arm. **a** Depicts reaches toward the right target, and **b** shows reaches toward the left target

A crossed reach to a target with an outside non-target had a mean deviation at passing of $-40.2 \text{ mm} (\pm 2.29)$, whereas an uncrossed reach in the same situation had an associated deviation at passing of $-35.8 \text{ mm} (\pm 2.28)$. This indicates that participants deviated more strongly from outside non-targets when performing crossed reaches (see also Fig. 4 on the next page). No other interactions were significant.

We found no significant differences between conditions for reaction time, movement time, and grip aperture. This last finding suggests that participants had a consistent grip aperture during the experiment and that they did not vary their grip aperture systematically as part of an avoidance response. This means that the deviation measures reported earlier (and measured using the index finger marker) are not confounded by grip aperture responses.

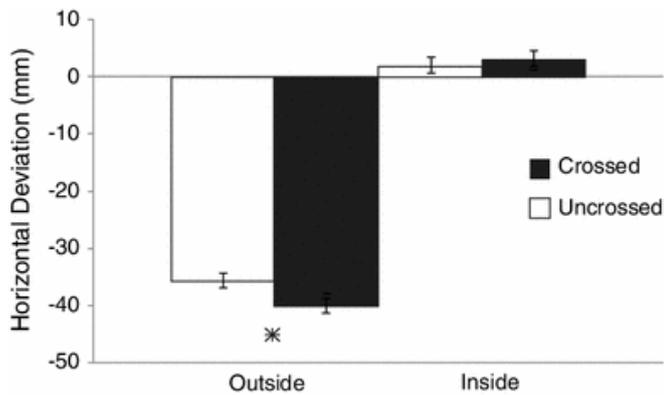


Fig. 4. Detailed interaction effect. Mean deviation at passing for crossed and uncrossed reaches when non-targets were on the outside or inside of the reaching arm. *Black bars* depict crossed reaches, while *white bars* depict uncrossed reaches. The *asterisk* shows significance at the $p < .001$ level. *Error bars* are standard error of the mean and the between subjects error correction for repeated measures as proposed by Cousineau (2005) for use in figures was applied.

Peak velocity

A main effect of target location was determined, $F_{(1, 16)} = 25.7, p < .001$. The mean peak velocity for uncrossed reaches was 1,352 mm/ms (± 45), and for crossed reaches, it was 1,387 mm/ms (± 44). Therefore, reaches that crossed the workspace were performed faster than uncrossed reaches.

A second main effect was found for non-target location, $F_{(1, 16)} = 5.87, p < .05$. The mean peak velocity for reaches with outside non-targets was 1,387 mm/ms (± 55), and with inside non-targets, it was 1,362 mm/ms (± 45). Taken together with movement time data and trajectory data, this implies that participants maintained a constant movement time by increasing speed during trials were the trajectory veered more away from the non-target (which by definition created a longer reaching path). No further main effects or interaction effects were found.

Time to peak velocity

We found main effects of target location, $F_{(1, 16)} = 5.54$, $p < .05$, and non-target location, $F_{(1, 16)} = 7.58$, $p < .05$, on time to peak velocity. Peak velocity was reached significantly later for outside non-targets 51.5 % of movement time (± 3.6) than for inside non-targets 19.2 % of movement time (± 2.2). The mean time to peak velocity for uncrossed reaches was 38.3 % of movement time (± 4.2) while crossed reaches attained peak velocity at 41.7 % of movement time (± 4.0).

A further interaction effect was found between factors target location and non-target location, $F_{(1, 16)} = 10.0$, $p < .01$. Mean time to peak velocity was 53.2 % of movement time (± 5.0) for reaches in conditions with outside non-targets when reaching across the midline and 46.2 % of movement time (± 5.4) for conditions requiring uncrossed reaching. Post hoc testing confirmed that outside non-targets elicited reaching peak velocity significantly later in the movement with crossed reaching vs. uncrossed reaching, $t_{(16)} = 2.31$, $p < .05$. The difference between crossed and uncrossed reaches with inside non-targets was not statistically significant, $p > .05$.

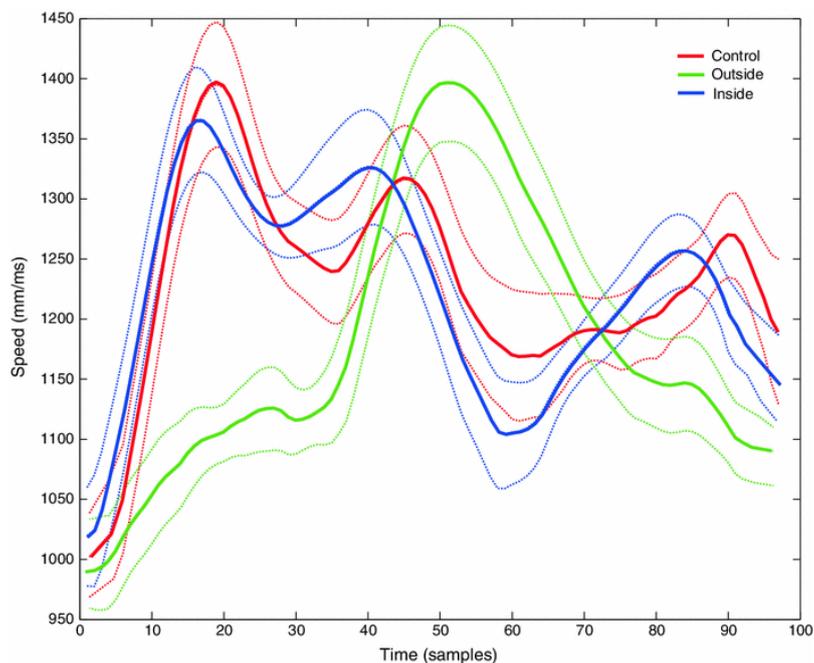


Fig. 5. Mean velocity profiles for inside and outside non-targets. Mean velocity profiles for inside (blue) and outside non-targets (green) as well as the control condition (red). Velocity on the y-axis and % movement time on the x-axis. The solid lines are means across participants, and the dashed lines are between subjects error [using the between subjects error correction for repeated measures as proposed by Cousineau (2005)]. Target location and hand used factors have been collapsed for this figure.

For both peak velocity and time to peak velocity, an effect of non-target location was found. As can be seen in Fig. 5, this effect is most likely due to different behavioral strategies by participants regarding moving speed in response to inside and outside non-targets. That is, if non-targets are on the outside of the reaching hand, the velocity of the hand is initially slower to around the point where the hand passes the obstacle when it quickly accelerates to a higher peak velocity compared to conditions with inside non-targets.

Discussion

The current study was designed to determine the cause of stronger ipsilateral non-target effects on reaching movements. As possible modulators of the reaching trajectory toward targets with ipsilateral non-targets, we considered handedness and non-target location and their possible interactions. To this end, we asked participants to perform reach-to-grasp actions toward a target object that could be at two different locations. These actions were performed with either the preferred or non-preferred hand by left-handers and right-handers. Another, non-target object was also present in the workspace, with exception of control trials which featured a single object. The additional non-target object could be on the inside or outside of the arm used to perform the reaches. We determined that handedness and hand used did not affect the kinematics of the reaching trajectories, whereas non-target location and target location did systematically affect trajectories toward the target. For the first time, we are able to unequivocally state that the observed trajectories in obstacle avoidance are the result of an interaction between limb position and non-target position. There seems to be no support for asymmetrical performance due to handedness or hand dominance in obstacle avoidance. This means that the effects that were found in earlier studies are not confounded by these latter factors and can be generalized across all possible positions in the workspace.

The main and interaction effects for target location can be explained by taking into account the type of movement that is performed. In our experiment, half the reaches were crossed, whereas the other half were uncrossed reaches. This means that either the right or left hand was transported from the starting position to the target that could be to the left or to the right of the starting position, so that right-hand-to-right-target and left-hand-to-left-target were uncrossed reaches and right-hand-to-left-target and left-hand-to-right-target were crossed reaches. The results indicated that crossed reaches, e.g., a reach with the left hand toward the right target, deviated more away from the non-target than uncrossed reaches, e.g., a reach with the left hand to the left target. Moreover, responses to non-targets were further increased when they were on the outside of the reaching hand as compared to the inside of the reaching hand. Biomechanical differences such as a larger displacement of the center of mass of the limb which

could necessitate the recruitment of a different set of muscle groups for task execution might be responsible for larger deviations to trajectories of crossed reaches (compared to uncrossed reaches). The trajectory toward a crossed target would then possibly require the limb to move along a more curved path to maintain optimal control of the limb during transport (for a succinct description as to how the brain would organize this, see: Feldman and Levin 2009). The fact that these biomechanical considerations may play a role is supported by the interaction effect of target location with non-target location because non-targets that had to be avoided would cause the center of mass to be displaced even more during a crossed reach, which was the case. Thus, the larger deviations we reported for crossed reaches could reflect the optimal path vis-à-vis expended energy for the transported limb through the workspace toward the target without knocking the non-target over.

Our results further show that special attention should be paid to the situation where the non-target is on the outside of the reaching hand. Participants deviated more strongly away from the non-targets on the outside of the limb performing the reach than when the non-target was on the inside. The effect generated by the ‘outsideness’ of non-targets accounts for previous results regarding enhanced interference by non-targets that were on the right side of the workspace and generalize this to an effect of ipsilateral non-targets. This effect is independent of which limb is used or which side of the workspace the non-target is on. The same holds for non-targets on the left side of the workspace that were not associated with the hand veering away from the non-target during movements. Indeed, this null-effect can be generalized to all workspaces where contralateral or inside non-targets are present. Apparently, non-targets on the inside of the arm do not require a ‘normal’ movement to be modified in order to avoid it successfully. Therefore, we can confirm that only if non-targets actually interfere with the transport or grip phase of a movement toward a target, i.e., they obstruct the movement, then automatic alterations are incorporated into the movement so that it veers away from a non-target to avoid a collision (Tresilian 1998). The contralateral or ‘inside’ non-targets may have been beyond the safety margin for collision-free movement and therefore may not have required an avoidance response. In the case of an ipsilateral non-target that obstructs the lower arm, the observed trajectory might then be caused by a generated motor program to move along a path that skirted the non-target at the preferred distance, which –in all cases- would mean the hand would also move more away from the non-target when compared to a normal trajectory. This is precisely what we have found for ‘outside’ non-targets, irrespective of hand used or hand preference.

To account for the surprising absence of an asymmetry due to handedness or hand dominance which have been reported in many domains, we refer to Mutha, Haaland, and

Sainburg(2013). Mutha et al. (2013) proposed a new view that motor lateralization or handedness is a reflection of the proficiency of the cerebral hemispheres for distinct movement control mechanisms. That is, each hemisphere has different control mechanisms for movements of its associated arm. However, each hemisphere has a different dominant control mechanism which suits the function the hand is engaged in and is expressed on a population level as handedness. Mutha et al. (2013) showed that right-handers using their dominant arm rely on predictive mechanisms regarding the dynamic properties of the arm to guide reaching direction and trajectory and that the reaching behavior of the non-dominant arm reflected optimal positional stability. This was done by occasionally and covertly shifting the start positions of the reaching movement either collinearly or orthogonally to the required direction of movement. No effects of orthogonal shifts were found, whereas collinear shifts had a differentiated effect on reaching movements: the dominant arm maintained the direction and straightness of the trajectory, while the non-dominant arm deviated to the previously learned goal position. This led the investigators to propose that two control mechanisms coexist in the brain and are, although associated with a particular hemisphere, independent of the effector. Following this, if obstacle avoidance is the ability to smoothly guide the hand around obstacles, which relies on the predictive control mechanism based on arm and hand dynamics and if this control mechanism is not specific for a particular arm, then obstacles are avoided similarly with the dominant and non-dominant arm and avoided similarly by right-handers and left-handers. Therefore, only the positioning of the target and obstacle should have an effect on the movement direction and movement trajectories. Our results support the notion that an identical control mechanism is selected for both arms independent of the actor's handedness. However, it could also be said that our task specifically—or obstacle avoidance in general—may have not been difficult enough to evoke differentiated responses from the trajectory controllers of the dominant and non-dominant hemispheres.

To reconcile, the relative position of a non-target with respect to the limb and its future path dictates the subtle and precise response of the motor system as to keep a preferred distance between the acting limb and the non-target. This process is not severely biased by which hand is used, the hand preference of the actor or the fact that hand and non-target are on the same side of space. It is influenced strongly, however, by the type of movement that is required (e.g., crossed or uncrossed) and the relative position of non-targets. Any effects previously described in literature concerning non-targets near the right hand are therefore generalizable to all non-targets on the outside of the reaching hand.

Chapter 5 – How obstructing is an obstacle? The influence of starting posture on obstacle avoidance

Menger, R., Van der Stigchel, S., & Dijkerman, H. C. (2012). How obstructing is an obstacle? The influence of starting posture on obstacle avoidance. *Acta Psychologica*, *141*(1), 1-8.

Abstract

The introduction of non-target objects into a workspace leads to temporal and spatial adjustments of reaching trajectories towards a target. Currently, there are two different explanations for this phenomenon: the non-target objects are considered as either physical obstacles to which we maintain a preferred distance (see Tresilian, 1998) or as distractors that interfere with movement planning (see Tipper, Howard, & Jackson, 1997). These components are difficult to disentangle, however. Our aim was to determine the unique contribution of the avoidance of a physical obstacle to the adjustments of reaching trajectories. In this study, we manipulate the degree of physical obstruction by non-target objects while keeping the a priori visual layout of the workspace more or less constant. This is achieved by placing participants in different starting postures with respect to the orientation of their limb segments. Participants reach towards and grasp target objects with non-targets present in the workspace in a frontal and a lateral starting posture. In the frontal conditions participants showed larger movements away from the non-target on the ipsilateral side of the workspace than in the lateral conditions. The results provide evidence for the interpretation that non-targets influence the movement trajectory partly because they are 'obstructing'.

Most times we manipulate things in the presence of other objects. In fact, our workspace is normally cluttered and our visual field crowded. Nonetheless, we are able to direct actions smoothly and effortlessly toward target objects in the presence of non-target objects. How these non-target objects are dealt with is a matter of some debate. One aspect that is, at least, agreed upon is that the introduction of non-target objects into a workspace leads to temporal and spatial adjustment of reach-to-grasp trajectories towards a target (Biegstraaten et al., 2003, Bonfiglioli and Castiello, 1998 and Castiello, 1996; C. S. Chapman and Goodale, 2008, Dean and Bruwer, 1994, Howard and Tipper, 1997, Jackson et al., 1995, Kritikos et al., 2000, McIntosh et al., 2004, Meegan and Tipper, 1998, Mon-Williams et al., 2001, Pratt and Abrams, 1994, Rice et al., 2008, Rice et al., 2006, Schindler et al., 2004, Tipper et al., 1997, Tresilian, 1998, Tresilian et al., 2005 and Welsh, 2011). These adjustments are relative to reach and grasp parameters that ordinarily occur when reaching towards objects that are presented alone. The paradigm used to study what aspects of non-targets affect movement trajectories is called obstacle avoidance. Currently, there are two accounts that serve to explain adjustments of reaching trajectories during obstacle avoidance: the non-target objects are considered as physical obstacles to which we plan and maintain a preferred distance (Tresilian, 1998) or as distractors that interfere with movement planning (Tipper et al., 1997).

The *physical obstacle* account describes deviating movements after the introduction of a non-target as the result of the preplanning of an avoidance movement to prevent collision with the non-target. The nervous system modifies the reaching movement in response to the presence of obstacles so as to minimize the likelihood of collision based on a preferred distance of the manipulandum to the obstacle. The modification process itself is ostensibly subtle and precise (Mon-Williams et al., 2001). Evidence in line with this account comes from many studies in which an increase in movement time is observed (Biegstraaten et al., 2003, Jackson et al., 1995, Mon-Williams and McIntosh, 2000, Mon-Williams et al., 2001, Saling et al., 1998 and Tresilian, 1998), suggesting that the movement is slowed down to increase spatial accuracy and avoid potential collisions. These adjustments are not a general response to the presence of non-target objects (Mon-Williams et al., 2001), on the contrary, the effect is specific to the lay-out of the workspace, in that non-target objects only elicit an avoidance response when the preferred distance to them is too small.

According to Tipper and colleagues (Tipper et al., 1997), the spatial adjustments that are observed in response to the introduction of non-target objects are caused by the automatic excitation of direction sensitive reaching neurons in area 5 of the posterior parietal cortex and in the motor cortex and their subsequent inhibition. Any overlap between the activations for target and non-target is inhibited and leads to two possible deviating movement trajectories (a

movement that veers towards or away from the non-target object) depending on the level of inhibition: when inhibition is strong, because excitation is strong due to a particularly salient non-target, the movement veers away from the non-target. In contrast, when excitation is weak, due to a less salient non-target, inhibition is weak and the movement veers towards the non-target. Such errors in the initial action planning are later corrected online during movement execution so that the hand smoothly ends up at the target. Thus, the nervous system, due to ineffective inhibitory mechanisms that are active during selection of a movement target during movement planning, inadvertently modifies movement planning in response to the presence of non-target objects. Simply put, non-target objects act as distractors when trying to plan a movement to the target. This hypothesis is substantiated by the report that stronger activations in reach-related areas in the parietal cortex are observed when non-target objects were present during reach movements than when they were not present (Chapman et al., 2007). It is important to note that changes to the movement trajectory are ultimately dependent on the strength of distraction by the non-target, which in turn is influenced by the non-targets' salience (Tipper et al., 1997).

The goal of this study was to determine the contribution of obstructional factors to movement adjustments related to the introduction of non-targets. Our manipulation was to change starting posture of a typical avoidance movement. Because reaching not only involves the hand, but also the arm, the orientation of the forearm can determine whether a non-target is an obstacle for the forearm or not. Changing the orientation of the lower arm ought not to influence the distracting effects of a non-target. One key feature of this manipulation therefore is that we can study 'obstructing' effects while keeping the visual lay-out constant.

It is interesting to note that several different starting postures have been used in the obstacle avoidance literature, without it being explicitly manipulated. The right hand is placed either midsagittally with respect to the trunk (see e.g. Tipper et al., 1997, Castiello, 1996, Kritikos et al., 2000 and Chapman and Goodale, 2008) or placed laterally to the trunk (see e.g. Tresilian, 1998, Mon-Williams et al., 2001 and Chapman and Goodale, 2010). The fingers on the starting location also differ. This varies between thumb and index finger in gentle opposition (e.g. Castiello, 1996), index finger only (e.g. Chapman & Goodale, 2010), and ulnar side of the hand on the starting location (e.g. Kritikos et al., 2000). In addition, the level of description of those orientations differ; from nominal description (which joints are flexed and extended) to detailed report of angles, to no information at all. The orientations of the major body segments involved in the to-be-performed movements are therefore quite diverse between studies.

It has been shown that starting posture affects reach-to-grasp movements when there are no non-targets present (Hesse and Deubel, 2009, Kritikos et al., 1998 and Timmann et al., 1996). This is supported by work by Rosenbaum and colleagues (Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995): their model states that starting posture determines, in concert with minimizing energetic requirements and required end posture, the movement that has to be performed. It follows from this that changing starting posture affects the reaching movement. Furthermore, this model has been elaborated to allow for obstacle avoidance (Rosenbaum, Meulenbroek, & Vaughan, 2001). This implies that starting posture, from a modeling perspective, affects avoidance behavior, i.e. the reaching trajectory towards a target object with an intermediate non-target object present which affords a collision.

Naturally, in obstacle avoidance experiments where posture was kept constant, any potential effect of starting posture was negated. However, if with different starting postures one can obtain entirely different results, starting posture becomes relevant: in the most extreme case starting posture could determine whether a non-target object was obstructing or distracting and as such what its effect was on the movement trajectories of participants. It is therefore of interest to study the effect of starting posture in itself for obstacle avoidance, as divergent starting postures may lead to different movement trajectories and therefore to other modifications of those trajectories by either obstacles or distractors.

Our experiment was designed to test two different starting postures; one with the hand frontal (or midsagittally) to the trunk and one with the hand lateral to the trunk. These postures were similar to the ones reported in earlier studies, for a frontal posture see e.g. Castiello (1996) and for a lateral starting posture see e.g. Tresilian (1998). In both starting postures the starting, non-target, and target locations were kept the same. This way, we can directly compare the effect of starting posture without varying the visual lay-out of the workspace, i.e. there was no visual difference between the non-targets when different starting postures were adopted yet the distance of the manipulandum to the non-target was different between these postures. Non-targets were presented ipsi- and contralaterally of the reaching hand and proximally and distally to the midline.

Reasoning in line with the physical obstacle account we expect differences between ipsi- and contralaterally placed objects, in that ipsilaterally placed non-targets are obstacles and need to be avoided particularly for the frontal posture, while contralaterally placed non-targets are not obstacles and therefore irrelevant to the movement. The hypothesis regarding increased physical obstruction by the non-target when adopting a frontal starting posture follows from the assumption that while a non-target is not a pure obstruction to the hand it may enter more

into the 'preferred space' around the lower arm while the hand travels to the target. The distractor interference account would also predict differences between ipsilateral and contralateral non-targets, or distractors, and between different proximities to the midline, but not between different postures. These differences would reflect the failure to inhibit automatic responses to the distractors that differ in 'strength' of attentional capture. One attribute that affects the strength of a distractor is position, where it has been reported that differently positioned distractors cause spatiotemporal adjustments that are specifically tuned to those locations (Tipper et al., 1997). In line with this we expect to find a range of different alterations to movement trajectories that are specific for non-target positions.

Methods

Participants

Twelve (2 men, 10 women) right-handed participants (determined by self-report and confirmed by questionnaire) participated in this study. All participants had normal or corrected to normal vision and were naïve to the purpose of the study. They were instructed to rapidly and smoothly execute a lifting movement as a response time task.

Materials and design

The participant sat in front of a 122 cm × 61 cm table. On this table there was a virtual workspace of 40 cm × 40 cm. In the workspace 2 elements had fixed locations; the start button and the target button. Both were shifted 3 cm rightwards from the center of the table. The start button was positioned 5 cm from the front edge of the table and the target button was situated 40 cm beyond that. The start button responded to button presses by participants and the target button responded to target objects being lifted from it. The non-targets have variable locations; they were placed at different distances from the midline (the line connecting start and target buttons), at widths of 8 and 12 cm.

Participants wore PLATO LCD goggles (Translucent Technologies, Toronto, Canada), which permitted manipulation of visual feedback and MiniBird magnetic markers (Ascension Technology Corporation, Burlington, USA) which allowed kinematic tracking with a sampling rate of 100 Hz over 3 s. These markers were placed at the tips of participants' right index finger and thumb to accurately measure their x, y, and z positions. These locations have been reported earlier as sites for markers (see e.g. Mon-Williams & McIntosh, 2000) and are considered to be the focus of prehension research (Ansuini, Tognin, Turella, & Castiello, 2007). Care was taken to avoid situations in which the width of the marker itself interfered with the movement. The

cables were fixed to the participants as well as to the edge of the table with tape and elastic, so that participants could move their arm without restriction.

Tall cylindrical objects ($2.75 \text{ cm} \times 2\pi \times 15 \text{ cm}$) were positioned at several locations. The target object was placed on the target button. The non-target objects were placed at a depth of 20 cm (half-way) from the start button, whereas width was 8 or 12 cm (medial and lateral) to the right or left of the midline. In total, there were thus 4 possible locations where objects could be placed as non-targets: Left-lateral, Left-medial, Right-lateral, and Right-medial. Including the control condition, where no non-target was placed in the workspace, there were thus 5 possible configurations of the workspace.

The starting posture was varied across 4 experimental blocks so that participants sat in a position where their lower arm was diagonal and in a position where their lower arm was in a straight orientation twice (see also Fig. 1). These experimental blocks were pseudo-randomized across groups of 4 participants (ABBA). Great care was taken to assure identical starting postures across the experiment. Participants were placed in line with the midline of the workspace with either their midsagittal line (sternum to navel) or the line between the coracoid process and the biceps brachii tendon. We used individual markings on the floor and workspace to quickly and accurately reorient the participants between conditions.

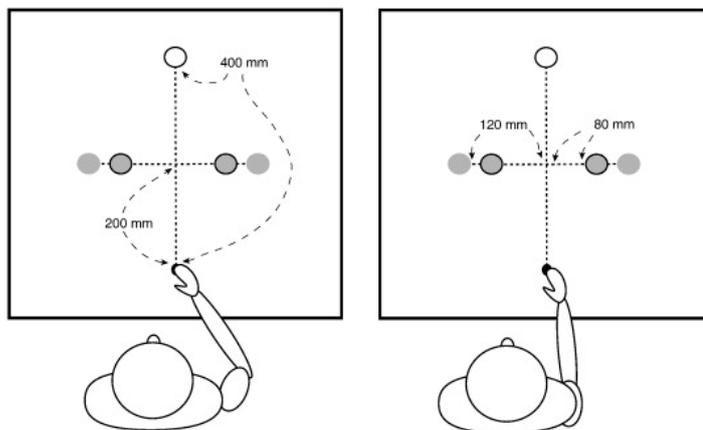


Fig. 1. Top-down view of the experimental setups. The black and white circles separated by the vertical dotted line represent the starting button and the target location, respectively. The 4 gray circles, connected by the horizontal dotted line, are possible locations of non-targets. Gray-ringed circles represent non-targets that are farther away from the midline, while black ringed circles represent non-targets that are closer to the midline. The left panel features the frontal starting posture (lower arm diagonal) and the right panel the lateral starting posture (lower arm straight).

Procedure

The experiment consisted of 120 trials, 12 repetitions of each of the 5 configurations discussed above (Section 2.2) for both starting postures. All experimental configurations were presented 6 times in a random order, which resulted in a sequence of 30 trials during a single experimental block.

Each trial started with an empty table and with the participants' hands and arms in the relevant starting posture. Starting posture was controlled using tactile cues along which the fingers had to be placed, markings on the floor to assure the correct position for the chair, trunk and feet, and by the experimenter who kept an eye on the overall disposition of the trunk. During this the participants had visual information of the workspace which was masked when they were ready to begin the trial. The non-target and target were then carefully placed on the table by the experimenter; the non-targets at randomly predetermined locations and the target at a fixed location. Next, the experimenter instructed the computer to open the glasses. Once vision was returned the participant had to wait for an auditory 'go' signal after a random duration between 800 and 1200 ms before starting the movement. This signal also prompted the start of the data collection. The movement task was to reach towards and subsequently lift the target from the table and to place it back immediately. Once the target was lifted data collection ceased and the participant had to return his or her hand to the starting button to impose the masking while the experimenter cleared the table.

Data processing

All analyses regarding the reaching trajectory were conducted on the x, y, and z data from the marker on the tip of the right index finger, except for the analysis of grip aperture which was performed on the index and thumb marker data taken together. Raw 3D data of each trial were filtered using a dual-pass Butterworth filter (2nd order, 20 Hz cut-off). Velocities and accelerations in each cardinal dimension (x, y, and z) were computed. These were used to define the beginning of the movement (Schot, Brenner, & Smeets, 2010). In this case the movement 'started' when marker position was sufficiently close to the starting location (3 mm), the threshold for marker velocity (5 mm/ms) was exceeded for a sufficient number of samples (50 ms). Per trial this yielded a number of sample candidates for the start of the movement. A continuous function then expressed which of the samples was actually closest to the threshold of e.g. minimal speed:

$$Fv = 1 - \frac{v}{v_{min}}$$

Trials were rejected for the following reasons: the reach never reached the minimum velocity (reported in this section), the reach was initiated before the starting cue was given, the reach did not end within the recording window (3 s), or because of unforeseen recording errors. Less than 10% of trials were rejected (data for 1 participant failed to meet this criterion).

Reach trajectories were normalized to have the same origin in 3D Cartesian coordinate system and the same number of position measurements, viz. 100 position measurements, per axis. In essence, each trial now had 100% movement time, that is, each movement was divided into 99 segments of equal duration. To this end, cubic spline interpolation was used. Trajectories were then averaged across conditions.

As demonstrated by Smeets and Brenner (1995), this type of normalization and subsequent averaging is sensitive to possible errors in determining the movement onset (or offset), that is, averaging across trials could lead to an average that does not resemble individual trials (see Fig. 6 of Smeets & Brenner, 1995). These authors propose position-based averaging instead as a way of dealing with this particular sensitivity. However, because in our experiment we had participants perform reaches to and from locations that were identical across trials and, more importantly, velocity profiles were therefore similar across trials, we argue that both time- and position-based averaging would yield the same results. In addition, we consider that the method that was used to determine the start of the movement (see Section 2.4) circumvented any possible errors in misaligning movement onset between trials, as the starting point of the movement was always within a small sphere with a radius of 3 mm. Taken together, this warrants that within condition comparison and over participant averaging was done on the basis of time-based averaging.

Dependent measures and analysis

Six measures were used, viz. the spatial measure deviation at passing, deviation at the moment that peak velocity was achieved, and initial direction of the movement, the temporal measure movement- and reaction time, and the grip aperture at the moment the hand passed the non-target were calculated for all trials. Deviation at passing was computed as the distance between the index finger marker and midline in the x-direction (transverse plane) at the moment the y-coordinate at the center of the non-target and index finger marker were identical. Deviation at peak velocity was calculated in much the same way: it was the distance between the index finger marker and the midline in the x-direction (transverse plane) at the moment of peak velocity. Peak velocity itself was computed from a velocity profile (v , t) in which both time and velocity themselves were first averaged as a function of position. This was possible because the distance moved was fairly identical between trials within a condition (see also Smeets &

Brenner, 1995). The time it took from movement start to reaching peak velocity was then computed. This information was used to ascertain the deviation in the x-direction at this precise moment. This measure has been used recently by Welsh as a kinematic marker of movement trajectories that reflects preprogrammed or feed-forward processes (Welsh, 2011). Movement time was the time between movement onset and the end of data collection, which coincided with the end of the reach-to-grasp movement. Reaction time was the time between the auditory cue to start the movement and actual movement onset by the participant. The initial direction of the movement was calculated as the angle between the midline and a vector through the (x, y) position of the marker after 15% of the trial's movement time had elapsed. To be more specific, the tangent to the curve was taken at $t = 15\%$ and the angle between this vector and the vertical midline of the workspace (connecting the middle of start button with the middle of the target button) was considered as the initial direction. To illustrate, an angle of -90° would mean a movement only to the right, 0° a movement straight forward and 180° a movement backward. We have chosen to define this measure as an angle instead of a distance because an angle reflects the curvature present in the movement. The curvature, in turn, can also be used to compare different trajectories, a practice that is often used in the study of saccade trajectories where deviation measures are also used (see Van der Stigchel, Meeter, and Theeuwes (2006) for review). Grip aperture was calculated by determining the length of the three dimensional vector between the thumb and index finger markers at the moment the hand passed the non-target, or more precisely, at the moment the y-coordinate at the center of the non-target and index finger marker were identical.

We compared the kinematic parameters of experimental trials for a particular condition with the parameters of the relevant baseline or control condition: for instance, we calculated the difference between the kinematic parameters of a reach from a frontal starting position towards a target with a non-target present on the right (or ipsilateral) side of the workspace and the kinematic parameters of a reach from a frontal starting posture towards a single target. In this case two types of deviation could occur: deviation away and deviation towards (the same holds for curvature). When deviation was away it meant that in a situation where there was a non-target on the ipsilateral side of the participant, the horizontal position of the hand was more to the left when compared to the hand position when there was no non-target present, whereas if the horizontal position of the hand was more to the right than in the situation with no non-target present, then the hand was said to deviate toward the non-target. Conversely, if the hand was more to the right with a contralateral non-target present in the workspace than when there was no non-target present, then the deviation would be labeled as 'away', whereas the label 'towards' was attributed when the hand was more to the left when the non-target object was on

the contralateral side of the workspace with respect to the hand position with only a target present. For the analysis of the results, deviation away was always labeled with a negative sign, while deviation towards was always labeled with a positive sign. This was done via the (conditional) subtraction of the relevant control condition from all experimental conditions. This means that all statistical analyses were performed on difference scores. So, for example, if the deviation at passing difference score for a ipsilateral distractor was -40 mm with a lateral starting posture and -60 mm for a frontal starting posture, then we assumed that with a frontal starting posture participants deviate more away from the non-target. This could have been irrespective of the absolute position of the hand, that is, the trajectories for the control and experimental conditions with the lateral starting postures may have been more to the left in the workspace (characterized by deviation at passing scores of e.g. -10 mm and -50 mm, respectively) than those of the frontal postures (e.g. 30 mm and -30 mm, respectively). The difference score is thus insensitive to absolute differences and reflects the changed behavior in response to non-targets.

For each subject, all the dependent measures were computed for every trial and then averaged for each of the 10 conditions. Where descriptive statistics are presented, “ \pm ” always refers to \pm standard error of the mean. Statistical comparisons within subjects were made with a repeated measures ANOVA with 3 factors: starting posture (2 levels; frontal, lateral), side (2 levels; left, right), and proximity (2 levels; medial, lateral). All comparisons between experimental conditions were made on the difference score between the experimental conditions and their relevant controls for all dependent measures (as described above). All further comparisons were made with Bonferroni-corrected t -tests.

Results

Because we subtracted control conditions (no non-target present) from experimental conditions (with non-target) in the subsequent analyses, we first performed a t -test to determine whether there was an effect of starting posture on reaching trajectory without non-targets present in the workspace. In control conditions mean deviation at peak velocity was 41.2 mm (± 7.6) for the frontal starting postures and 37.6 mm (± 5.2) for the lateral starting postures. A paired t -test revealed a significant difference ($p < .05$) between these conditions for deviation at peak velocity. Similar tests for initial direction, movement time and reaction time showed no statistically reliable differences. We also performed a paired sample t -test on the grip aperture in frontal versus lateral starting postures. Results indicated that there was no significant difference in grip aperture at the moment the hand passed the non-target, $t(11) = 1.66$, $p = .13$, for the different starting postures when no non-targets were present.

This implied that starting posture alone affects reaching trajectory (see also Fig. 2). This is in line with previous results (Kritikos et al., 1998). The timing of the movement and initial direction did not seem to be affected by starting posture. However, in our view, these results warranted a yoked comparison between experimental and their specific control conditions, i.e. conditions with the same starting posture, because the comparison between experimental conditions could otherwise be biased by the unique effect of starting posture possibly obscuring the effect of its interaction with the non-target object in which we are interested.

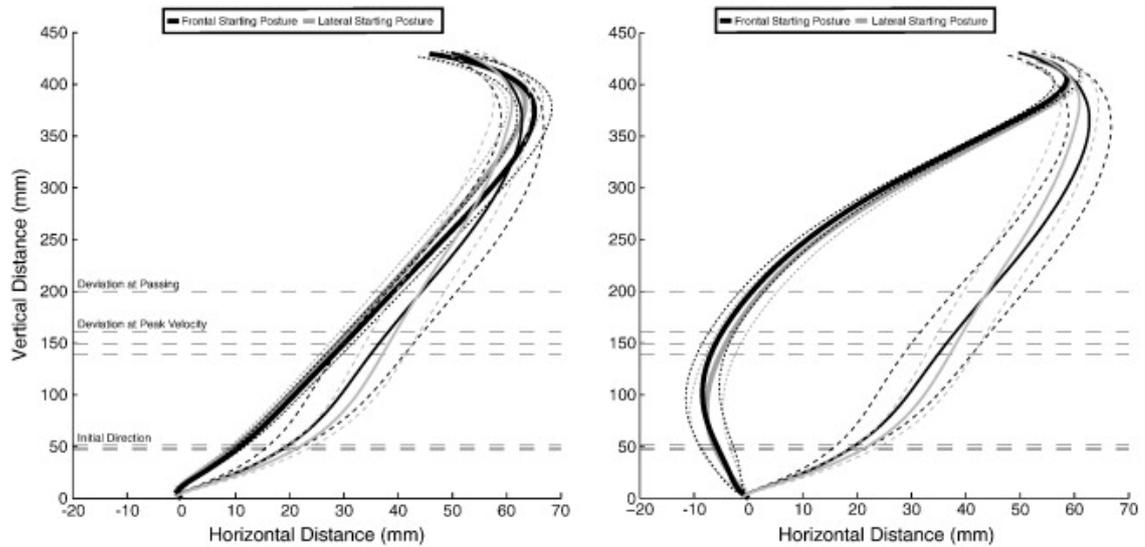


Fig. 2. Movement trajectories for the experimental and control conditions. The thick curves indicate the average movement trajectories across participants as seen from above for contralateral (left panel) and the ipsilateral (right panel) non-target conditions (proximity conditions have been collapsed) with the different starting postures. The thin curves represent the average movement trajectories across participants as seen from above for the control condition with the different starting postures. Horizontal distance from the midline (0) is displayed in mm on the ordinate, vertical distance to target is displayed on abscissa in mm. The solid black lines show the mean movement trajectories with a frontal starting posture and the solid gray lines show the mean movement trajectories with a lateral starting posture. Color-coded dashed lines show standard error of the mean for the mean trajectories across participants for these conditions, with larger dashes for the control conditions and smaller dashes for the experimental conditions. Horizontal gray dashed lines indicate the mean distances at which the measures' initial direction, deviation at peak velocity and deviation at passing were taken for all conditions. Lines at one standard deviation from those means are also provided for the measures' initial direction and deviation at peak velocity. Please note that the sideways translation at the top of the curves is caused by the participants' grip that spans the width of the object. In addition, the markers are on top of the participants' fingers, adding the width of their fingers to the translation. Please note that the curves cannot be compared directly to values in text, because when averaging movement paths over time, the difference of the mean trajectories (the figure) can differ from the mean of the difference between trajectories (values in text).

Deviation at peak velocity

Because we wanted to compare this measure across conditions we first had to establish that the moment peak velocity reached by participants was equal across conditions, that is, that participants consistently reached their peak velocity after a particular time had elapsed. We ran a repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) across the experimental conditions on time to peak velocity. This analysis showed no significant differences. Peak velocity was therefore attained at around the same moment for all conditions. Next we ascertained whether peak velocity was attained at around the same depth across conditions and whether that depth differed from the depth at which the hand passed the obstacle. We performed a repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) across the experimental conditions on the depth (y-distance) at which peak velocity was reached. We found no significant differences between conditions. We then compared the mean distance of when peak velocity was reached (M: 150 mm, SD: 11 mm) with the distance at which the hand passed the obstacle (200 mm) and a one-sample *t*-test demonstrated that these distances are significantly different from each other, $t(11) = -12.9$, $p < .0001$. Therefore, peak velocity was consistently reached at roughly the same moment in each movement, at around the same distance which was different from the distance at which the hand passed the obstacle.

We performed a 3 factor repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) across the experimental conditions on deviation at peak velocity.

The ANOVA showed that side, $F(1, 11) = 44.5$, $p < .001$, had a significant effect on the deviation at peak velocity. This suggested that the reaching trajectory at the moment of peak velocity was different when non-target objects were placed ipsilaterally versus contralaterally. In particular, ipsilateral non-targets led to more deviation away from the target than contralateral non-targets (see also Fig. 2, both panels).

In addition, starting posture, $F(1, 11) = 7.85$, $p < .05$, had a significant effect on the deviation at peak velocity. When seated frontally participants deviated more away than when seated laterally. We found no effect of proximity on deviation at peak velocity. Fig. 2 illustrates the effect of starting posture on movement trajectory.

A trend towards significance ($p = .071$) was revealed for the interaction between side of the non-target and its proximity to the midline.

Deviation at passing

We repeated this analysis for deviation at passing. A similar pattern was revealed for deviation at passing: again side ($F_{(1,11)} = 49.0$; $p < .001$) and starting posture ($F_{(1,11)} = 7.38$; $p = .022$) had a significant effect on movement trajectory, this time at the point where the hand passes the non-target. The directions of the effect were the same: non-targets on the ipsilateral side caused more deviation away from the non-target, while contralateral non-targets prompted less and more diverse responses; the frontal starting posture yielded larger deviations away and towards than the lateral starting posture. Again no main effect of proximity was found. Neither was any significant interaction effect found.

Movement time

A 3 factor repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) across the experimental conditions on movement time was performed. These results indicated that starting posture, side, and proximity to the midline did not have a significant effect on movement time (p 's $> .05$). No significant interaction effect was found.

Reaction time

An identical analysis was performed on median reaction times. The results showed that only non-targets' proximity to the midline influenced reaction times, $F_{(1, 11)} = 8.69$, $p < .05$. When non-targets were closer to the midline participants reacted slower than when the non-target was placed farther away from the midline. This may be a reflection of increased processing of the non-targets that are closer to the midline relative to those non-targets that were placed more distally, because the former are more likely to collide with the hand when it is transported to the target or because the former elicit greater inhibition. The analysis showed no significant interaction effects.

Initial direction

A 3 factor repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) was performed across the experimental conditions on initial direction. The results show that side, $F_{(1, 11)} = 25.8$, $p < .001$, had a significant effect on initial direction. More of interest was the result that starting posture, $F_{(1,11)} = 4.75$, $p = .054$ trended toward significance.

We found a significant interaction effect between the two starting postures and whether the non-target was placed ipsi- or contralaterally, $F_{(1, 11)} = 8.36$, $p = .016$. Post-hoc t -tests

confirmed this effect for frontal vs. lateral starting posture with the non-target on the ipsilateral side, $t_{(11)} = -2.83$, $p = .012$, and demonstrated no effect for frontal vs. lateral starting posture with the non-target on the contralateral side, $t_{(11)} = 0.820$, $p = .42$. Although a trend was found for starting posture, the interaction suggested that this differed in strength for side of the non-targets. That is, the initial direction was more different between postures when non-targets were placed on the ipsilateral side of the workspace. Apparently, with a lateral starting posture the movements with non-targets present on the ipsilateral side of the workspace were centered more around the midline, as indicated by mean initial directions of $-35.9^\circ (\pm 13)$ and $-38.8^\circ (\pm 12)$ while with a frontal posture they were more away from the midline, as indicated by mean initial directions of $-53.3^\circ (\pm 12)$ and $-53.1^\circ (\pm 10)$. On the contralateral side, however, there were much less pronounced and systematic differences between the two starting postures.

Grip aperture

We used a 3 factor repeated measures ANOVA (starting posture [2 levels; lower arm diagonal, lower arm straight], side [2 levels; left, right], proximity [2 levels; medial, lateral]) across the experimental conditions to analyze grip aperture at the moment the hand passed the non-target. A similar pattern was revealed for grip aperture as for the reaching trajectory parameters: we found a main effect of starting posture on grip aperture, $F_{(1, 11)} = 5.51$, $p < .05$, that is, grip aperture was smaller during movements that started with a frontal posture than in movements that started with a lateral posture when non-targets were present in the workspace. In addition, we found a main effect of side, $F_{(1, 11)} = 6.46$, $p < .05$, which indicated that the grip aperture was significantly smaller when non-targets were on the ipsilateral side of the workspace compared with grip apertures in the presence of contralateral non-targets. Again we found no significant effects for the different levels of proximity; in this case grip aperture was not significantly different when the non-target was closer or farther away from the participant. Furthermore, we found a significant interaction effect between the factors starting posture and side for grip aperture at the moment the hand passes the non-target, $F_{(1, 11)} = 12.4$, $p < .01$. This indicated that the grip aperture was more different between starting postures when the non-target was on the ipsilateral side of the workspace. Post-hoc t -tests confirmed that the grip aperture with an ipsilateral non-target present was smaller during a movement that started from a frontal posture than that of a movement that started from a lateral posture, $t_{(11)} = -3.86$, $p < .01$. Non-targets on the contralateral side did not prompt differentiated grip apertures for the different starting postures.

In the following we will refer to the spatial parameters of the reaching trajectories together as the movement trajectory. Because each of these measures is indicative of a unique

and separate moment in the movement trajectory, then, if they are taken together and demonstrating the same effects, it can be assumed that the whole trajectory is affected by an experimental manipulation. On the contrary, any effect that is present for one measure but not for others must be interpreted as a local effect, restricted for instance to the middle of the movement if there were only an effect for e.g. deviation at passing. This could be due to increased or decreased availability of feedback information, for the middle and the beginning of the movement respectively.

Discussion

The current study was designed to test the effect of different starting postures on reaching trajectories when non-target objects were present. We introduced non-target objects into participants' workspace at several locations while they had to reach-to-grasp a target object. Participants were seated in one of two starting postures, viz. with the forearm being placed diagonally or straight ahead. We found that the movement trajectories were different when participants had to use a different starting posture. This is not surprising, since movement trajectory planning is thought to be based on calculating the most efficient transformation from a starting posture to an end posture (the ready-to-grip hand near the target), so the same end posture preceded by different starting postures leads to dissimilar transformations, i.e. movements (see (Rosenbaum et al., 2001). What is surprising, however, is the fact that starting posture interacted with non-target object location at the beginning of the movement. Apparently, when objects are on the right side and closer to the reaching hand, the initial movement trajectory deviates more away from a non-target object when a frontal posture is assumed than when a lateral position is adopted. This is in line with Tresilian's account that we keep a preferred distance between our manipulandum and the non-target object, because we want to avoid potential collisions with those objects (Tresilian, 1998 and Tresilian et al., 2005). The results we obtained from the analysis of grip aperture seem to subscribe to this idea, in that the grip aperture at the moment the hand passed the non-target was smaller for more 'obstructing' (e.g. ipsilateral) non-targets, which is a behavioral response that seems to be geared towards minimizing the risk of collision with the non-target (Mon-Williams et al., 2001).

In the introduction we mentioned that by varying posture we would be able to make a non-target object more or less of an obstacle while keeping the visual lay-out constant. The response observed when posture was changed was evident: the results suggest that with a lateral starting posture the ipsilateral non-target became less of a physical obstacle. For the first time, we are now able to state that this is the case, because the visual features of the non-target were not changed, because among other things the position and size of the non-target remained

the same. Earlier studies that attributed adjusted movement trajectories because of the presence of non-targets to avoiding a physical obstruction varied position of these objects (Tresilian, 1998). In turn, this means that visual features of the non-target are also changed. Since it has been shown that position also influences the distracting effects (Tipper et al., 1997), any changes in movements that were interpreted as a consequence of a physical obstacle could have been due to distracting effects. We show, however, that there is a suitable manipulation that allows for manipulating one of these effects separately from the other. Our results indicate that non-targets' level of obstruction can be modified. Furthermore, the degree of obstruction of a non-target is an important, but not the only, contributor to modifications of the movement trajectory that are made in response to the presence of non-targets in the workspace. Moreover, we have shown that starting posture has an effect on the avoidance movement trajectory and that in itself warrants careful consideration of starting posture when designing experiments on obstacle avoidance.

Nonetheless, it could be argued that changing starting posture changed the layout of the visual field and thereby distracting properties of non-targets. As we did not use a chin rest to stabilize head position and had no fixation point, an ipsilateral non-target object could appear somewhat more to the right in the lateral condition than in the frontal condition, which could result in less distractor interference and in this particular case, less of a movement away from the non-target. Following this rationale, the opposite effect should then be expected on the contralateral side, that is, increased distractor interference from contralateral non-targets resulting in movement trajectories that veer more towards those objects. A single-sample *t*-test was performed on the deviation scores of all contralateral conditions from the control condition for all spatial parameters to check for this possibility. All statistical comparisons were Bonferroni-corrected and indicated no significant departure from '0'. These results do not indicate increased distractor interference, suggesting that varying postures, in this experiment at least, does not change how distractors (could) affect our reaching. Furthermore, we believe that the change in postures did not yield a sufficient change in visual angle to affect the distracting properties of the non-targets.

It has been theorized that non-targets that are not relevant for the movement have less of an effect on the movement than those that are relevant (Tipper et al., 1997). Our results suggest that movement trajectories around non-targets that are closer to the midline do not differ statistically from non-targets that are farther away from the midline. If it is true that by placing non-targets farther away from the midline they become less relevant to the immediate avoidance movement and are therefore less distracting, then we should have found an effect of proximity to the midline. In our experiment the more contralaterally placed non-targets may

have been irrelevant to the movement in that they were never distracting or obstructing our participants. This could account for the lack of a main effect of proximity in our data. An additional analysis of a right (ipsilateral) side effect of proximity of the non-targets to the midline could vindicate the argument that spatial adjustments to *relevant* non-targets could indeed be based on distractor interference. However, paired t-tests between the setups with proximal and distal non-targets, all on the ipsilateral side, did not reveal any significant effects for proximity to the midline on our spatial parameters. Thus, this means that when both starting postures were used, proximity to the midline of the ipsilateral non-target did not affect reaching movements. Another explanation could be that the resolution of 'proximity' was too low, that is, the different proximity conditions may have prompted too similar movement responses.

One alternative way of framing our results is by arguing that starting posture biases where attention is allocated. This means that even though we kept the non-target in the same location (a priori visual layout is the same), a non-target could capture different amounts of attention based on the starting posture of the actor. Conceivably, a particular starting posture may elicit a preferred movement plan to the target that passes closer to a non-target than that of another posture. In essence, the non-target then comes closer to the arm, which is why it captures more attention (or: becomes more salient) during movement planning. This would then result in stronger competition during selection-for-action and therefore cause the movement trajectory to veer more away from the non-target. The speculation that prepared actions can be influenced by non-target objects is supported by the premotor theory of attention (Rizzolatti & Craighero, 1998) that states that attention itself derives from the activity of sensorimotor circuits. Indeed, this hypothesis requires a strong and direct coupling between visual attention and premotor activity. Our results support this idea. The degree of obstruction of a non-target therefore influences the amount of attention captured by the non-target.

We conclude that starting posture is a suitable method to manipulate the degree in which a non-target object obstructs movement without changing the degree in which it could visually distract the actor. Our evidence indicates that non-target objects definitely act as physical obstructions to movement. One key factor in this is that an object need not be an obstacle for the hand, while it may be one for the lower arm. Previous studies may have been too focused on the hand in isolation. Any experiment into obstacle avoidance should therefore consider that starting posture also affects reaching trajectories.

Chapter 6 – The Effect of Similarity: Non-Spatial Features Modulate Obstacle Avoidance

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2013). The effect of similarity: Non-spatial features modulate obstacle avoidance. *PLoS ONE* 8(4): e59294.

Abstract

The introduction of non-target objects into a workspace leads to temporal and spatial adjustments of reaching trajectories towards a target. If the non-target is obstructing the path of the hand towards the target, the reach is adjusted such that collision with the non-target, or obstacle, is avoided. Little is known about the influence of features which are irrelevant for the execution of the movement on avoidance movements, like color similarity between target and non-target objects. In eye movement studies the similarity of non-targets has been revealed to influence oculomotor competition. Because of the tight neural and behavioral coupling between the gaze and reaching system, our aim was to determine the contribution of similarity between target and non-target to avoidance movements. We performed 2 experiments in which participants had to reach to grasp a target object while a non-target was present in the workspace. These non-targets could be either similar or dissimilar in color to the target. The results indicate that the non-spatial feature similarity can further modify the avoidance response and therefore further modify the spatial path of the reach. Indeed, we find that dissimilar pairs have a stronger effect on reaching-to-grasp movements than similar pairs. This effect was most pronounced when the non-target was on the outside of the reaching hand, where it served as more of an obstacle to the trailing arm. We propose that the increased capture of attention by the dissimilar obstacle is responsible for the more robust avoidance response.

During our everyday activities we reach towards and grasp many objects. Although these objects are seldom the only items present in our direct surroundings, we are able to steer our hand toward them and evade any obstacles that are present. This ability is served by a complex system that encodes potential obstacles to an arm movement during motor planning so that they are successfully avoided during movement execution. Tresilian first described that the deviations to movements that are found after the introduction of a non-target to a workspace are the result of the preplanning of an avoidance movement to prevent collision with the non-target (Tresilian, 1998). The nervous system is thought to modify the reaching movement in response to the presence of obstacles so as to minimize the likelihood of collision based on a preferred distance of the arm to the obstacle. The modification process itself is ostensibly subtle and precise (Mon-Williams, Tresilian, Coppard, & Carson, 2001). For instance, when wrist posture is changed, the obstructing effects of a non-target object may change as well (Tresilian, 1998). Evidence in line with this account comes from many studies in which an increase in movement time is observed when a non-target stimulus is placed in the workspace (Tresilian, 1998; Mon-Williams et al., 2001; Biegstraaten, Smeets, & Brenner, 2003; Jackson, Jackson, & Rosicky, 1995; Mon-Williams & McIntosh, 2000; Saling, Alberts, Stelmach, & Bloedel, 1998), suggesting that the movement is slowed down to increase spatial accuracy and avoid potential collisions. These adjustments are not a general response to the presence of non-target objects (Mon-Williams et al., 2001), on the contrary, the effect is specific to the layout of the workspace, in that non-target objects only elicit an avoidance response when the preferred distance to them is too small. For instance, Chapman and Goodale have noted that the obstacle avoidance system is sensitive to changes in obstacle size and obstacle location (Chapman & Goodale, 2008).

A number of other studies have shown that presenting non-target objects in a workspace in a position where they do not directly obstruct the reach toward a target also leads to spatial and temporal modifications of reaching-to-grasp movements (Howard & Tipper, 1997; Kritikos, Bennett, Dunai, & Castiello, 2000; Kritikos, Dunai, & Castiello, 2001; Meegan & Tipper, 1998; Tipper, Howard, & Jackson, 1997; Welsh, Elliott, & Weeks, 1999; Welsh, 2011). In this case the non-target is regarded as a distractor. It is thought that the distractor interferes with the planning of the action toward the target object by evoking a competing response that needs to be inhibited before an accurate reach toward the target can occur (Tipper et al., 1997). This results in spatio-temporal adjustments to reach movements which are in turn modified by various features of the distractor. Among the features that have been investigated in these studies are distractor size (Kritikos et al., 2001), orientation (Kritikos et al., 2000), and location (Tipper et al., 1997).

Although the explanation offered by the obstacle avoidance account can explain data more parsimoniously than the distractor interference account, the simple fact that obstacles need to be avoided to prevent a collision may not exclude other factors from further modifying the spatial path of the reach. This is true as long as additional modifications of hand movements through a workspace where obstacles need to be avoided can be revealed. So far, however, the competition between a target and a distractor has been manipulated by changing features that are also directly relevant for the execution of movement, that is, by changing features that made them more or less obstructing (e.g. size, orientation).

The aim of the current study was to investigate the effect of similarity between target and non-target on reaching behavior. More explicitly, we were interested in whether the similarity between target and non-target, defined by color, would modulate the movement trajectories of participants when they needed to avoid obstacles. Because similarity in color is not directly movement relevant, any alterations to movement trajectories are directly attributable to non-spatial features of the non-target, without a possible role for biomechanical control laws in explaining alterations to movement trajectories. Furthermore, it is known that color itself does not have an influence on the reach trajectories when controlling for chromaticity and luminance (Gentilucci, Benuzzi, Bertolani, & Gangitano, 2001). While color-matched targets and non-targets have not been studied earlier in an obstacle avoidance paradigm, there have been investigations into similarity in distractor interference setups for eye movements and hand movements. We will discuss these studies below and note some limitations.

For eye movements it has been reported that saccade trajectories deviate more away from similar distractors than dissimilar distractors (Ludwig & Gilchrist, 2002, 2003; Mulckhuyse, Van der Stigchel, & Theeuwes, 2009). This has been explained by the stronger oculomotor competition between the target and distractor when they are similar. This in turn results in a stronger top-down inhibition to resolve the competition, which leads to larger deviations away from the distractor. This line of reasoning could be applicable to hand movements as well: when there is strong competition between two similar objects, the inhibition of the automatic movement response to the 'distracting' object should also be strong, which should be reflected in a hand movement that veers away from a similar distractor more strongly than when a dissimilar distractor is presented (in this case a dissimilar pair of objects is associated with less inter-object competition). Of course, this hinges on the assumption that eye movements and hand movements are planned by systems that are sensitive in the same way to a given form of information (i.e. similarity information), which may not be justified. Indeed, several studies show that targets for the eye and hand are selected by independent, effector-

specific, systems (Thompson & Westwood, 2007; Sailer, Eggert, Ditterich, & Straube, 2000; Jonikaitis & Deubel, 2011), which makes it difficult to generalize results from eye movement studies to hand movement studies.

Empirical evidence for the effect of target-distractor similarity in prehension (Kritikos et al., 2000) indicated that when the features of target and distractor are different, the distractor has a greater impact on prehension parameters. It is interesting to note that the features with which similarity in their study was manipulated were size and orientation. Therefore, any effect of similarity could possibly be attributable to an avoidance response to the physical properties of the non-targets instead of increased competition between target and non-target caused by those properties of the non-target. As mentioned earlier, it would therefore be informative to study similarity with a feature that does not affect the occupation of volumetric space, as it would afford a direct comparison with eye movement literature and not suffer from the aforementioned confound of possibly increasing obstructiveness.

In this study we asked participants to reach towards and grasp a target with a non-target present in the workspace. The non-target could be placed in different locations relative to the target. The target and non-target could be either similar or dissimilar in color, while they were identical with respect to all other features. We measured participants' reaching trajectories and extracted kinematic parameters from them. We were interested in finding a difference between similar and dissimilar conditions, because that would imply that using color to establish similarity is a relevant intervention in an obstacle avoidance paradigm. This would point out that non-spatial visual properties that have been found to modulate distractor effects can also modulate obstacle avoidance maneuvers.

Experiment 1

In this experiment, we tested the reach-to-grasp behavior of participants towards a single target in the presence of either a non-target in the left hemisphere or a non-target in the right hemisphere. Participants reached with their right hand, so that the left hemisphere non-target was on the inside of the reaching arm and the right hemisphere non-target was on the outside of the reaching arm. Non-targets were either a different or the same color as the target. In addition, we observed reaching behavior to grasp a target in the absence of non-targets.

Methods

Ethics Statement

The faculty's institutional review board, the WMO Advisory Committee, under the Medical Research Act issued a formal written waiver that this research project did not require approval from a Medical Ethics Review Committee. Thus, the institutional review board issued a formal written waiver for the need of ethics approval.

Participants

Ten (2 men, 8 women) right-handed participants contributed to this study. All participants had normal or corrected-to-normal vision and were naïve to the purpose of the study. Each participant gave written informed consent prior to the start of the experiment.

Materials

The participant sat in front of a 122 cm×61 cm table. This table featured a workspace of 40 cm×40 cm. In the workspace there were two fixed elements; the start button and the target. Both were shifted 3 cm rightwards from the center of the table. A virtual line connecting the middles of the start button and the target was considered as the midline of the workspace. The start button was positioned 5 cm away from the front edge of the table and the target was situated 40 cm beyond that. The non-targets were positioned at widths of 10 cm to the left and right of the midline of the workspace, that is, the non-targets were either positioned on the inside or outside of the reaching arm. Their depth was always 20 cm into the workspace (halfway in between the starting button and the target). The target was placed on a trigger that responded to when the target was lifted of it. See Figure 1, left panel, for an overview of the setup. The target and non-targets were tall wooden cylindrical objects (2.75 cm×2π×15 cm). We made two sets; one painted green and one painted red.

Participants wore PLATO LCD goggles (Translucent Technologies, Toronto, Canada), which permitted manipulation of visual feedback and participants wore MiniBird magnetic markers (Ascension Technology Corporation, Burlington, USA) which allowed kinematic tracking with a sampling rate of 100 Hz over a recording window of 3 s. These markers were placed on the tips of participants' right index finger and thumb. The cables were fixed to the participants as well as to the edge of the table with tape and elastic bands, so that participants could move their arm without restriction and without influencing the recordings.

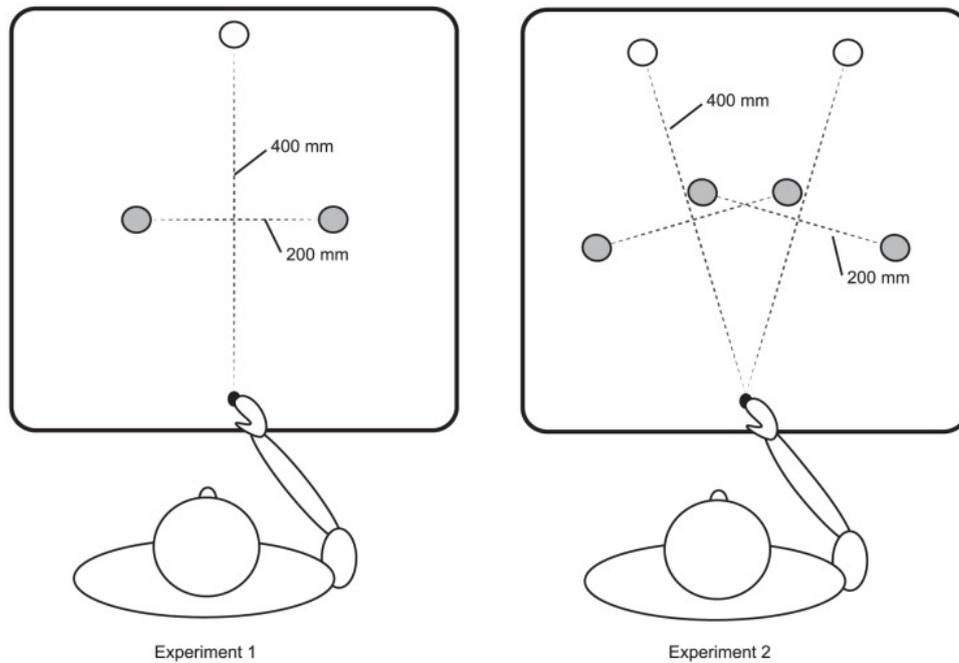


Fig. 1. Top-down view of the experimental setups. Filled circles represent possible non-target locations, while an empty circle represents the target locations. The distance between the starting location of the hand and the target location was 400 mm. Midway towards the target the non-targets were placed at 200 mm distance to the starting location. Non-targets were removed 100 mm from the midline of the workspace. Panel A represents the setup of Experiment 1 and panel B that of Experiment 2.

Design & Procedure

There were two possible locations where objects could be placed as non-targets and a single target location. The non-targets could be either similar or dissimilar in color to the target. In addition, the target could be either red or green. The number of experimental configurations of the workspace then becomes eight, viz. two levels of similarity (Similar vs. Dissimilar) x two levels of non-target side (Inside vs. Outside) x two levels of target color (Green vs. Red). The workspace also had two configurations in which only a red or green target was presented. The total number of configurations was 10. Participants reached towards the target with each configuration 10 times, which meant we recorded a total of 100 trials. The trials were pseudo-randomized across the first and second half of the experiment, that is, participants completed five repetitions of all configurations in the first half of the experiment and in the second half of the experiment.

Participants were positioned with their midsagittal line (sternum to navel) in line with the midline of the workspace. Each trial started with an empty table and with the participants' hand on the starting button. The participants had no access to visual information at this point. The non-target and target were then carefully placed in the workspace by the experimenter,

minimizing any auditory cues about the position of the target and non-target. Next, vision was returned to the participant and they had to wait for an auditory 'go' signal after a random duration between 800–1200 ms before starting the movement. Upon the auditory signal data collection commenced. The task was to lift the target and place it back as rapidly and smoothly as possible. Once the target was lifted, the end of movement recording was triggered. After the participant had returned his or her hand to the starting button the visual masking was imposed again and the experimenter cleared the table for the next trial. Eye fixation was not restricted during the reaching movement.

Data processing

All analyses regarding the reaching trajectory were conducted on the data from the marker on the tip of the right index finger. Raw 3D data of each trial were filtered using a dual-pass Butterworth filter (2nd order, 20 Hz cut-off). Velocities in each cardinal dimension (x, y, and z) were computed. Positions and velocities were used to define the beginning of the movement (Schot, Brenner, & Smeets, 2010). In this case the movement 'started' when a few separate conditions were met: (1) the index finger marker position needed to be within 3 mm of the starting location, (2) the index finger and thumb needed to be travelling faster than 5 mm/ms, (3) for at least 50 ms. A three dimensional velocity vector was determined by vector sum addition of speeds in each cardinal direction (x, y, and z) for prerequisite (2) and (3). Per trial a number of sample candidates would meet these criteria for the start of the movement (i.e. close enough to the starting button and travelling faster than the minimal speed for the given duration). A continuous function then expressed which of the samples was actually closest to the threshold of the given minimal speed: $F_v = 1 - v/v_{\min}$. This particular sample would then be chosen as the start of the movement. Trials were rejected for the following reasons: the reach never exceeded the minimum velocity (reported above), the reach was initiated before the starting cue was given, the reach did not end within the recording window (3 s), or because of unforeseen recording errors. No participants had more than 10% of movements rejected, which was the maximum of allowed rejections.

Reach trajectories were normalized to have the same origin in a 3D Cartesian coordinate system and to have the same number of position measurements. To this end, cubic spline interpolation was used.

Analysis

For each participant, all the dependent measures were computed for every trial and then averaged for each of the 10 configurations. Difference scores were computed for every

kinematic parameter by subtracting experimental and control conditions from each other. We used the following kinematic parameters: x-deviation at the moment the hand passes the obstacle (in mm) Chapman & Goodale, 2008), movement duration (in milliseconds), reaction time (in milliseconds), and the initial direction of the movement (slant of the movement vector with respect to the midsagittal line in degrees after 150 ms, with clockwise as positive and midsagittal as 0). We have chosen to define this last measure as an angle instead of a distance because it allows for a more direct comparison between this study and the results from eye movement literature (Ludwig & Gilchrist, 2002, 2003; Mulckhuyse et al., 2009; Al-Aidroos & Pratt, 2010) (regarding similarity) in which angular outcome measures are used regularly.

All difference scores were subjected to a repeated measures analysis of variance having two levels of similarity (Similar vs. Dissimilar), two levels of non-target location (Outside vs. Inside) with respect to the reaching arm and two levels of target color (Red vs. Green). Interaction effects were further explored using post-hoc paired t-test analyses with Bonferroni's correction for significance.

Results

Deviation at Passing

There was a main effect of similarity, $F(1, 9)=13.09, p<.01$, indicating that the mean deviation at passing for dissimilar pairs ($M=-10.3$ mm, $SD=1.05$) was significantly greater than that of similar pairs ($M=-9.36$ mm, $SD=1.01$). Ostensibly, participants deviated more away from a dissimilar non-target than from a similar non-target. The main effect of non-target side gave an F ratio of $F(1, 9)=72.62, p<.001$. This indicates that the mean deviation at passing for inside non-targets was significantly different from the outside non-targets (compare panels A & B of Fig. 2; the reaching movement deviates less from the inside non-targets than from outside non-targets, respectively). There was no main effect of color. The interaction effect between similarity and non-target side was significant, $F(1, 9)=7.69, p<.05$. Post-hoc analyses using Bonferroni's criterion for significance indicated that participants deviated significantly more away from the dissimilar outside non-target than the similar outside non-target, $t(9)=2.83, p<.025$, while the difference in deviation at passing between similar and dissimilar non-target on the inside of the arm was not significant. A separate analysis performed on conditions with inside non-targets alone showed no significant departure from control conditions.

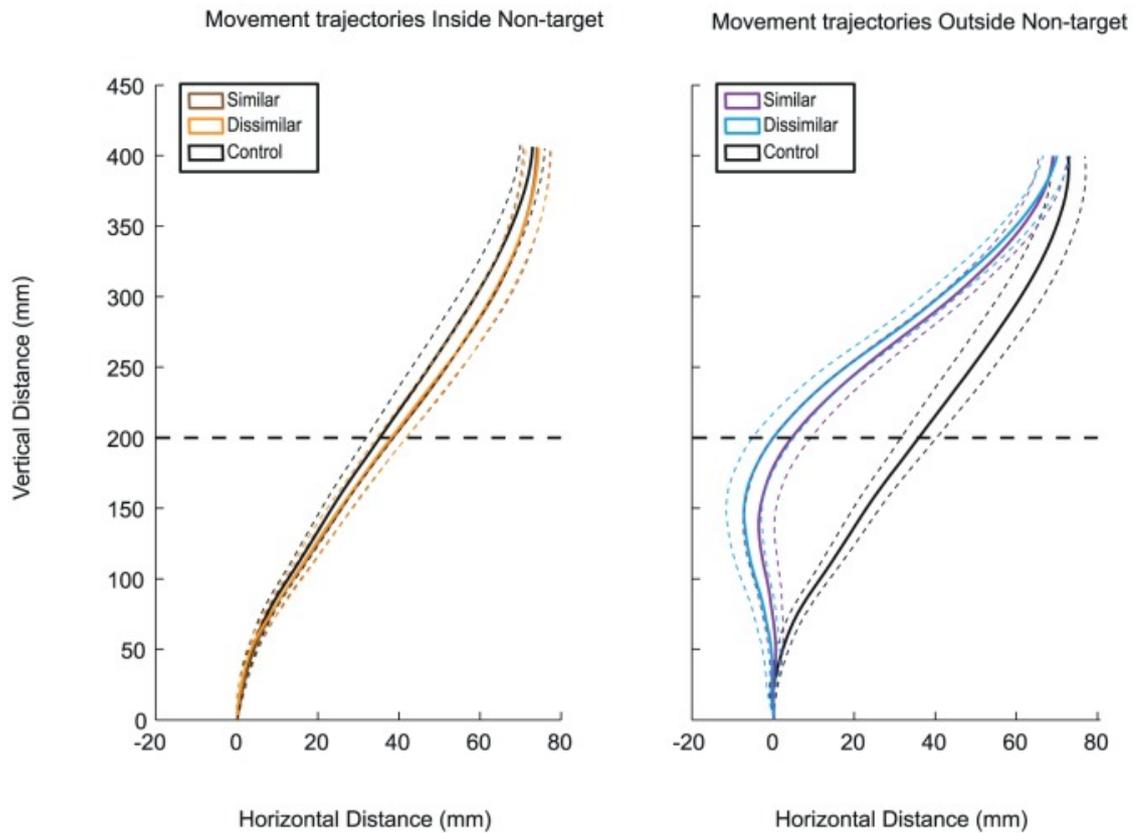


Fig. 2. Average movement trajectories across participants for Experiment 1 across participants and in the x, y plane. The left panel shows the hand trajectories when the non-target was on the inside of the hand, while the right panel shows the same for an outside non-target (with reference to the participant's reaching hand). The solid lines indicate average trajectories in the experimental and control conditions. The dashed lines represent between subjects movement error (SEM) around those trajectories. Color conditions (R and G) were collapsed into a single similar (RR and GG) or dissimilar trajectory (RG and GR), indicated by brown and purple (for the inside non-target) and orange and blue (for the outside non-target) lines respectively. The control condition is plotted in black. The horizontal dashed lines indicate the planes at which deviation at passing was measured.

Initial Direction

Analysis revealed that there were no significant effects of any factor on initial direction. We discovered two trends towards significance, however, one for non-target side with $p=.053$ and one for the interaction between similarity with non-target side, $p=.051$. This is in line with the effects described above.

Movement Time

None of the factors were significant for movement time.

Reaction Time

The analysis showed no significant main effects for reaction time. There was, however, one significant interaction effect between similarity and non-target side, $F(1, 9) = 11.2, p = .01$. Further investigation using Bonferroni-corrected t-tests revealed that participants reacted significantly slower, $t(9) = -2.39, p < .025$, in the dissimilar conditions ($M = 351$ ms, $SD = 47$) than in the similar conditions ($M = 333$ ms, $SD = 53$) when the non-target was presented on the outside of the arm (right side of the workspace), whereas there was no significant difference in reaction time between the different similarity conditions when non-targets were presented on the inside of the arm (left side of the workspace).

Taken together, these parameters imply that the movement trajectory as a whole was affected by similarity, as can be seen in Figure 2, at least as long as the non-target is on the outside of the arm.

Discussion

The purpose of this experiment was to uncover the role of color-defined similarity between target and non-target by investigating hand reaching trajectories in an obstacle avoidance paradigm. We hypothesized that similarity of target and non-target would be reflected in differences in movement trajectories because of analogous results from previous research into eye and hand movements with the distractor interference paradigm. The results support this hypothesis as the trajectories of the hand are different when target and non-target have the same color compared to when they have different colors. This effect is a replication of Kritikos and colleagues (2000) who found an analogous effect for size and orientation and Ludwig and Gilchrist (2003) who report a similarity effect of visually presented targets and distractors for eye movements. This 'similarity' effect thus extends to color-defined similarity in physical objects and we now have support for an additional modifier of the hand trajectory in obstacle avoidance beyond the avoidance of a collision.

There is a further distinction that we can make with regard to the direction for the similarity effect; our results indicate that a dissimilar pair causes more deviation away than a similar pair. This is in line with Kritikos and colleagues (2000) results but not with the results of Ludwig and Gilchrist (2003). We refer to the general discussion for a detailed treatment of the direction of the similarity effect.

The results also indicate an effect of non-target location on reaching trajectories. This could have been because the right side non-target (on the 'outside of the arm') is actually more

of an obstacle to the trailing lower arm than the left side non-target. All reaches were made with the right hand, so the enlarged movement trajectories ‘around’ the right side non-target may reflect the constraints placed on the movement of the lower arm which forced it in a direction away from the non-target to avoid collision—and moving the hand with it (for a detailed discussion see (Menger, Van der Stigchel, & Dijkerman, 2012)).

Of particular interest is the interaction we found between non-target side and similarity between target and non-target. We can discount obstacle avoidance as a cause, because similarity was manipulated using color which is a feature that does not necessitate movement adaptations in itself, contrary to a feature like non-target orientation, which—if manipulated—leads to a different physical layout. Because in our experiment the physical location of the non-target was constant and the starting posture was controlled, the difference between movements with similar and dissimilar pairs present in the workspace cannot be due to biomechanical considerations. The effect is therefore due to a subtle bias caused by the relation between non-target and target. It may be that a particular level of obstruction by the non-target is required before this effect of similarity can affect the behavior of participants, which could explain why we find the effect of similarity only on the right side of the workspace where more robust avoidance maneuvers were observed.

Experiment 2

In Experiment 1 we showed that a non-target of a different color than the target gave rise to larger avoidance effects in the reach-to-grasp movement than a non-target with the same color as the target. This effect appeared to be driven by the right non-target position. To account for the dominant effect of the right non-target position we proposed that this non-target position may have been more obstructive to the trailing arm. Furthermore, we speculated that the requirement of more robust avoidance maneuvers in the right non-target condition may have made the similarity effect more readily detectable. In that case, the detection of the effect of similarity is facilitated by the biomechanical constraints placed on the movement system. It is worthwhile to investigate whether the similarity effect can be replicated under slightly different biomechanical constraints so as to exclude an effect of task ecology. We performed Experiment 2 to check whether non-spatial features of the obstructing non-targets can that still further modify avoidance responses when reaches are made in different directions (other than straight ahead) into either the left or right hemispace.

To this end we modified the setup of Experiment 1 such that participants had to reach to grasp towards a target that could be present in one of two possible locations that were 30

degrees apart. Targets were presented in isolation and in the presence of non-targets that were to the left or right of the target. Non-targets were similar or dissimilar to the target with regard to their color. In half the trials the non-target was on the outside of the reaching arm, while the non-target was on the inside of the reaching arm in the other half of the trials.

To recap, we expected that non-targets that were dissimilar to the target would evoke larger avoidance responses than similar ones. In addition, any such (dis)similarity effect was expected to be confined to situations where the non-target was on the outside of the reaching hand, irrespective of the location of the target.

Methods

The method for Experiment 2 was similar to that of Experiment 1; as such only the differences in methodology are reported here.

Ethics Statement

The faculty's institutional review board, the WMO Advisory Committee, under the Medical Research Act issued a formal written waiver that this research project did not require approval from a Medical Ethics Review Committee. Thus, the institutional review board issued a formal written waiver for the need of ethics approval.

Participants

Ten right-handed participants volunteered to participate in this study (4 men, 6 women). All had normal or corrected-to-normal vision. No participants were excluded based on their failure to meet our mistrial criteria. Each participant gave written informed consent prior to the start of the experiment.

Materials

The setup of Experiment 1 was rotated 15 degrees clockwise and counterclockwise to create two new target and four new non-target locations. In the workspace there were two fixed elements; the start button and a target at one of two possible locations. Virtual lines connecting the middles of the targets with the start button were considered as the midlines of two (overlapping) workspaces. The start button was positioned 5 cm from the front edge of the table and the target buttons were situated 40 cm along 'their' midlines beyond that. The non-targets could be positioned at widths of 10 cm to the left and right of the midlines of the workspaces. Because the participants always used their right hand for grasping, the 'left' non-targets were on the inside of the reaching arm irrespective of target location, whereas the 'right' non-targets

were on the outside of the reaching arm irrespective of target location. Non-target depth was always halfway from the start button to the target along the midline from starting button to target location. The targets were placed on triggers that responded to the removal of the targets. See Figure 1, right panel, for an overview of the setup.

Design & Procedure

There were four possible locations where objects were placed as non-targets and two target locations where targets were placed. Per target location there were two possible non-target locations. Furthermore, the non-targets could be either similar or dissimilar in color to the target. In addition, the target could be either red or green. The number of experimental configurations of the workspaces was 16, viz. two levels of similarity between targets and non-targets (Similar vs. Dissimilar) x two levels of target side (Left vs. Right) x two levels of non-target side (Inside vs. Outside) x two levels of target color (Green vs. Red). The experiment also had four control conditions in which only a red or green target was presented at either target location. The total number of configurations was 20. Each configuration was executed eight times, to a total of 160 trials. Trials were randomized across the first and second half of the experiment.

Analysis

For each participant, all the dependent measures were computed for every trial and then averaged for each of the 20 configurations. We calculated the spatial measures with respect to the midline of the workspace associated with a particular condition in which the movement was performed. This means that the scores within this experiment and between Experiment 1 and 2 are directly comparable. Difference scores were computed for every kinematic parameter by subtracting experimental and control conditions from each other. We used the following kinematic parameters: x-deviation at the moment the hand passes the obstacle (in mm), movement duration (in milliseconds), reaction time (in milliseconds), and the initial direction of the movement (slant of the movement vector with respect to the midsagittal line in degrees after 150 ms).

All difference scores were subjected to a repeated measures analysis of variance having two levels of similarity (Similar vs. Dissimilar), two levels of target location (Left vs. Right), two levels of non-target location (Outside vs. Inside) and two levels of target color (Red vs. Green). Interaction effects were further explored using post-hoc paired t-test analyses with Bonferroni's correction for significance.

Results

Deviation at passing

There was no main effect of similarity. For non-target side we found a main effect, $F(1, 9)=449.2$, $p<.001$. This indicated that participants deviated significantly more away at passing an outside non-target ($M=-47.1$ mm, $SD=2.73$) than an inside non-target ($M=1.51$, $SD=1.09$). In addition, target side had a significant main effect on deviation at passing, $F(1, 9)=5.70$, $p<.05$. This means that mean deviation at passing when reaching for the right side target ($M=-25.6$ mm, $SD=1.89$) was significantly greater than that of a left side target ($M=-20.1$ mm, $SD=2.24$). A main effect of color was not found.

We observed an interaction effect of similarity with target side $F(1, 9)=7.80$, $p<.025$. Post-hoc analyses using Bonferroni's criterion for significance indicated that average deviation at passing was significantly more away in the dissimilar pair with the right target condition ($M=-25.6$ mm, $SD=1.95$) than in the similar pair with the right target condition ($M=-20.1$ mm, $SD=2.30$), $t(9)=2.55$, $p<.025$, whereas if the reach was towards the left target then the similarity conditions did not differ significantly from each other. Furthermore, we determined that there was a three-way interaction effect of similarity with target side and non-target side $F(1, 9)=8.08$, $p<.025$. Post-hoc testing indicated that reaches veered more away from a dissimilar 'outside' non-target when the target was on the right side of the workspace than from a similar non-target, $t(9)=4.75$, $p<.001$. This effect was not apparent when the participants reached towards the left target or when non-targets were on the inside of the reaching arm (all p 's $>.05$). Again, it appears that the effect of similarity, or rather dissimilarity, is confined to a specific situation.

This is further substantiated by a separate comparison of inside non-targets with the control condition. Although there was no overall effect of inside non-targets on the hand movement, further (Bonferroni-corrected) testing revealed that there was one 'inside' condition that showed a significant departure from a reach toward a target in isolation: when the dissimilar non-target was present and participants reached toward the right hemispace target their reaching trajectories differed significantly from control conditions, $t(9)=-4.27$, $p<.005$.

Initial Direction

We found a main effect of similarity on initial movement direction, $F(1, 9)=6.10$, $p<.05$. Target side also had a main effect on initial direction, $F(1, 9)=106.9$, $p<.001$. Non-target side did not have a significant effect on initial direction, although it did display a trend towards significance. We found an interaction of similarity with target side, $F(1, 9)=8.0$, $p<.025$ along similar lines as

the interactions reported above, and an interaction between target side and non-target side $F(1, 9)=133, p<.001$.

As can be seen in Figure 3 the different setups yielded quite distinct movement patterns. Please note that the x-axis was scaled differently because for grasping the right target object the index finger had to move ‘around’ it while the index finger could stay on the inside of the left target object for a successful grasp. Therefore, the horizontal distance for the movements to the right target (Figure 3 right panel) was larger (due to the added width of the object and the finger) than the distance to the left (Figure 3 left panel).

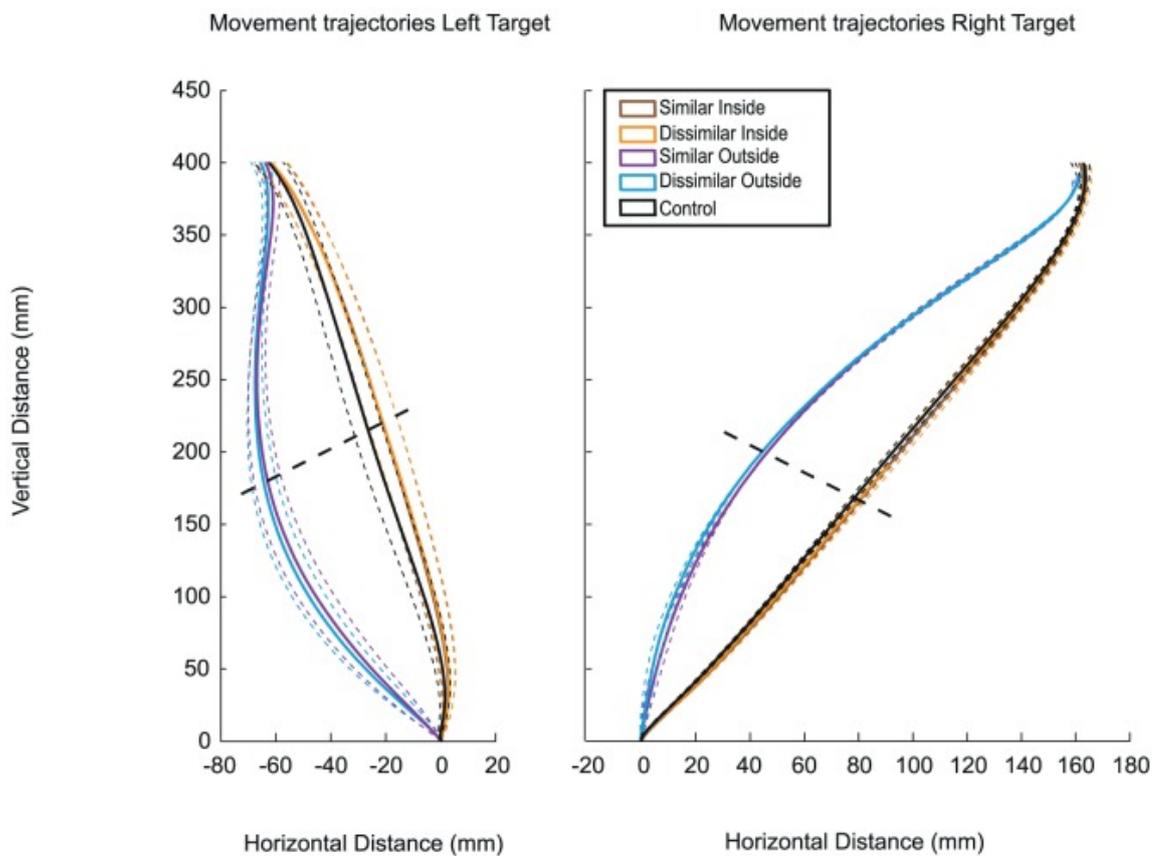


Fig. 3. Average movement trajectories across participants for Experiment 2 across participants and in the x, y plane. The left panel shows the hand trajectories towards the target on the left, while the right panel shows the hand paths towards a right side target (with reference to the participant). Each panel contains trajectories towards the target with inside and outside non-targets. The solid lines indicate average trajectories in the experimental and control conditions. The dashed lines represent between subjects movement error (SEM) around those trajectories. Color conditions (R and G) were collapsed into a single similar (RR and GG) or dissimilar trajectory (RG and GR), indicated by brown and purple (for the inside non-target) and orange and blue (for the outside non-target) lines respectively. The control condition is plotted in black. Please note the difference in scaling of the x axis compared to the previous figure. The oblique dashed lines indicate the planes at which deviation at passing was measured.

The trajectories that resulted from movements with non-target present on the outside of the reaching arm were distinct from the control conditions, whereas non-targets on the inside of the arm prompted responses that were closer to a reach toward a single target. The effects of the non-targets on the movement trajectories were therefore strongest for the outside non-targets which was reflected in the interaction effect mentioned above. In addition, the similarity effects appear to be strongest in these cases as well, see also Figure 3.

Reaction time

We found no significant differences between conditions for reaction time.

Movement Time

We found no significant differences between conditions for movement time.

Discussion

In Experiment 2, participants were instructed to reach for and pick up a target placed 15 degrees to left and 15 degrees to the right of their midsagittal plane. The target was presented alone or accompanied by a non-target. The non-target was either similar or dissimilar in color to the target and was placed halfway between the start and target location to either the left or to the right of the reaching arm, thereby putting it on either the outside or inside of the reaching arm.

Our results indicate that non-target location had an influence on reaching trajectories, that is, non-target location influenced reaching behavior when the non-target was in a specific location, namely, to the right or on the outside of the reaching arm. Conversely, we found no systematic evidence to support avoidance effects by non-targets to the left or on the inside of the reaching hand. It is interesting to note that this 'right side' effect exists when a target is to the left as well as to the right of the starting hand location. More importantly, our results indicate that similarity influences reaching behavior. Key kinematic parameters were influenced by our manipulation of similarity using color. As such, we have replicated the similarity effect of Experiment 1 for additional reaching directions.

Interestingly, the similarity effect again appears to be driven by a particular configuration of the workspace; when the non-target is on the outside of the reaching hand and the target is located on the right the effect is most explicit. In this situation the non-target is located in a position that more easily allows collisions, not necessarily with the hand in

isolation, but rather with the lower arm, which might explain why a bias was detected at all. Perhaps a difference due to the manipulation of non-spatial properties of the non-target is only detectable in situations where a particular level of obstruction is generated by the non-target.

General Discussion

In two experiments, participants reached for and grasped a target that was either presented alone or in the presence of a non-target. Our main manipulation was the similarity of target and non-target. We used color to set the similarity of the target and non-target. Our secondary manipulation was the location of the non-target, which was presented either on the inside or on the outside of the reaching arm. Our aim was to investigate the effects of a non-physical, or non-spatial, feature of the non-target on the avoidance trajectory of the hand around it when it was being guided toward a to-be-picked-up target.

The results indicate that similarity is used to prompt spatial modifications to reaching trajectories. That is, dissimilar targets and non-targets appear to prompt reach trajectories that deviate further away from the non-target than similar non-targets and targets. This stronger avoidance effect seems robust for different reaching directions. In addition, the effect appears to be most pronounced when the non-target is placed on the 'outside' of the reaching arm.

Our results imply that using color to manipulate target-non-target similarity is a way to further manipulate the avoidance responses around non-targets. It is important to note that this effect should not be confused with that caused by a physical property of the non-target, as for the avoidance movement around a physical obstacle the color of that obstacle should be irrelevant. Therefore, our results support the idea that avoidance movements may also be further modified by non-spatial features of the non-target (in addition to very useful spatial features such as its location). This is in line with previous empirical evidence on similarity between target and non-target (Kritikos et al., 2000). These authors found that dissimilarity in size and in orientation of target and distractor caused more interference on reaching trajectories. These authors speculated that their results were indications of a more general principle: 'it is not so much size or orientation that is crucial, but rather whether the non-target is the same as or different from the target' (p. 148, Welsh et al, 1999). Our findings that demonstrate the same effect of similarity, although defined by the non-spatial feature color and in an explicit obstacle avoidance paradigm, seem to subscribe to this.

Our study indicated an opposite direction of the effect of similarity on hand movements to that reported for eye movement studies (Ludwig & Gilchrist, 2003; Mulckhuysen et al., 2009;

Al-Aidroos & Pratt, 2010); indeed, these authors find that when the visual target and the visual distractor are similar that eye trajectories deviate more away, whereas our results show stronger avoidance responses for dissimilar non-targets. One possible explanation for this discrepancy could be that eye movements and hand movements are not governed by a common attentional mechanism, which is one of the two current interpretations for the relation between eye and hand movements (Thompson & Westwood, 2007; Sailer, et al., 2000; Jonikaitis & Deubel, 2011). The other interpretation favors the idea that targets for the eye and the hand are selected by a common mechanism (Song & McPeck, 2009; Neggers & Bekkering, 2000). If that would have been the case, then the departure of our results from the general tendency in eye movement literature that similar non-targets are associated with more deviation, would be quite interesting. This study, however, did not aim to distinguish between the two interpretations. Nevertheless, because the modification of avoidance responses by similarity information is different from the modification of eye movement by the same information, our data seem to point to effector-specific control systems.

Our results indicate a difference in movement trajectories between color similar and dissimilar pairs. The similarity in color between target and non-target is a feature that should not increase or decrease the likelihood of collision and should therefore not affect avoidance movements in that similarity is not a feature that is directly relevant for movement. Avoidance of a collision is still the main drive behind the modification of the spatial path of the reach through the workspace when non-targets are present. However, the avoidance response can be further modified as is evident from our similarity effect. This is based on the results from the configurations in two experiments where the non-target was on the outside of the reaching arm. As stated earlier, we hold that in these configurations the obstruction offered by the non-targets is higher and that the subtle biasing influence of color-defined similarity becomes more readily apparent. Although this statistical interpretation of our data is viable, we speculate that the enhanced influence of 'distracting' features of the non-target, such as its similarity, may lead to the observed biases in the movement trajectories. Simply put, any obstacle that needs to be avoided needs to be noticed first. As such, if different degrees of noticing or attentional capture are assumed, then our results may imply that hand movements veer away differently from similar and dissimilar non-targets because these types of non-targets capture different degrees of attention. Our results indicate that dissimilar non-targets may compete more for attentional resources with the targets than similar non-targets. Following Tipper and colleagues (1997), the dismissal of the irrelevant dissimilar non-targets may then require increased resources which leads to increased spatio-temporal interference as evidenced from the changes in the kinematic parameters of the movement trajectories.

There has been extensive research into the neural substrates required for obstacle avoidance (McIntosh, McClements, Schindler, Cassidy, Birchall, et al., 2004; Schenk, Schindler, McIntosh, & Milner, 2005; Rice, McIntosh, Schindler, Mon-Williams, Démonet, et al., 2006; Schindler, Rice, McIntosh, Rossetti, Vighetto, et al., 2004; Rice, Edwards, Schindler, Punt, McIntosh, et al., 2008). It has been suggested based on this work that automatic avoidance of obstacles is a dorsal stream function. Our results add an interesting new dimension to this statement, since our results suggest that not only 'dorsal stream' features, such as size and orientation, are relevant to obstacle avoidance, but that 'ventral stream' features also play a role. In this case color was the ventral stream feature. Whether there is cross-talk between the two streams in healthy participants (Verhagen, Dijkerman, Grol, & Toni, 2008) or the dorsal stream is capable of processing color to some extent is a question beyond the scope of this paper. Furthermore, in a recent paper, evidence was brought forward that indicated that conscious processing of visual information influenced obstacle avoidance (Hesse, Lane, Aimola, & Schenk, 2012). Taken together with the results of the current study, this casts doubt on the presumed automatic and subconscious nature of this ability. However, further research should investigate more effects of ventral stream features in obstacle avoidance and, if possible, in participants who have impaired processing of said features.

**Chapter 7 – It is the flash which appears, the movement will follow:
Investigating the relation between spatial attention and obstacle
avoidance**

Menger, R., Dijkerman, H. C., & Van der Stigchel, S. (2015). It is the flash which appears, the movement will follow: Investigating the relation between spatial attention and obstacle avoidance. *Psychonomic Bulletin & Review*, 22(5), 1292-1298.

Abstract

Obstacles are represented in the attentional landscape. However, it is currently unclear what the exclusive contribution of attention is to the avoidance response. This is because in earlier obstacle avoidance designs, it was impossible to disentangle an effect of attention from the changing features of the obstacle (e.g., its identity, size, or orientation). Conversely, any feature manipulation could be interpreted as an attentional as well as an obstacle effect on avoidance behavior. We tested the possible tuning of avoidance responses by a spatial cue in two experiments. In both experiments, spatial and nonspatial cues were separately given as go cues for an obstacle avoidance task. Participants had to reach past two obstacles in Experiment 1, and past a single obstacle in Experiment 2. We found that when the right obstacle was flashed, participants veered away more and produced more-variable trajectories over trials than in conditions with nonspatial and left spatial cues, regardless of the presence or absence of another obstacle. Therefore, we concluded that the tuning of avoidance responses can be influenced by spatial cues. Moreover, we speculated that a flashed obstacle receives more attentional weighting in the attentional landscape and prompts a stronger repulsion away from the obstacle.

According to Baldauf and Deubel (2010), the planning of a complex movement entails the creation of a so-called “attentional landscape” that weights the attentional distribution across all action-relevant locations in the visual layout of the workspace. In addition to locations, the weighting is sensitive to motor-related aspects of the task, such as the required accuracy, with more weight being attributed to a location that requires more accuracy. Movements are then executed toward the (highest) peak in the landscape and away from low(er) activity regions or valleys. Cisek (2007) has further argued that the peaks in attentional landscapes instantiated by action-relevant objects are simultaneously parallel motor plans for interacting with objects. For instance, Wood et al. (2011) have shown that visual salience dominates early visuomotor competition in reaching behavior. These researchers manipulated the salience of potential targets using varying degrees of luminance and found that participants directed their early reach trajectories toward more luminant—and therefore salient—targets in an array of multiple potential targets.

Other experiments have shown that the capture of attention by a nontarget can change the motor responses to target objects (Chang & Abrams, 2004; Tipper, Howard, & Jackson, 1997; Welsh, 2011; Welsh & Elliott, 2004; Welsh, Elliott, & Weeks, 1999). However, these nontarget objects were not obstructing, and sometimes were not even physical objects at all. So, although these studies may shed light on the effect of distracting stimuli on motor behavior, we cannot be certain that the results for attentional manipulations in obstacle avoidance would be the same. Indeed, the changes in motor responses evoked by salient distractors and visual cues are thought to be due to the biased resolution of competition between a target and distractor during action selection (i.e., which object to reach for), whereas obstacle features (e.g., location, size) must be incorporated in the motor plan that brings the hand and arm around the obstacle and toward the target. After all, in obstacle avoidance, the goal is *not* to interact with the obstacle. This means that a separate motor plan to interact with an obstacle is redundant (once the target is identified). Instead, the detected obstacle information should be incorporated into the motor plan toward the target. This means that an obstacle does not act as a distinct attractor of motor activity, but rather as a *repeller* of motor activity.

Given that obstacles are represented in the attentional landscape, it remains to be seen what the exclusive contribution of attention itself is to the avoidance response. In earlier experiments, attentional manipulations had co-occurred with changing features of the obstacle (e.g., its color similarity to the target; Menger, Dijkerman, & Van der Stigchel, 2013), or feature manipulations of the obstacle co-occurred with attentional changes. Now, for the first time, the present experiments offer the opportunity to study the effect of attention without changing the spatial features of the to-be-avoided obstacles.

In the present experiments, we studied the relation between attentional capture and obstacle avoidance. As such, we had participants perform reaches for and evasions of physical objects. Furthermore, we manipulated attentional capture by flashing LEDs embedded within the obstacles as a cue for movement onset. We expected that the tuning of the avoidance response could be influenced by a spatial cue. The spatial cues were given by flashing two LEDs on a single obstacle on one side of the workspace. We compared this to a baseline cue in which an LED was flashed on both obstacles present in the workspace. We confirmed the nonspatial nature of this cue in Experiment 2 by comparing it with a no-flash condition. Moreover, we hypothesized that the capture of spatial attention immediately prior to obstacle avoidance would shift the trajectories farther away from the obstacles. This directionality of repulsion—for example, a right-obstacle flash leading to more deviation away from the right obstacle—was checked in Experiment 2 with a single-obstacle setup.

Method

Participants

Ten participants (seven women, three men) volunteered via informed consent for Experiment 1, and another ten (six women, four men) for Experiment 2. They participated in this study in exchange for curricular credit. All participants were right-handed, had normal or corrected-to-normal vision, and were naïve as to the purpose of the study. The faculty's institutional review board under the Medical Research Act issued a formal written waiver that this research project did not require approval from a Medical Ethics Review Committee.

The sample size was determined using power analysis software, namely G*Power (Franz Paul, Universität Kiel, Germany). We obtained a partial eta-squared (η_p^2) value from an earlier study (Menger, Van der Stigchel, & Dijkerman, 2012). The effect size, f , was determined to be .57. This related to the difference in deviations of the hand movements between the target-with-similar-obstacle condition and the target-with-dissimilar-obstacle condition (i.e., a main effect of target-distractor similarity on the deviation of the hand from the obstacle). The effect size of .57 would be detected with a precision $\alpha = .05$ (two-sided) and with $\beta = .05$ (power = 95%).

Apparatus and stimuli

Participants were seated behind a table with an unmarked workspace (450 × 300 mm). Within the workspace, four elements were present: the target object, two nontarget objects, and the starting button (see also Fig. 1). The target object stood on a trigger that responded when the target was removed. Tall, cylindrical objects (5.5 cm × 15 cm) were used as the targets and

nontargets. The target was placed at 400 mm depth and 0 mm width with reference to the starting location, whereas the nontargets were placed at 200 mm depth and at ± 100 mm width. Two red-colored LEDs were embedded (near the top and the bottom) within the left and right nontargets and faced toward the participant. The LEDs were programmed to emit bursts of light for 30 ms. The movement kinematics were recorded using MiniBird magnetic markers (Ascension) at a sampling rate of 100 Hz over 3 s. The markers were attached to the tips of the participants' index fingers and thumbs (see also Mon-Williams & McIntosh, 2000). Furthermore, by securing the cables to the participants' arms and hands, great care was taken to avoid interference by the markers themselves with the movements.

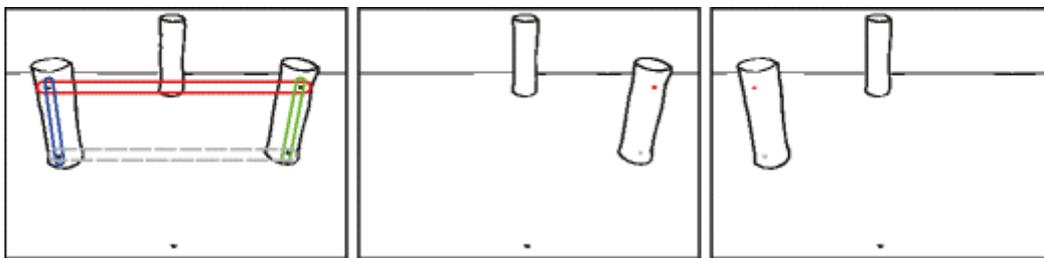


Fig. 1. View of the layout of the experimental workspaces from a participant's perspective. The left panel shows the dual-obstacle setup, whereas the middle and right panels show the two single-obstacle setups. In the left panel, colored ovals show the configurations of LED stimulation: "top" stimulation, "right" stimulation (spatial), "left" stimulation (spatial), and "bottom" stimulation (catch trials). The starting location of the hand (black cross) was at (0, 0), and the front point (for the participant) of the target was at (0, 400). The left obstacle's inside point was located at (-100, 200), and the right obstacle's inside point was located at (100, 200).

Design

For each condition in Experiment 1, two LEDs were always flashed simultaneously. The location of the LED flashes was varied across four conditions: top, left, right, and bottom (see also Fig. 1). Trials in the bottom condition served as no-go catch trials (20%), and those in the other conditions served as go trials. There was no difference in the required responses in these go conditions.

Experiment 1 consisted of 108 trials: 30 repetitions of each experimental condition (top, left, and right) and 18 catch trials. The trials were randomized such that the first half of the repetitions of each condition took place in the first half of Experiment 1, and the second half of the repetitions in the latter half of Experiment 1. The experimental trials were preceded by 16 practice trials (four repetitions of each condition).

In the additional Experiment 2, three conditions were tested in three batches: top, bottom, and no LED stimulation, in dual, single-left, and single-right nontarget setups (see Fig. 1). A sound was played as a go cue, while the location of the simultaneous flash informed the participant of the required response: Top flashes and no flashes counted as the go trials, whereas bottom flashes counted as no-go (catch) trials. All other details were identical to those of Experiment 1.

Procedure

Participants were mid-sagittally aligned with the center of the workspace. They were instructed to rest their right thumb and index finger on the starting button in a closed pincer posture until task execution was required. The experiments were self-paced: Once participants had pushed the starting button, a random interval between 800 and 1,200 ms elapsed before any LED(s) would flash. Depending on the condition, the flash(es) could indicate the go signal or the no-go signal. When a no-go condition was presented, the participants were not allowed to move, and after a short delay (3 s) they were allowed to proceed with the next trial. When a go condition was presented, participants were instructed to smoothly and rapidly reach for the target object with their right hand. Their goal was to lift the target from the table and place it back with the same hand. We further instructed participants to grasp the middle of the target object with their thumb and index finger.

Dependent measures and analysis

All analyses on the reaching trajectories were performed on the x , y , and z data from the index finger marker, except for grip aperture, which was calculated from the data from both markers. The raw 3-D data were filtered using a dual-pass low-bandwidth Butterworth filter (2nd order, 20-Hz cutoff) and were normalized using a cubic spline interpolation into 100 samples (see also Mon-Williams, Tresilian, Coppard, & Carson, 2001; Tresilian, Mon-Williams, Coppard, & Carson, 2005). Velocities were calculated in each cardinal dimension and were used to define the beginning of the movement (Schot, Brenner, & Smeets, 2010). Here, the movement onset was determined when the marker position was sufficiently close (3 cm) to the starting button and the velocity exceeded 5 mm/ms for at least 50 ms.

Trials were rejected when participants started to move before the go signal or if participants moved during no-go trials. One participant was rejected from further analysis in Experiment 1 because he exceeded our no-go failure criterion of 67% correct no-go responses.

Using the position, velocity, and stimulus presentation data, we calculated the following measures: reaction time (time between the flash and movement onset), movement time (time

from movement onset until movement offset), grip aperture (3-D distance between the thumb and index finger markers), peak velocity (maximum velocity attained during a movement), time to peak velocity (time from movement onset until the peak velocity was reached), position at passing (distance between the location of the index finger and the nontarget at the moment that the hand passed the vertical position of the middle of the nontarget), and error at passing (the within-subjects error for deviations at passing across repetitions for a condition).

Results

We performed an initial repeated measures analysis of variance (ANOVA) on the data from Experiment 1 with an extra factor Block (two levels: first and second) and the within-subjects factor Flash Location (three levels: top, right, left). Our analysis showed no significant difference between reaches performed in the first versus the second half of Experiment 1 for all dependent measures (all p 's > .05). Therefore, the split-half data were collapsed.

Position at passing

The results of Experiment 1 are shown in Figure 2. We confirmed that position at passing was significantly affected by the locations of the flashes, $F(2, 18) = 5.814$, $p = .015$, $\eta_p^2 = .45$. The means of the position at passing for the three locations of the flashes were 27.4 mm (± 0.9) for the top flash condition, 20.4 mm (± 4.9) for the right flash condition, and 28.6 mm (± 4.3) for the left flash condition. These data are also displayed in Figure 3. Panel A which shows that when flashes were presented on the right nontarget, participants moved their hand the most to the left, and for flashes on the left, the participants moved their hand the most to the right. Therefore, the participants deviated away from the flashed locations. Further Bonferroni-corrected comparisons revealed that the horizontal position of the hand after right flashes only differed significantly from that under left flashes, $t(9) = 3.88$, $p = .006$, and not from top flashes, $p > .05$.

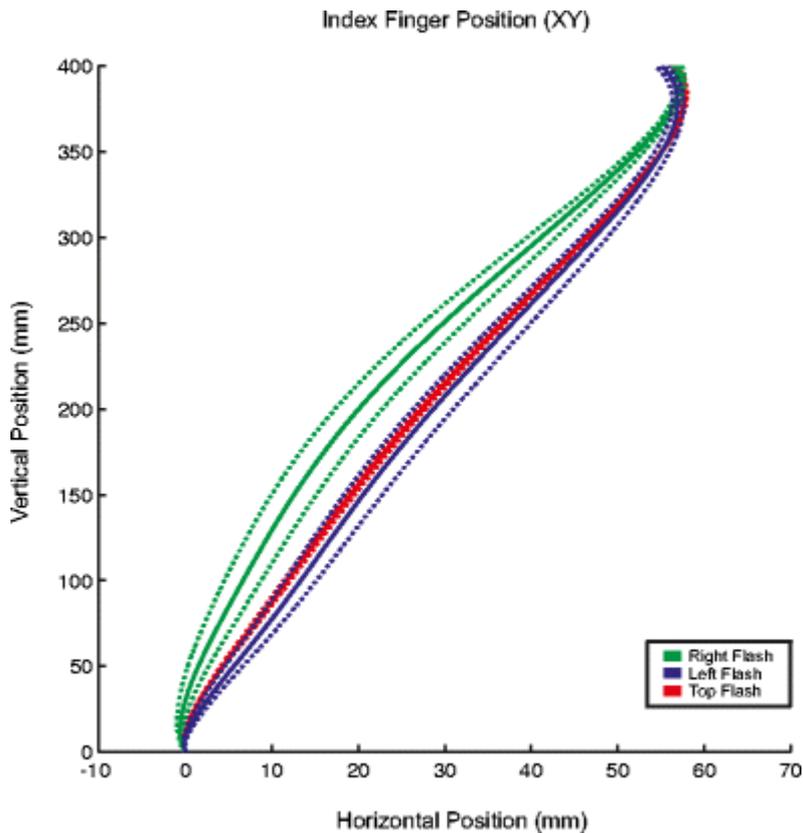


Fig. 2. Mean trajectories of the index finger for Experiment 1. Mean movement trajectories were calculated across participants in the x, y plane. *Solid lines* represent the mean trajectories for reaches, whereas *dotted lines* represent the between-subjects standard errors of the means, which have been corrected for repeated measures by using the Cousineau (2005) method. Line is used to depict the different conditions, in which the left, right, or top obstacle LEDs were flashed. Please note that the endpoint of the reach is near the edge of the target object, which means that half the width of the object and the whole width of the finger “inflate” this endpoint.

In Experiment 2, we found a significant interaction between batch (three levels: dual obstacles, single left obstacles, and single right obstacle) and flash (two levels: on and off), $F(2, 18) = 4.963, p = .019, \eta_p^2 = .357$. Trajectory data from these conditions are displayed in panels A and B of Fig. 4. Panel A shows data from the dual-nontarget setup, whereas panel B shows trajectory data from the single-nontarget setups (on either the left or the right of the workspace). Further Bonferroni-corrected testing revealed that this effect was driven by a significant difference between the flashed and not-flashed right nontarget conditions, $t(9) = 2.49, p = .034$. Therefore, participants deviated more away from a right nontarget when it was flashed. Moreover, a flash on the left of the workspace or a flash not limited to a single location (i.e., top) did not affect the reaching trajectories. This was a replication of the results from Experiment 1, as well as confirmation of the nonspatial nature of the top flash cue in Experiment 1.

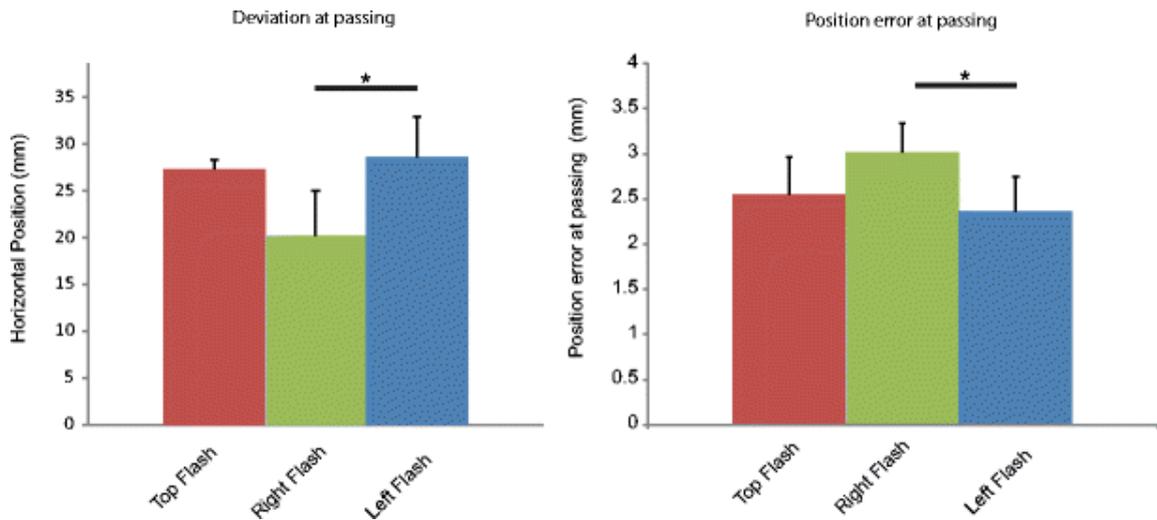


Fig. 3. Detailed main effects in Experiment 1. Bar charts show the mean deviation at passing and the mean position error at passing. Error bars show the standard errors of the means. Asterisks denote significant paired t tests (Bonferroni-corrected). Line is used to depict conditions in which the left, right, or top obstacle LEDs were flashed.

Position error at passing

The data of Experiment 1 indicated an effect of flash location on the within-condition variance for horizontal position over trials, or position error at passing: $F(2, 18) = 13.75, p < .001, \eta_p^2 = .26$. The mean position errors at passing were $2.6 (\pm 0.4)$ for the top flash condition, $3.0 (\pm 0.3)$ for the right flash condition, and $2.4 (\pm 0.4)$ for the left flash condition, which are also displayed Figure 3. Panel B results show that the mean over trial errors was highest when flashes were on the right, whereas it was lowest when the flashes were presented on the left. The intermediate score was for the top flashes. A tandem of Bonferroni-corrected paired t tests revealed that the mean error score was higher for the right than for the left, $t(9) = 2.97, p < .05$. This implies that participants made more variable movements in the condition in which the most obstructing object in the workspace was flashed.

We did not find any effect of flash location on position errors at passing in Experiment 2.

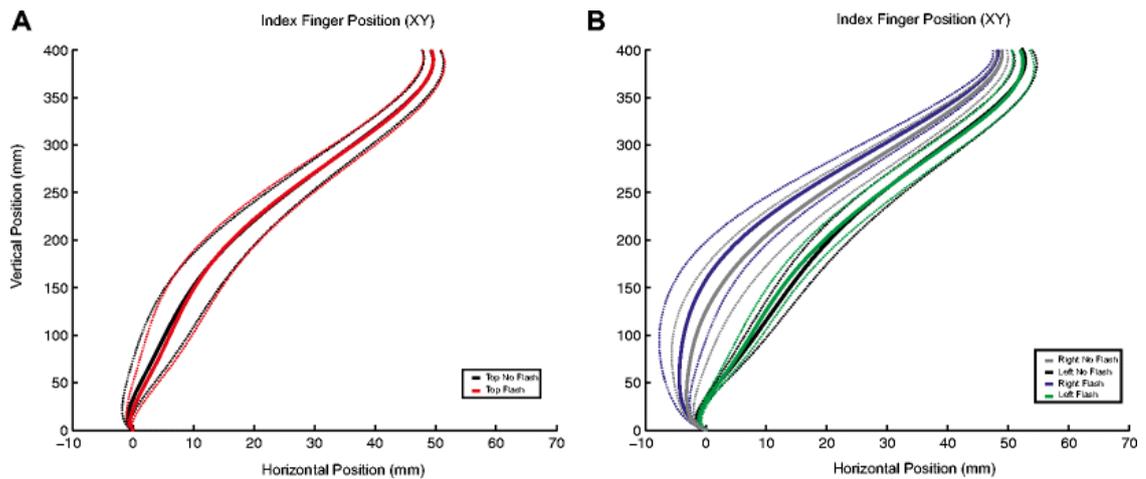


Fig. 4. Mean trajectories of the index finger for Experiment 2. Mean movement trajectories were calculated across participants in the x, y plane. *Solid lines* represent the mean trajectories for reaches, whereas *dotted lines* represent the between-subjects standard errors of the means, which have been corrected for repeated measures by using the Cousineau (2005) method. Panel A shows reaches performed with two obstacles, whereas panel B shows reaches performed with a single obstacle, at either the left or the right of the workspace. In panel A, the trajectories for conditions in which no LEDs or both top obstacle LEDs were flashed are depicted. Panel B shows the results when the right or left top obstacle LEDs were flashed, as well as conditions in which there was no flash with an obstacle on the right or the left.

Reaction time, movement time, peak velocity

We observed no main effect of flash location on the reaction times, movement times, or peak velocities in either experiment. The fact that reaction times did not differentiate the flash location conditions was expected, because the flashes were used as a general go signal and their individual natures did not necessitate unique response mappings. In addition, participants did not speed up their movements: Peak velocities, times to peak velocity, and movement times were invariant. A separate analysis showed a trend, $p = .08$, toward significance for the effect of flash location on 2-D trajectory lengths (determined by numerical integration of the average spline curve of each condition for each participant). Taken together, this shows that participants moved with the same peak velocity and movement time along curves that were not different in length.

Grip aperture

We found no effect of flash location on the grip apertures in either experiment. This means that participants did not manipulate the opening between their fingers as part of their avoidance response to the different locations of the flashes coming from the nontargets.

Discussion

We investigated whether a spatial cue can influence obstacle avoidance. In our experiments, visual cues were go cues for an obstacle avoidance task: Participants had to reach for and grasp a target object while avoiding one or two obstacles. We showed that the avoidance response is tuned by a spatial cue. Specifically, the differences seemed primarily driven by the location of the spatial cue: Only when the right obstacle was flashed (a right-object spatial cue) did participants' avoidance behavior differ from that to the nonspatial cues. Given that the physical objects were equally obstructing in all conditions, the only thing that could have led to the occurrence of larger avoidance responses was the presence of spatial cues. So, we have now demonstrated the exclusive effect of attention on obstacle avoidance. However, this effect is limited to obstacles that are already more obstructing, because the left-obstacle spatial cue did not have an effect on avoidance movements. The asymmetric avoidance responses observed here, but also previously (Chapman & Goodale, 2008; Dean & Bruwer, 1994; Menger et al., 2012, Menger, Van der Stigchel, & Dijkerman, 2013; Mon-Williams et al., 2001), occur because only the right obstacle interferes more with the transport of the lower limb as the arm extends toward the target object (Menger et al., 2012). Therefore, the hand has to take a more curved trajectory around it. This study further serves to demonstrate that, in terms of the attentional landscape, the spatial location of a more-obstructing object is likely associated with greater activity. We speculate that the subsequent tuning of this activity by a spatial cue is only by virtue of its having a certain level of activity already.

Chapman, Gallivan, Culham, and Goodale (2011) showed that when obstacles interfere with grasp planning, there is top-down modulation in the early visual cortex. Specifically, these authors demonstrated that objects that physically interfere with to-be-performed actions are detected by the contralateral (with respect to the reaching hand) posterior intraparietal sulcus (IPS), which then suppresses the neural representation in early visual cortex areas that is associated with these objects. In addition, Chapman and colleagues (2011) showed that the modulation of visuomotor planning areas by the IPS is dependent on the degree of interference or obstruction afforded by the object. This means that the more the object obstructed movements, the more activity was registered in IPS. In broad strokes, Chapman and colleagues (2011) defined obstacle avoidance along the following lines: Positive neural activity is evoked by physical objects in the visual cortex, and this activity represents a retinotopic map of the workspace. This map can be pictured as a landscape with hills and valleys of activity, both noting locations that are relevant for actions. Movements are drawn toward high-activity regions (hills) in this landscape and are repulsed from low-activity regions (valleys). So,

obstacles first will give rise to activity in the landscape and will attract attention. Only when obstacles are tagged by the IPS as interfering with a movement to the target will the activity (hill) be suppressed to a relatively low level (valley). The function of the IPS in this case appears to be to reduce the activity of peaks in a visual attentional landscape, to ultimately have the hand move away from certain objects while it travels toward the goal object.

In our experiments, we offered a spatial cue by flashing LEDs on obstacles. This led to the capture of attention at the obstacle location. This should have served to enhance the activity of peaks in the visual attention landscape associated with the obstacles. Possibly, this enhancement could lead to the obstacle becoming more of an obstacle as measured in motor responses, because the IPS would have already tagged the object as an obstacle at that location. In other words, the obstacle is “marked” by the IPS as a repeller, and attentional capture at the location of the obstacle causes the avoidance system to treat the obstacle as an even stronger repeller.

One caveat is in order, though: In our experiments there was much trial-by-trial consistency in the locations of the targets and nontargets, and this may have led to a static and prebiased attentional landscape (which might be an unfair reflection of real-life dynamic attentional landscapes). Unlike Chapman et al., (2011), we did not use long delays between revealing what objects were obstacles and what were targets, which allowed the landscape to start out neutral and change dynamically over time. The static nature of the landscape and the feedforward nature of motor commands might further reconcile our results with those of most other studies that have used salient distractors, which have shown that distractors can attract trajectories rather than repel them. That is, here it is likely that the extensive experience that participants had with the obstacle setup and the to-be-performed movement ensured that the incoming visual transient from the LED flash was never processed as a target, and therefore was never distracting. This sort of filtering of the incoming visual transient has been described previously in electrophysiological studies (e.g., Ikeda & Hikosaka, 2003).

So, although our results may partly be explained by the experience that participants had with the setup, it is still interesting to see that flashing LEDs can change the weighting of the attentional landscape, as observed through stronger avoidance responses. To wit, a nontarget may prime an additional activation in the attentional landscape that competes with the activation for the target. Top-down processes operate on that competition by “tagging” the obstacle response code. Whether the IPS tag attenuates the obstacle activation to a low hill or valley in the attentional landscape or switches on a different motor-programming module (“avoid” rather than “move to”) is beyond the scope of this article. However, we speculate that

our attentional manipulation may have modulated the gain of the IPS response on a trial-by-trial basis; that is, similarly to how Chapman et al. (2011) demonstrated increased IPS activity with increased obstruction, we speculate that attentional capture leads to a more obstructing obstacle, in terms of IPS activity.

To recap, we have found evidence for the effect of stimulation on obstacle avoidance movements. This effect seems to be driven mainly by a spatial cue on a location that obstructs the movement of the arm as it extends toward the target object. We consider that the cue may have changed the attentional distribution across the action-relevant locations in the workspace. Because peaks in the attentional landscape are thought to be intrinsically coupled with motor plans, we observed an effect on hand movements. Specifically, we found that a flash on the more-obstructing object served as a stronger repeller of the heading of the hand.

Chapter 8 – When Two Worlds Collide: the Role of PeriPersonal Space in Obstacle Avoidance

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Abstract

Multisensory coding of the space surrounding our body, the peripersonal space (PpS), is crucial for motor control. Recently, it has been proposed that an important function of PpS coding is that it allows anticipation of the tactile consequences of contact with a nearby object. Indeed, performing *goal-directed* actions (i.e. pointing and grasping) induces a continuous remapping of PpS as a function of on-line sensorimotor requirements. Here, we investigated whether remapping of the PpS can be induced by obstacles, e.g. objects that are not the target of the grasping movement. Our aim was to show that the PpS also calculates the tactile results of potential collisions. In the current experiment, we used a cross-modal obstacle avoidance paradigm, in which participants reached past an obstacle to grasp a second object. Participants indicated the location of tactile targets delivered to the hand during the grasping movement, while a visual cue was sometimes presented simultaneously on the to-be-avoided object. The tactile and visual stimulation was triggered when the reaching hand passed a position that was drawn randomly from a continuous set of predetermined locations (between 0 and 200 mm depth at 5 mm intervals). We observed differences in visuotactile interaction during obstacle avoidance dependent on the location of the stimulation trigger: visual interference was enhanced for tactile stimulation that occurred when the hand was near the to-be-avoided object. We show that to-be-avoided obstacles, which are relevant for action but are not to-be-interacted with (as the terminus of an action), automatically evoke the tactile consequences of interaction. This shows that PpS remapping extends to obstacle avoidance and that this process is flexible. The PpS therefore not only calculates the tactile results of actions but also of potential collisions.

In the course of each day, we perform many obstacle avoidance movements. To illustrate, a typical human may drive to work in his or her car, while braking and steering to avoid other cars and other objects on the road. Next, he or she may continue to walk to the office, while avoiding garbage bins, other people, and lantern posts etc. Finally, he or she may sit down behind a desk to manage the analog and digital desktop, while not tipping over a well-deserved cup of coffee or tea. The ease and expertise with which our typical humans perform these basic avoidance behaviors betray the automatic and unconscious nature of what must be a very complex skill. Indeed, to perform avoidance actions nearly all available sources of information -- visual, proprioceptive, tactile, and audio- must be combined dynamically and in real-time. The study of this type of obstacle avoidance behavior can reveal interesting interactions between these different streams of information. To be more specific, obstacle avoidance can shed light on the information the brain processes in order to program complex movements. That is, the lessons we can learn from obstacle avoidance may allow for a more accurate conceptual understanding of visuomotor control.

There are a number of studies that show effects of obstacle features on the spatiotemporal characteristics of avoidance movements (Chapman & Goodale, 2008, 2010;; de Haan, Van der Stigchel, Nijens, & Dijkerman, 2014; Menger, Dijkerman, & Stigchel, 2013, 2014; Menger, Van der Stigchel, & Dijkerman, 2012, 2013; ; Mon-Williams & McIntosh, 2000; Mon-Williams, Tresilian, Coppard, & Carson, 2001; Rice et al., 2006;; Tresilian, 1998). The response to obstacle locations has been described as subtle and precise (Mon-Williams et al., 2001), meaning that each individual obstacle location gives rise to a unique avoidance response (for a review, see Menger, Dijkerman, Van der Stigchel (*submitted*)). Because most of the studies into obstacle avoidance have focused on the processing of visual information and its incorporation into a motor plan, what is lacking from our current understanding about obstacle avoidance is how different sources of not-purely visual information interact in order to program and control avoidance movements. In other words, are there crossmodal interactions between vision and the tactile sense during obstacle avoidance? Moreover, what can those crossmodal interactions say about the role obstacles play in the coding of peripersonal space, i.e. the sector of space closely surrounding one's body? Here, therefore, we are interested in the crossmodal interactions that do or do not occur during obstacle avoidance in order to better understand how peripersonal space may facilitate avoidance behavior.

It is likely that obstacles will activate multisensory networks in the brain because obstacles are -almost by definition- near to the body and, as such, within the peripersonal space (Rizzolatti, Fadiga, Fogassi, Gallese, 1997) of individuals. Bimodal neurons in premotor and parietal areas responding both to tactile stimuli on the body as well as to visual stimuli near the

body (Duhamel, Colby, Goldberg, 1998; Graziano, Hu, Gross, 1997; Rizzolatti, Scandalora, Matelli, & Gentilucci, 1981)¹ will likely also respond to obstacles. The particular processing of the peripersonal space serves two hypothesized functions (Rizzolatti et al. 1997; Brozzoli, Ehrsson, & Farne, 2014) which are both in line with the function of obstacle avoidance: to successfully guide the hand to a goal object while avoiding non-goal objects, i.e. through efficient voluntary motor control, and automatic defensive actions.

To be more specific, the first hypothesized function of peripersonal space is the planning of movements towards items and individuals in the space closely surrounding us and predicting the consequences of these movements. These predictions are crucial in order to effectively interact with them. This assumption is based on the research by Brozzoli et al. (2010) who showed that when grasping objects, a flash on one side of a target object improved processing of tactile stimuli on the finger that would touch that part of the object at the end of the grasping movement. This effect was particularly clear during execution of the grasping movement. These findings suggest a dynamic link between visual information on a nearby object and tactile processing on the approaching hand. Indeed, performing goal-directed grasping movements induced a continuous remapping of peripersonal space as a function of on-line sensorimotor requirements (Brozzoli, Pavani, Urquizar, Cardinali, & Farne 2009; Brozzoli et al. 2010). Recently, it has been proposed that peripersonal coding also allows anticipation of tactile consequences of contact with a nearby object (Kandula, Hofman, & Dijkerman, 2015). Further behavioral evidence comes from demonstrations of visuotactile interactions when objects are near the hand (Spence, Pavani, Maravita, & Holmes, 2004; Pavani & Castiello 2004; Brozzoli et al. 2009). These behavioral claims are supported by an fMRI study that showed that parietal visuo-tactile cortical areas are activated when objects are near specific parts of a human body (Brozzoli, Gentile, Petkova, & Ehrsson 2011). Taken together, there is ample support for the assumption that peripersonal space is involved in the voluntary control of (more or less dynamic) action.

Second, objects and people in our close surroundings may also approach us and, as such, may warrant a defensive movement. Facilitation of detection of these objects or people and initiating defensive postures or actions is thought to be another function of peripersonal space (Rizzolatti et al. 1997; Brozzoli et al., 2014). Evidence for a defensive mechanism comes from

¹ The neural areas associated with the peripersonal space have been defined in the monkey brain, e.g. the predictive consequences of actions were shown with single cell recording in parietal visuo-tactile neurons that discharged for objects near specific parts of a monkey's body (Ishida et al. '10).

monkey studies by Cooke and Graziano (e.g. Cooke & Graziano, 2004; Graziano & Cooke, 2006) who found that the monkeys executed defensive movements like squinting or blocking when the regions that corresponded with looming or nearby objects were artificially stimulated.

Visuotactile interaction has been demonstrated during grasping actions (see Brozzoli et al. 2009; 2010). This means that some form of contact –either the subject will contact the object or the object will contact the subject- with the object was expected. There are, however, situations where objects are relevant for to-be-performed actions but not to-be-contacted such as in obstacle avoidance. Therefore, here we were interested to study whether peripersonal space remapping could be induced by objects that are not a target of the action, but that are nevertheless relevant when performing the action. This way, we can tell whether predicting the tactile consequences of action includes automatically predicting contact and collisions with all relevant objects in the peripersonal space, even if they are not the terminus of action.

In order to test this, we used a cross-modal obstacle avoidance paradigm, in which participants reached passed an obstacle to grasp a second object. Participants indicated the location of tactile targets delivered to the hand during the movement, while a visual distractor was sometimes presented on a to-be-avoided object. Tactile and visual stimulation was triggered when the reaching hand passed a position drawn randomly from a set of predetermined locations. As reviewed by Spence, Pavani, Maravita, & Holmes (2004) there already have been several studies that show that the crossmodal congruency task can provide an experimental index of common spatial location across different sensory modalities. That is, the cross-modal congruency task has been used in a variety of experimental settings to determine the multisensory representation of visuotactile space in normal participants. As such, this paradigm is suited for investigating the contributions of visual, tactile, and proprioceptive inputs to the multisensory representation of peripersonal space.

Methods

Participants

Ten participants (5 men and 5 women) volunteered for this study in exchange for curricular credit and gave their informed consent. All participants were right-handed and had normal or corrected-to-normal visual acuity, and were naïve as to the purpose of the experiment. Our faculty's institutional review board under the Medical Research Act ruled that this experiment

did not need approval from a Medical Ethics Review Committee. The experiment was conducted according to the guidelines provided by the Helsinki Declaration (WMA, 2013).

Sample size was determined using power analysis software, viz. G*Power (Franz Paul, Universität Kiel, Germany). We obtained a partial η^2 from an earlier study (Menger et al. 2012). The effect size, f , was determined to be .57. This related to the difference in deviation of the hand movement between the target with similar obstacle condition and the target with dissimilar obstacle condition (i.e. a main effect of target-distractor similarity on the deviation of the hand from the obstacle). The effect size of .57 will be detected with a precision $\alpha = .05$ (two-sided) and with $\beta = .05$ (power = 95%). We should therefore be able to detect any effect on trajectory with this sample size.

Materials and Apparatus

Participants were tested individually in a quiet dimly illuminated room. They were seated at a white table with two embedded buttons; one start-button, located near the participant, and one target-button located at a reachable depth of 400 mm at 0 mm width, respective to the midline. Participants were midsagittally aligned with the midline of the workspace. Hollow plastic cylinders (50 mm and 150 mm height x 50 mm diameter) served as target object and as non-target object. The tall object was the non-target, while the short object functioned as target. The target object was made shorter to prevent problems with occlusion of the infrared markers. The target object was weighted down with sand to ensure participant's responses were analogue to our earlier experiments with wooden objects. The target object was placed on the target button, while the non-target was always placed at 200 mm depth and 100 mm width to the right of the midline (from the participant's perspective). The target button would respond to the object being lifted from it and triggering it would signify the end of a trial. Two red-colored LEDs were embedded (near the top and the bottom) within the non-target which were facing toward the participant. The LEDs were programmed to emit bursts of light for 30 ms. See Fig. 1 for a representation of the experimental setup.

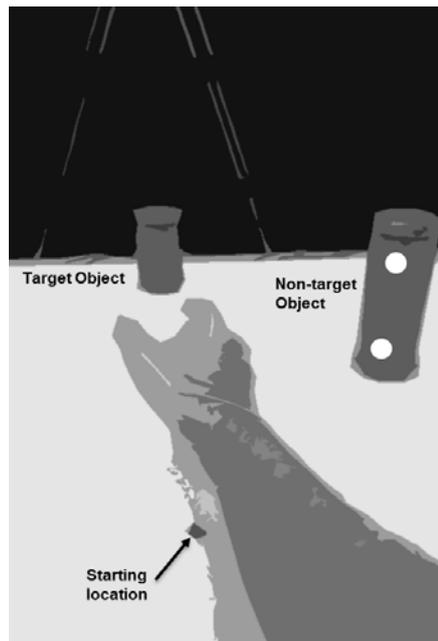


Fig. 1. Stylized representation of the experimental setup, showing the target object, the non-target object (with white circles emphasizing the LED locations), the starting position and the experimenter's hand.

The tactile stimulation was achieved by use of vibro-tactile motors that presented 180 Hz vibrations for a period of 100 ms to either the index finger or the thumb of the 'acting' hand, that is, stimulation took place during task execution. The motors were attached to the middle of the most proximal digit of both fingers. Participants were asked to report the location they felt the tactile stimulus by pressing one of two buttons on the response box with their non-dominant hand: the left button for the thumb stimulation and the right button for the index finger stimulation.

Movement kinematics were recorded using 3D Investigator™ Motion Capture System (Northern Digital, Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. The markers were attached to the tips of the participants' index fingers and thumbs (see also Mon-Williams & McIntosh, 2000) in such a way as to minimize occlusion by objects. Furthermore, by securing the cables to the participants' arms and hands, great care was taken to avoid interference by the markers itself on the movements. A custom built microcontroller interfaced with the motion capture system and a stimulus computer to allow for real-time integration of kinematic data into stimulus presentation. This setup was made so that we could present LED stimulation during movement when a certain location was reached. In short, we configured a set of virtual tripwires that automatically and quickly produced stimulation based on marker location. If a tripwire (defined in space as a 2D plane) was triggered then stimulation would occur within 5 ms.

Design

We used a continuous design, where 40 different locations between the starting location and the non-target object's midpoint acted as 'tripwires' for stimulation. Tactile stimuli could be presented alone or together with a simultaneous visual stimulus on the non-target object. The presentation of the visuotactile stimuli was considered as congruent when the tactile stimulus was on the index finger and incongruent if the tactile stimulus was presented on the thumb, because the visual stimulus was always on the non-target in the right visual field to the right of the reaching arm. Similarly, the tactile stimuli were considered as congruent when presented to the index finger and incongruent when presented to the thumb, because the non-target was always located to the right of the reaching hand. Furthermore, a catch-trial condition was included, where participants never received tactile stimulation during task execution. This was to ensure that participants did not simply wait for the stimulation to occur in order to perform better on the tactile discrimination task. The catch-trials were presented 16 times (10%). The conditions in our design are therefore: *tactile congruent*, *tactile incongruent*, *visuotactile congruent*, *visuotactile incongruent* and *catch*. The total amount of trials therefore numbered $40 \times 4 + 16 = 176$. Five repetitions of each condition were presented as practice trials prior to the experiment.

Procedure

Participants had to reach-to-grasp objects while avoiding an obstacle. During this action unimodal or multimodal stimuli could be delivered, tactile or visuotactile stimuli respectively. They were instructed to have their right thumb and index finger on the starting button in a closed pincer posture until task execution was required. The experiment was self-paced: once participants pushed the starting button a warning signal would alert them to the start of the trial and after a random interval between 800-1200 ms a different auditory signal would prompt them to execute their task. The task was twofold: perform a reach to grasp the target object in order to lift it, while also reporting -via a response box- the location of a tactile stimulus on their acting hand. We further instructed the participants to grasp the middle of the target object with their thumb and index finger and react as quickly as possible to the tactile stimulation while also smoothly and quickly reaching for the target object.

Analysis

We gathered data on measures of response interference in the tactile discrimination task and in the obstacle avoidance task. Therefore, we looked at the accuracy and speed of tactile

discrimination responses, and at parameters of the avoidance trajectories which might show interference.

For data from the former category, the tactile discrimination data, we analyzed %error of responses (number of incorrect responses), absolute reaction time (time between stimulus presentation and response box button press) and the Crossmodal Congruency Effect (CCE; the difference scores between reaction times in congruent and incongruent conditions). Regarding reaction times (RTs), we maintained the following criteria: any RTs below 150 ms were considered anticipations and were excluded from data analyses. Additionally, RTs over 500 ms were considered out-of-bounds. Less than 5% of the trials were removed using these criteria.

Because of the continuous design we were able to calculate the slope between space (the locations of the tripwires) and RTs as well as CCEs. We performed Repeated Measures Analyses of Variance (RM ANOVA) on these slopes and %Error, with within-subjects factors *Modality* (2 levels: tactile, visuotactile) and *Validity* (2 levels: congruent, incongruent). CCE slopes were analyzed with a Paired t-test on the effect of *Modality* (tactile, visuotactile).

For data from the second category, the obstacle avoidance data, we looked at Peak velocity (the maximum velocity attained during movement), Movement time (the time from movement onset until the end of the reach-to-grasp movement), Deviation at passing (distance between the location of the index finger and the edge of the non-target at the moment the hand passed the vertical position of the middle of the non-target), and Error at passing (the standard error of the mean calculated for the deviation at passing measure across all the repetitions of a condition by a particular participant, i.e. the less error at passing, the less stereotypical a movement). We performed Repeated Measures Analyses of Variance (RM ANOVA) on these measures, with within-subjects factors *Modality* (2 levels: tactile, visuotactile) and *Validity* (2 levels: congruent, incongruent).

All kinematic analyses were performed on the x, y, and z data from the index finger marker. The raw trajectory data of each trial was filtered by using a dual low-pass second-order Butterworth filter with a cut-off frequency of 20 Hz (see also: Mon-Williams et al. 2001; Tresilian et al. 2005). The filtered trajectory data was then normalized using a cubic spline interpolation into 100 samples (see also: Smeets and Brenner 1995; Tresilian, Mon-Williams, Coppard, & Carson, 2005).

Results

%Error

A main effect was found for validity, $F(1, 9) = 24.5$, $p < .001$, $partial \eta^2 = .73$, on the amount of errors participants made in the tactile discrimination task. Figure 2 shows the percentage of errors made in tactile discrimination judgments.

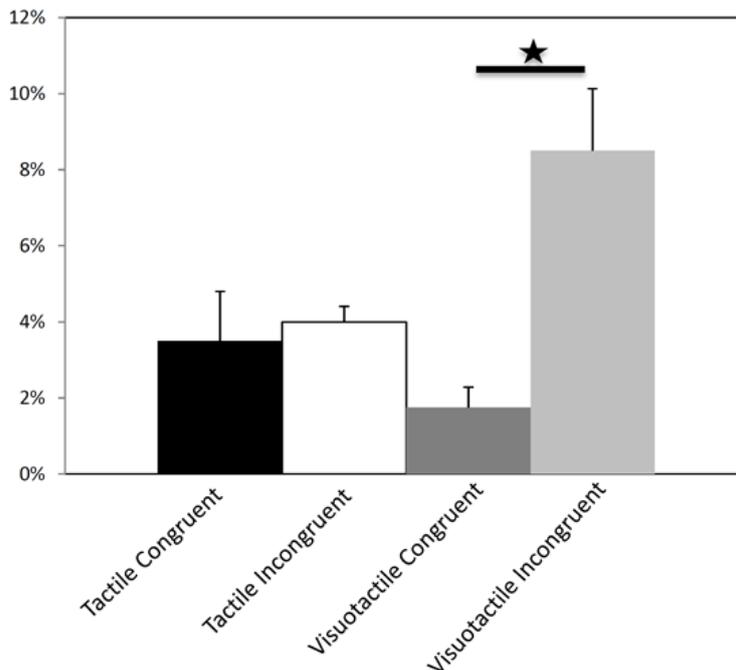


Fig. 2. Mean performance scores in %Error across participants for the tactile congruent (black), tactile incongruent (white bar), visuotactile congruent (dark grey), visuotactile incongruent (light grey) conditions. Error bars are standard error of the mean. Please note that the analysis reported in the results section was based on *numbers* of incorrect responses.

The fewest errors were made in the Visuotactile Congruent (VC) condition, then the Tactile Congruent (TC) condition which was on par with the Tactile Incongruent (TI) condition. The most errors were –by far– made in the Visuotactile Incongruent (VI) condition. According to our model, the amount of errors was larger in the incongruent conditions (TI and VI) than in the congruent (TC and VC) conditions, indicating it was harder for participants to judge the site of tactile stimulation when it did not correspond with the side of the hand the non-target object was on. The effect appears to be driven by the visuotactile condition, as the difference between the tactile congruent and incongruent conditions was small.

We further found an interaction effect between validity and modality, $F(1, 27) = 6.36$, $p < .001$, $partial \eta^2 = .41$, for amount of errors made in the tactile discrimination task. Further

Bonferroni-corrected paired t-testing revealed that the amount of errors was higher for VI condition than for VC condition, $t(9) = 3.86, p < .0125$, but not for the tactile only condition. This implies that participants made the most mistakes when the non-target object was flashed while the site of tactile stimulation was on the opposite side of the hand.

Absolute Reaction Time

We contrasted space, as distance from the target at which the tactile stimulus was given, with mean median reaction times across participants (RTs) in Figure 3 for all conditions. As stated in the analysis subsection above, we calculated the slopes of between space and RTs for all participants for each condition. The average of these slopes can be seen in Figure 3. From this graph, several preliminary conclusions can be made; in some conditions, viz. TC and TI space does not seem to have an effect on RTs, while in others there seems to be a relation, e.g. VC and VI. Next to this apparent effect of Modality, there appears to be an effect of Validity, at least, at a baseline level, that is, the setting of the intercepts seems to be determined by Validity.

Main effects of Validity, $F(1, 9) = 9.73, p < .05, \text{partial } \eta^2 = .51$, and Modality, $F(1, 9) = 9.63, p < .05, \text{partial } \eta^2 = .52$, were determined for individual slopes in a RM ANOVA. This means that slopes were more pronounced in congruent conditions than in incongruent conditions, as well as more pronounced in the visuotactile conditions than in tactile conditions. This in turn indicates that space may modulate reaction times more during congruent and visuotactile conditions than in incongruent and tactile conditions respectively.

Furthermore, we found an interaction effect between modality and validity for the individual slopes for space versus reaction times, $F(1, 27) = 5.14, p < .05, \text{partial } \eta^2 = .36$. Further investigation with Bonferroni-corrected paired t-testing showed that the individual slopes for the congruent and visuotactile conditions (VC) were most pronounced and differed from the VI, TI and TC conditions, all p 's $< .0125$. This indicates that the relation between space and RTs is strongest in this particular condition where visuotactile stimulation was congruent, that is, on the same side of the hand. Simply put, RTs seem to go down when the hand nears the obstacle, but only when the obstacle is flashed and the tactile stimulation is on the side of the flash. If the tactile stimulation is on the other side or when there is no visual stimulation accompanying the tactile stimulus, then space does not modulate RTs.

Crossmodal Congruency Effect

The crossmodal congruency effect (CCE) measure is shown in figure 4. This difference score which was computed between the valid and invalid iterations of tripwire stimulations at the

same depth, has been known to show the amount of interference offered by multisensory interactions.

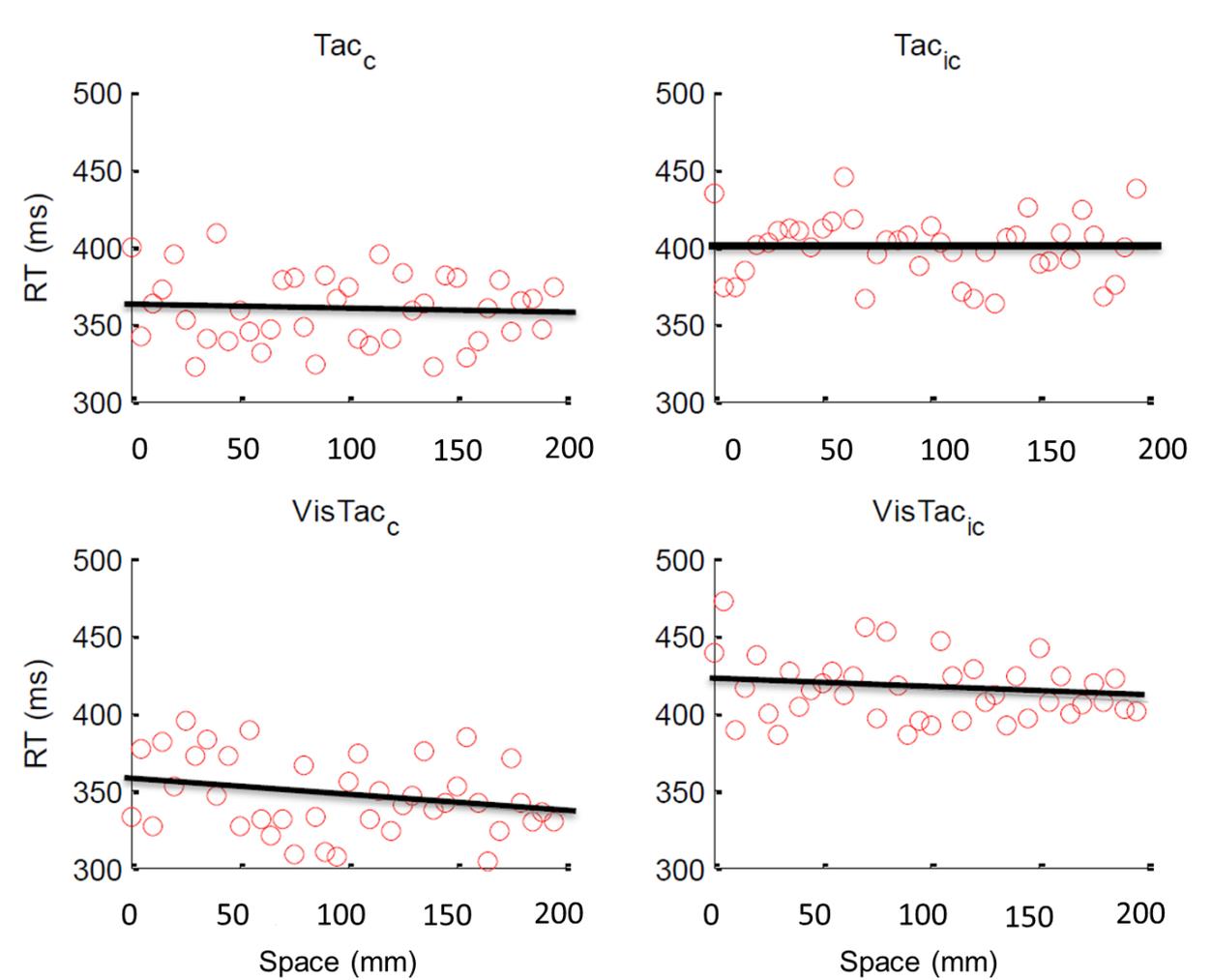


Fig. 3. Overview of absolute reaction times in the tactile congruent (top left), tactile incongruent (top right), visuotactile congruent (bottom left), visuotactile incongruent (bottom right) conditions. Red circles represent mean scores for that ‘tripwire’ location across participants. The black lines represent the least mean squares regression lines to show the mean relation between space and absolute reaction time. Please note that the analysis reported in the results section was based on *individual slopes*.

That is, the valid stimulation conditions exhibit a facilitatory effect on response times, while the invalid stimulation conditions exhibit an inhibitory effect on response times (see also Spence, Pavani, & Driver, 2004; Spence, Pavani, Maravita, & Holmes, 2004). Although the exact contribution of each factor (valid and invalid stimulation) remains unclear in this metric, the CCE measure does allow for easy and quantified crossmodal comparisons. We have plotted the CCE against space (depth of stimulation in mm) for both visuotactile and tactile stimulation conditions. The graphs show an apparent effect of space on the visuotactile CCE, while an effect of space on the tactile CCE appears absent.

We ran a least mean squares regression on the average CCE's across participants per stimulation modality and the results showed that our model had a RSQ of .048 in the visuotactile modality condition and an RSQ of 0.01 in the tactile condition. We analyzed the individual slopes of the relationship between space and the CCE for the visuotactile condition (mean \pm SD: $.42 \pm .08$) and the slopes for the relationship between space and the CCE for the tactile condition (mean \pm SD: $.17 \pm .07$) with a paired t-test, which showed a difference between visuotactile and tactile CCE's, $t(9) = 2.3, p = 0.043$. Given these data, we can conclude that in the visuotactile condition crossmodal interaction increased when participants' hands neared the obstacle.

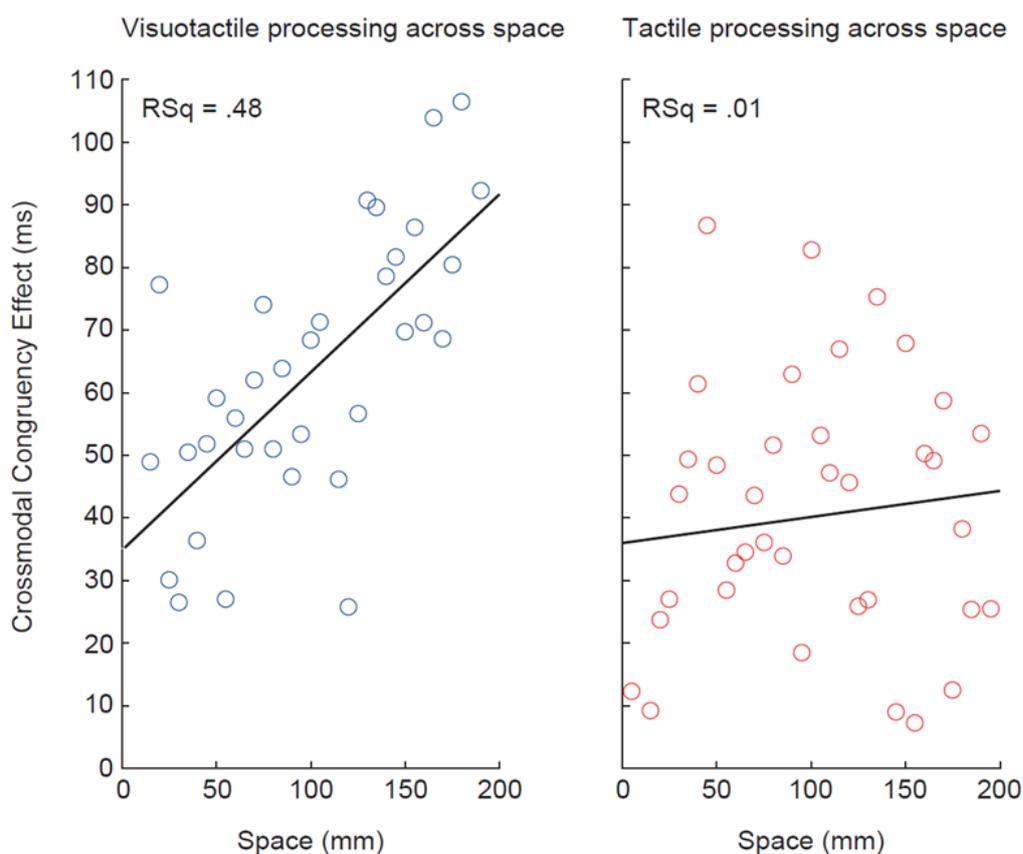


Fig. 4. Difference scores between participants' reaction times to valid and invalid stimuli under visuotactile (left Panel) and tactile stimulation (right Panel) across space. The solid lines indicate least mean squares regression lines which shows that space accounts for 48% of variation in the visuotactile conditions, while only for 1% in tactile conditions. In the experiment, we let participants reach-to-grasp an object with an obstacle present in the workspace. During this action we presented a tactile stimulus that could be accompanied by a visual stimulus. The combination of tactile stimulation and the obstacle location could be either congruent or incongruent. In the visuotactile condition the visual distraction offered by the obstacle was enhanced by a flashed LED. This allowed us to calculate the crossmodal congruency effect as a measure of the strength of interference on visuotactile processing.

Kinematic data analysis

For the kinematic data analysis we found no main effects for any measure (Reaction Time, Peak velocity, Grip Aperture, Deviation at passing, and Error at passing), except for the movement time measure. For movement time we found a main effect of validity, $F(1, 27) = 7.08, p < .05, \text{partial } \eta^2 = .48$. This indicates that invalid trials were performed slower than valid trials, regardless of the modality. We found no main effect of modality, nor did we establish an interaction between modality and validity. To sum up, we determined that the effects we found in reaction times and CCE were not due to differences in movement trajectories, which were in fact quite similar across all conditions (see also Figure 5). The main effect of movement time remained unsupported by additional nonsignificant effects related to speed of movement or movement path length.

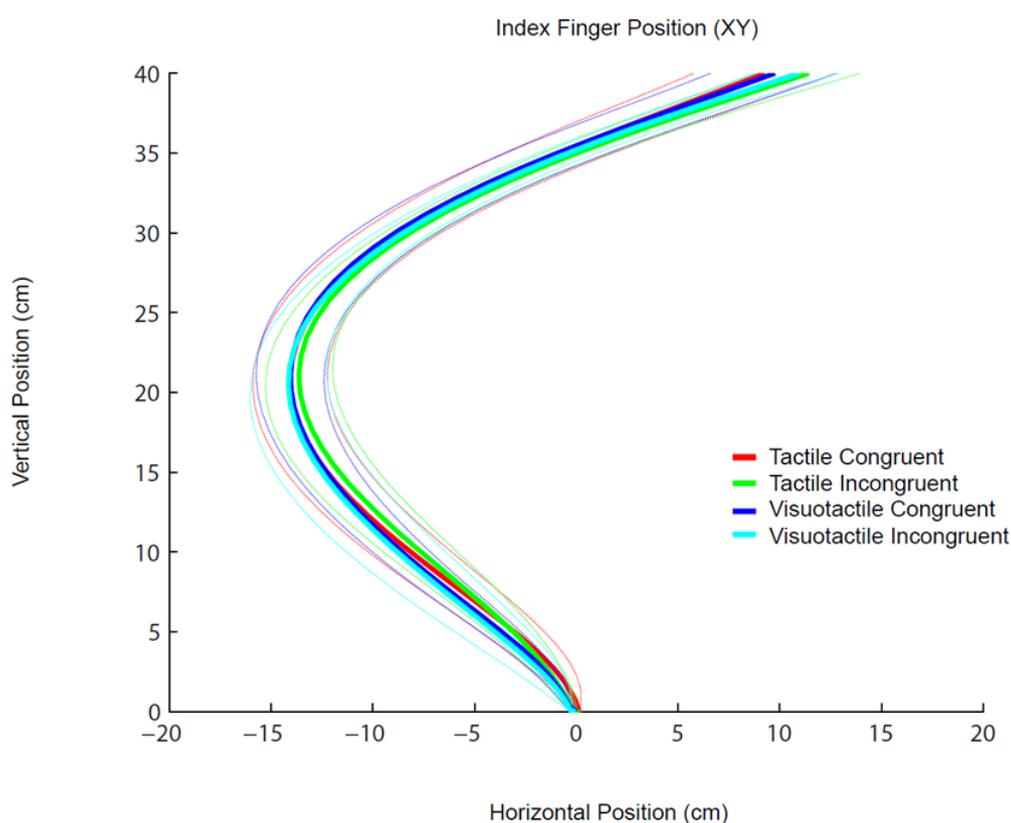


Fig. 5. Mean movement trajectories in the X, Y plane. Thick lines represent mean movement trajectories, whereas thin lines represent an upper and lower bound defined by adding and subtracting the standard error of the mean.

Discussion

Although there has been increasing interest in how various sensory cues may be weighted and integrated to enable a multisensory representation of peripersonal space (e.g., see Rizzolatti et al. 1997; Spence & Driver, 2004), this is the first study to investigate this for obstacle avoidance. Our aim was therefore to investigate whether the PpS not only calculates the tactile consequences of goal-directed actions but also of potential collisions. In this study, participants performed reaches towards a target object, while a to-be-avoided non-target object was also present in the workspace. During this action participants were subjected to tactile stimulation or visuotactile stimulation. Moreover, this stimulation could be congruent or incongruent: the stimuli were presented on the same side of the acting hand or on opposite sides of the acting hand. We used the spatial location of the hand to trigger stimulation in order to carefully map participants' responses across space. Importantly, movement tracking was used to determine that the participants' kinematics were similar between conditions, which allows for drawing meaningful conclusions about the tactile discrimination task data.

The data showed main effects for modality and validity. These main effects are required in order to attain a meaningful interaction, or cross-modal congruency effect (CCE). For a CCE to occur there needs to be difference between unimodal and bimodal conditions. We confirmed the presence of this prerequisite by finding that visuotactile responses were faster and more accurate than tactile responses. Second, we found support for a main effect of validity, which indicates that congruent stimuli were processed faster than incongruent stimuli. Crucially, we found that the modality effect was further modified by the congruent stimuli, i.e. a visual and tactile stimulus on the same side of the hand led to faster discrimination responses than when they were on the opposite side of the hand. Having established that our CCE is genuinely occurring, we can now draw conclusions about the effect of space on the CCE, which is the crux of our experiment.

We demonstrate that multisensory interactions increase when a hand nears an obstacle. This is a novel demonstration as, so far, there have only been demonstrations of increased visuotactile interactions when a hand nears a to-be-interacted-with object; e.g. increased multisensory interactions when grasping an object (Brozzoli et al., 2010). Our data extend the results by Brozzoli et al. (2010) who were the first to show cross-modal congruency effects increase when actors' hands approach a target object. These authors also showed differential modulations of peripersonal space for two different actions, namely pointing and grasping. Crucially, Brozzoli et al. (2010) demonstrated that grasping triggered enhanced cross-modal

interactions as the actor's hand neared the terminus of action compared to pointing. So, these enhancements occur only when the target object was to be interacted with. We replicate their data with our experiment: we also show an increased cross-modal interaction as the hand nears the obstacle. Apparently, avoiding obstacles fits along the continuum set by pointing and grasping. In fact, when speculating about where obstacle should fit along that line, we consider that obstacle avoidance (CCE between 30 ms and 90 ms) might be closer to Grasping (CCE between 20 ms and 80 ms as reported by Brozzoli et al. (2010)) than pointing (CCE between 20 ms and 50 ms as reported by Brozzoli et al. (2010)). Furthermore, our experiment offers two important extensions. First, we have used space in order to trigger visuotactile stimuli instead of time. Whereas Brozzoli and colleagues (2010) probed cross-modal interaction prior to, at the start of, and during action execution, we probed cross-modal interaction at 40 different locations. This means that the resolution of our experiment was higher. In addition, our continuous design allowed us to quantify the relationship between space and the cross-modal congruency effect. This way, we can effectively point to a relation between space and the CCE, or rather between space and cross-modal interactions underlying the peripersonal space.

Now, we show increased multisensory interactions when the object is to be avoided, that is, when it is relevant *for* but not the terminus *of* action. This result redefines the automatic and flexible nature of online peripersonal space remapping during movements. The results suggest that during voluntary movements, the anticipated tactile consequences of contact with a nearby object are automatically evoked, even when contact with the object is not planned. We conclude that the anticipatory multisensory-motor interface between the body and environment also takes collisions into account when driving any voluntary action. Our data firmly support the posited functions of the PpS (Rizzolatti, 1997; Brozzoli et al., 2014): in order to successfully control the movement trajectory of a hand around obstacles (and towards a goal), the PpS incorporates current visual stimuli and predicted tactile consequences. Above all, this is in order to move efficiently and to protect the manipulandum (e.g. a hand) from harm by anticipating the negative consequences of actions.

Although the CCE has seen widespread use as an index for measuring the multisensory representation of peripersonal space (see Maravita et al. 2003 for a review), there are two alternative explanations for the disparate performances by participants during congruent and incongruent trials. First, it is possible that purely the competition between responses elicited by a target stimulus and a distractor stimulus affects processing times. That is, on incongruent visuotactile trials, the tactile stimulus is the target stimulus, whereas the visual stimulus is the distracting stimulus. The distracting effect on incongruent trials is mainly due to the disparity between the locations of the visual stimulus and the tactile stimulus. In bold strokes, both the

tactile and visual stimuli evoke responses associated with the side on which they are presented. Given that the distractor activates the wrong response, and that this response needs to be inhibited before the correct response can be given, slower responses to the target will occur (see Tipper, Howard, & Jackson, 1997 for a detailed discussion of the mechanism underlying this process) than in situations where the stimuli are presented on the same side. In that case, the performance by people on congruent trials might show response facilitation, since the target and the distractor stimuli would both activate the same, “correct” response.

Second, the slower performance by participants during trials with incongruent stimuli might reflect a perceptual interaction between vision and touch, similar to the ventriloquism effect reported by Bertelson & de Gelder (2004). In this case, one stimulus is mislocalized toward the other; i.e. the tactile stimulus is mislocalized (closer) to the visual stimulus location (or vice versa). Possibly, the reason for this is the phenomenon of tactile suppression (see e.g. Juravle, McGlone, & Spence, 2013). Tactile suppression is the inhibition of tactile perception during movement execution. Coupled with the idea posited by Alais & Burr (2004) that for bimodal stimulation localization the more reliable stimulus dominates localization, then we can conclude that in our experiment the visual stimulus dominates the tactile stimulus which leads to a mislocalization of the tactile stimulus toward the visual stimulus. This means that it would be more difficult for people to determine the true location of the tactile stimulation for incongruent stimuli compared to congruent stimuli, resulting in longer processing times for incongruent stimuli. Conversely, the tendency toward localizing visual and tactile stimuli to one spatial location may also speed up congruent responses, because --in this case- the locations are already closer together. According to Spence et al. (2004), however, such (mis)localizations may “account for only small components of the overall cross-modal congruency effects reported” (p. 166). We therefore also consider the contribution of the ventriloquism effect to the CCE as relatively small. Thus, we consider the response competition explanation for the CCE, where the competition evoked by two conflicting signals needs to be overcome, the most likely.

One caveat is in order when interpreting response competition effects; both the labels facilitatory and inhibitory may be attributed to the effects of congruent and incongruent stimulation. That is, we can both argue that congruent stimuli facilitate processing and that incongruent stimuli inhibit processing, while the observed effect remains the same: a difference in measured response times between conditions. In all, this subtle nuance means we can only point to *differences* between the bimodal congruent and incongruent conditions, instead of proclaiming *facilitatory* or *inhibitory* effects. The main point of the discussion yet remains: the cross-modal congruency effect increases when the actor’s hand comes closer to the non-target.

Taken together, we consider that the results of this cross-modal congruency study on obstacle avoidance behavior generate promising leads: first of all, we have quantified PpS remapping relative to distance for obstacle avoidance behavior, so the boundaries of remapping (e.g. radial or cardinal) could be further explored. Secondly, since avoidance behavior combines both hypothesized functions of the PpS, which are defending the organism from harm and guiding voluntary action, it would be interesting to explore the relative hierarchy of these functions.

Chapter 9 – General Discussion

The goal of this dissertation was to gain a better insight in obstacle avoidance behavior and the visual information processing required for guiding goal-directed actions. This chapter provides an overview of the results from Chapters 2 to 8 and their theoretical implications. Importantly, the findings point toward modulatory effects of attention and ventral stream features on complex visuomotor planning and control. Furthermore, the peripersonal space (PpS) network through which the consequences of action are predicted has been identified as playing a role in obstacle avoidance. The reported findings also provide guidelines for further testing in the obstacle avoidance paradigm. Specifically, I have identified important motor constraints for obstacle avoidance movements and I have quantified the effect of available obstacle position information. These findings should be taken into account when designing experiments into obstacle avoidance, or more generally speaking, experiments with complex visuomotor tasks.

Generally speaking, obstacle avoidance movements are affected by dorsal stream features. Such features include, but are not limited to, obstacle position, size (height, width, and diameter), and orientation. Specifically, it has been well-researched that the lateral (left to right) and sagittal position (from near to far in depth) of obstacles affects movements around those obstacles; near obstacles lead to larger avoidance movements than far obstacles and obstacles that are on the right side of the workspace give rise to larger veering movements than obstacles located on the left side of the workspace. Moreover, larger objects give rise to larger avoidance responses than smaller objects. Lastly, when objects are slanted inward, this leads to more pronounced avoidance movements than when the object is slanted outward. Possibly, the base of an object is considered less obstructing than the apex.

Previous literature on these mentioned effects (see Chapter 2) was primarily qualitative, in that a relationship between e.g. size and avoidance movement trajectories was either established or not. In Chapter 3, a description is offered of the steps that were taken to allow for a quantitative interpretation of the movement trajectory analyses. Here, a successful attempt was made to establish a formal relationship between obstacle position and avoidance responses. These results provide evidence for a fine-grained spatial resolution of the obstacle location representation. In addition, the recorded function can be used to predict avoidance effects stemming from obstacle location by itself.

Next to reviewing dorsal stream features that prompt changes to normal avoidance behavior, Chapter 2 dealt with the contextual and motor factors which were known to influence obstacle avoidance behavior were also reviewed in Chapter 2. In Chapter 4 the effect of the handedness of participants was explored. As a 'motor factor' handedness did not influence avoidance responses, nor did using the preferred hand vs. the non-preferred hand affect

avoidance responses. In contrast, one motor factor that was shown to influence obstacle avoidance behavior was the starting posture of participants (see Chapter 5). This result should be considered when designing experiments; the fact that handedness does not overtly affect avoidance movements can be used for designing experiments that can quickly toggle the interpretation of an object as obstacle or irrelevant object by offering last-minute information on which hand should be used to proceed with the avoidance task. Furthermore, starting posture should be strictly controlled in any obstacle avoidance experiment, or more generally speaking, each experiment that uses a visuomotor task. Moreover, the same strictness should apply to the end posture of the movement. If the end posture is left uncontrolled, then movement trajectories will vary freely according to their end postures. Needless to say, this produces variance in the measures collected from the movement trajectories. It should be stressed that this variance can be simply prevented and therefore dispersion in the data reduced, by providing an ecological end-point of movement like for example a to-be-lifted wooden cylinder or glass.

The investigation of the effects of ventral stream features represents another tangent of this dissertation. Ventral stream features are features that are often non-spatial in nature. However, as is obvious, size and shape can also help determine what an object is; a hollowed-out cylinder with an intact base and made out of clear material that affords grasping and is within reach is regularly identified as a glass. In this regard, is the identity of 'a glass' truly non-spatial? This small philosophical crisis notwithstanding, there are features of objects that are known not to be processed in the dorsal stream, but that are, instead, processed in the ventral stream. Hence, any effect of such a feature points toward the involvement of the ventral stream in visuomotor planning and control. In Chapter 6 such an effect of a non-spatial object property on avoidance movements was described. Apparently, ventral stream features of obstacles affect avoidance movements, but they only modulate effects of dorsal stream features. In my interpretation, the dorsal stream features evoke a base avoidance response which is further tweaked by ventral stream features.

Building on this finding, another study (Chapter 7) was performed where the exclusive contribution of attention on avoidance movement trajectories was investigated. In other words, an attempt was made to try to tweak the base avoidance response in a different way by proffering a spatial cue for the obstacle. The point here was that this manipulation did not change a feature of the object, like in the previously described case. Any effect on avoidance behavior would be solely due to our manipulation of attention and not due to either an exclusive manipulation of ventral or dorsal stream information. The results of this flashing experiment confirmed our hypothesis that a spatial cue on an obstacle increases the repulsive effect of

obstacles. The premotor preparation for action, represented by an attentional distribution across the action-relevant locations in the workspace, can therefore be influenced. Accordingly, there is now accumulated evidence that 1) corroborates effects for dorsal stream features, that 2) further extends the input for information gathering processes underlying obstacle avoidance with ventral stream features, and that 3) also show a modulatory effect on obstacle avoidance of spatial attention.

In the final research chapter of this thesis, the link between obstacle avoidance and the PpS was investigated. The aim of this study was to examine whether or not a flexible remapping of PpS could occur during obstacle avoidance movements and particularly with regard to the obstructing object. The findings indicated that the PpS not only determines the tactile consequences of goal-directed actions but also the consequences of potential collisions. This is commensurate with the proposed functions of the PpS, which are: guiding voluntary action and preventing harm. Indeed, both these functions seem to be combined in obstacle avoidance; a goal-directed action that needs to be efficient as well as self-protecting. With these findings we have confirmed an operant mechanism in the brain that plays a major role for information processing and control regarding obstacle avoidance.

What can be concluded from all this is that there is a confluence of the dorsal and ventral streams; both ventral and dorsal stream features have been shown to affect obstacle avoidance behavior. Moreover, information processing was shown to be modulated by attention. In bold strokes, what an object is and how much attention you pay to it determines how much you avoid it. What is more, the interaction between tactile and visual information when avoiding obstacles points out that for this skill there is a convergence from many different sources of information. However, this information processing should not be considered a black box. There are many avenues open for investigation, which, if assiduously pursued, will lead to clear insights into the behavior. In fact, as demonstrated in this thesis, it is possible to derive simple equations from behavioral measures that appear to govern such behavior, which can be used to predict behavior. The next step here is to incorporate more terms into the equation so that all the heterogeneous factors affecting avoidance behavior that are described in this thesis may be more accurately and robustly approached. Moreover, the 'tweaking' role of ventral stream features and attention may be modeled in such an equation by adding or calibrating a gain parameter. Alternatively, the equation could feature higher order parameters to increase its accuracy as well as become a likely representation of the actual and operational behavioral rule humans use to guide their hand towards a target object around an obstacle. It should be clear that we can still learn much about obstacle avoidance, although several inroads have been laid which will hopefully be explored in the future.

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Contributions

Chapter 1

Authored by Rudmer Menger, with helpful comments by Stefan Van der Stigchel and Chris Dijkerman.

Chapter 2

First and subsequent drafts were authored by Menger. Van der Stigchel and Dijkerman edited the document and contributed concepts and theories.

Chapter 3, 4, 5, 6, 7, & 8

Van der Stigchel and Dijkerman obtained funding for the experiments. Study designs were established collectively by Menger, Dijkerman and Van der Stigchel. Menger collected all the data and performed the required statistical analyses. Van der Stigchel and Dijkerman aided in the interpretation of the results and provided links with relevant theories and concepts. Menger wrote the first and subsequent drafts of these articles, while Dijkerman and Van der Stigchel edited the manuscripts. Revision of the manuscripts was performed by Menger, with support from Van der Stigchel and Dijkerman.

Chapter 9

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Finally, all authors declare that there are no conflicts of interest with regard to the performed research.

Nederlandse samenvatting

We hebben allemaal die *ene* vriend die of dat *ene* familielid dat het tijdens feestjes of diners altijd presteert om zijn glas wijn om te stoten. Hoewel een dergelijk voorval natuurlijk onhandig is, gebeurt het doorgaans weinig. We kunnen zeggen dat botsingen met voorwerpen vaak succesvol voorkomen worden. Obstakelvermijding is dus een automatische maar complexe vaardigheid die mensen bezitten. ‘Automatisch’ omdat we veel verschillende lichaamsdelen kunnen gebruiken om obstakelvermijding te bewerkstelligen zonder dat we daar bij nadenken. Het bewegen naar een doel terwijl irrelevante voorwerpen ontweken worden kan immers gebeuren in een auto, te voet, of met een hand. Obstakelvermijding is bovendien een ‘complexe’ vaardigheid omdat het veelal gebeurt in dynamische en rijkelijk gevulde omgevingen. Dat wil zeggen, het bewegingsprobleem dat door ons brein wordt opgelost als we een obstakel vermijden is zeer ingewikkeld.

Om te begrijpen hoe mensen in staat zijn om obstakels te vermijden is het nodig om te begrijpen hoe het brein informatie verwerkt zodat een beweging uitgevoerd kan worden. Mensen bewegen doorgaans niet in een vacuum: we zijn omringd met verschillende objecten en oppervlakten waarmee we kunnen interacteren. Deze objecten en oppervlakten reflecteren licht van de zon, hetgeen vervolgens op ons netvlies terecht komt. De visuele cortex in het brein verwerkt deze informatie langs twee verschillende zogeheten stromen (netwerken in het brein): de dorsale stroom en de ventrale stroom. De dorsale stroom loopt van het achterhoofd, waar de occipitale cortex zich bevindt, naar de bovenkant van het brein, de parietale cortex. De dorsale stroom verwerkt visuele informatie met het doel om bewegingen te sturen. Dit betekent dat hier vooral informatie verwerkt wordt over *waar* objecten zich bevinden. De ventrale stroom daarentegen loopt van de visuele cortex naar de onderste regionen van de temporale cortex (bij de slaap) en verwerkt informatie om voorwerpen te kunnen identificeren. Dit betekent dat hier vooral informatie verwerkt wordt over *wat* objecten zijn. Om succesvol te kunnen bewegen in onze omgeving maken we gebruik van beide soorten informatie; we moeten weten wat objecten zijn en waar ze zijn.

Echter, aan het ‘einde’ van deze twee stromen houdt de informatieverwerking niet op. Bewegingen dienen voorbereid en gecontroleerd te worden door het brein op basis van deze informatie. Dit gebeurt in de premotor en motor cortex van het brein. Voor het plannen van een beweging moeten er twee zaken geregeld worden: bewegingsselectie en bewegingspecificatie. Bewegingsselectie gaat erom dat het juiste object waarnaar de beweging plaats moet vinden geselecteerd wordt. Neem als voorbeeld het drinken van een slok water tijdens een diner; het

volstaat dan niet dat je het glas wijn, dat naast een glas water stond, oppakt. Bewegingsspecificatie gaat om hoe de beweging precies wordt uitgevoerd: bijvoorbeeld hoe de arm door de beschikbare ruimte wordt getransporteerd, hoe ver de vingers zijn geopend, of de beweging snel of voorzichtig plaatsvindt en of bijvoorbeeld de romp ook meewerkt aan de armbeweging.

Het controleren van een geprogrammeerde beweging gebeurt door middel van een feed-forward mechanisme (het omgekeerde van feedback). Dit betekent dat een beweging geprogrammeerd wordt op basis van eerdere ervaringen in vergelijkbare omstandigheden. Het uitvoeren van de snelle, natuurlijke beweging geschiedt vervolgens zonder dat er feedback verwerkt wordt. De reden hiervoor is dat de signaalverwerking door ons zenuwstelsel te langzaam is om adequaat te reageren op verstoringen; een correctiesignaal zou simpelweg te laat arriveren, want de beweging is al voorbij. Zodra er een fout wordt gemaakt in de beweging, dan wordt daar voor volgende bewegingen wel degelijk rekening mee gehouden door het feed-forward plan aan te passen op basis van de laatste ervaringen. Vergelijk dit met een situatie waar je propjes gooit richting een prullenbak: zodra het propje door de lucht vliegt kun je aan de baan niks meer veranderen. Je kan wel de resultaten inzien: mis of raak. Indien je raak gooit, weet je dat je niks hoeft te veranderen aan je beweging. Gooi je mis, dan weet je of je harder moet gooien of zachter of meer naar rechts of links. Zo werkt de controle van een armbeweging in een situatie waar een voorwerp ontweken moet worden, simpel gezegd, ook.

Om te bewegen moeten we dus informatie verwerken. Daarbij geldt dat we niet slechts passieve ontvangers van die informatie zijn: we zoeken actief naar bruikbare informatie en we negeren irrelevante informatie. Ons brein beschikt over aandachtsprocessen die het mogelijk maken om voor ons huidige en volgende doel op korte termijn afdoende informatie te verzamelen. Zodra we het domein van obstakelvermijding betreden kan aandacht ook een rol spelen, want aandacht beïnvloedt zowel het verzamelen van informatie als ook de verwerking van informatie. Het is mogelijk om dat als volgt in te beelden: stel een landschap van pieken en dalen voor. Dit landschap is een representatie van activiteit in ons brein. Er is daarin een groep neuronen die ieder gekoppeld zijn aan een bepaald stukje ruimte in onze nabije omgeving (waar we bij kunnen). Zodra er een relevant object in die ruimte aanwezig is gaan op de bijbehorende plek in het landschap de neuronen aan; dit leidt tot een piek van activiteit. Staat er niks relevants dan blijft het landschap op dergelijke plekken plat. Voor voorwerpen die ontweken moeten worden is het voor te stellen dat in de representatie, oftewel het neuronale landschap, een vallei is. De resultante van alle activiteit in het landschap leidt tot een unieke beweging; het brein programmeert een beweging in de richting van een piek en om valleien heen. Aandacht

kan dan de aantrekkingskracht van pieken en de afstotende kracht van valleien sterker of zwakker maken.

Samenvattend kan gezegd worden dat informatie in onze omgeving wordt verwerkt om bewegingen te programmeren en dat dit proces beïnvloed kan worden door aandacht. Obstakelvermijding zelf kan op drie manieren onderzocht worden: ten eerste kunnen onderzoekers de beschikbare informatie manipuleren; ze kunnen bepaalde informatie aanbieden en kijken wat daar het effect van is. Ten tweede kunnen zij de aandacht ergens op laten vestigen en kijken wat daar het effect van is. Ten derde kunnen zij de bewegingscomponent beïnvloeden om te zien wat daar het effect van is. Mogelijke effecten zijn meetbaar doordat de ontwijkingsbeweging zelf meetbaar is. Een gecontroleerde wijziging binnen een experimenteel raamwerk leidt dan of wel, of niet tot een consistente verandering in bewegingen.

Deze dissertatie is zeker niet het eerste onderzoek naar obstakelvermijding. Sterker nog, een aantal studies zijn al verricht en deze werken zijn dan ook samengevat in hoofdstuk 2. In grote lijnen zijn de resultaten van het literatuuronderzoek dat obstakelvermijding zich kenmerkt door subtiele en precieze bewegingen. In essentie is elke beweging rond een obstakel een unieke en op maat gemaakte reactie op een specifieke omgeving. Dit wil zoveel zeggen als dat we geen stereotype manier hebben om op elk obstakel te reageren. Onder gelijke omstandigheden produceren we echter wel stereotype bewegingen. Dit betekent dan weer dat er wel wetmatigheden ten grondslag liggen aan obstakelvermijding. Desalniettemin hebben voorgaande studies slechts een algemeen beeld geschetst van bijvoorbeeld het effect van de locatie van een obstakel: als een object dichtbij de hand staat zal de vermijdingsreactie sterker zijn. In hoofdstuk 3 wordt daarom een experiment beschreven met als doel om de relatie tussen locatie en de sterkte van de vermijdingsbeweging precies te bepalen. Deze relatie is vervolgens gekwantificeerd en dus is het nu mogelijk om op basis van een obstakellocatie de kracht van de vermijdingsbeweging te voorspellen. Dit is een eerste en succesvolle poging geweest om een wetmatigheid in obstakelvermijdingsbewegingen bloot te leggen.

Uit het literatuuronderzoek kwam verder ook naar voren dat er een aantal interessante effecten waarneembaar waren in obstakelvermijdingsexperimenten. Een voorbeeld daarvan is dat de vermijdingsreacties sterker zijn als het obstakel zich rechts (en uiteraard voor) een persoon bevindt (vergeleken met obstakels die links staan). Een ander voorbeeld is dat in sommige experimenten de kracht van de vermijdingsreactie stukken sterker was dan in andere experimenten. Dat wil zeggen, onder ogenschijnlijk gelijke omstandigheden werden uiteenlopende reacties gemeten. In beide gevallen heb ik geprobeerd de oorzaak te zoeken in

hoe de beweging werd uitgevoerd. Eén hypothese was dat wellicht het gebruik van de voorkeurshand leidde tot grotere vermijdingsbewegingen. Dit bleek niet het geval (zie hoofdstuk 4). Ik heb namelijk vastgesteld dat het wel of niet gebruiken van je voorkeurshand geen effect heeft op obstakelvermijding. De reden dat obstakels die rechts staan van een persoon meer ontweken worden is dus te vinden in de relatieve positionering van het obstakel ten opzichte van de bewegende hand (en arm).

Een andere hypothese was dat de sterkte van vermijdingsreacties afhangt van hoe de beweging gestart wordt, met andere woorden: vanuit welk startpostuur de beweging aanvangt. Mijn resultaten gaven aan dat het startpostuur inderdaad bepalend is voor de vermijdingsreactie (zie hoofdstuk 5). Ook hier geldt weer dat de relatieve positionering van het obstakel ten opzichte van de bewegende hand, hetgeen natuurlijk sterk wordt beïnvloed door het startpostuur, de belangrijkste bepaler is van de kracht van de vermijdingsreactie.

Nu is vastgesteld dat obstakelvermijding gedreven wordt door wetmatigheden die gebaseerd zijn op eigenschappen van het obstakel die door de dorsale stroom verwerkt worden. Bovendien zijn er nu aantoonbaar belangrijke componenten van de beweging die streng gecontroleerd moeten worden. Hiermee was het toneel gereed gemaakt voor onderzoek naar de eventuele effecten van aandacht op obstakelvermijding en van obstakeleigenschappen die verwerkt worden in de ventrale stroom. De rol van de dorsale stroom moet hier overigens niet worden onderschat; uit patiëntenstudies blijkt dat effectieve en natuurlijke obstakelvermijding bijna niet te realiseren is als de dorsale stroom in een brein niet werkt. Dit neemt niet weg dat verwerking van informatie via de ventrale stroom een effect kan hebben op obstakelvermijdingsgedrag.

In hoofdstuk 6 is dit dan ook specifiek onderzocht. Daartoe zijn twee experimenten gedaan waarbij niet-ruimtelijke eigenschappen van obstakels gewijzigd werden. Omdat de plaats, grootte, oriëntatie etc. van de obstakels niet veranderde zou een niet-ruimtelijke wijziging geen effect moeten hebben op de bewegingen. Er is echter tweemaal een effect vastgesteld, wat zoveel wil betekenen als dat de dorsale stroom samenwerkt met de ventrale stroom tijdens obstakelvermijding. Een andere mogelijke interpretatie is dat de manipulatie van de obstakels in deze experimenten per ongeluk ook een aandachtsmanipulatie was.

In een ander onderzoek, hetgeen in hoofdstuk 7 gerapporteerd wordt, zijn experimenten gedaan die gericht waren op het met opzet vestigen van de aandacht op obstakels teneinde veranderingen in vermijdingsbewegingen te genereren. Er is geprobeerd om de aandacht van proefpersonen vlak voor de uitvoering van een vermijdingsbeweging te vestigen op een obstakel om te zien of deze dan ook sterker vermeden zou worden dan wanneer de

aandacht er niet op gevestigd werd. Dit bleek het geval te zijn. Het is dus denkbaar dat er op deze wijze in het eerder genoemde neuronale landschap een dal dieper gemaakt kan worden.

Het onderliggende mechanisme dat de gevolgen van bewegingen van het lichaam zelf voorspellen kan is de zogeheten *peripersonal space*. Dit is een gebied rond je lichaamsdelen waarvoor bimodale neuronen in je brein coderen. Let wel, dit is een ander gebied dan waar eerder over gesproken is. Hier gaat het specifiek om neuronen die zowel actief zijn als er iets in de peripersonal space te *zien* is, als ook wanneer men in die regio *aangeraakt* wordt (het zijn zeer waarschijnlijk deze neuronen die ervoor zorgen dat bepaalde mensen 'kietelig' zijn). De betrokkenheid bij het uitvoeren van doelgerichte bewegingen van deze neuronen is onlangs aangetoond; zodra een hand een te manipuleren object nadert begint het peripersonal space netwerk meer activiteit ten toon te spreiden. In hoofdstuk 8 extrapoleer ik deze bevindingen naar obstakelvermijding en toon ik aan dat ook voor obstakelvermijding een dergelijke toename van activiteit is waar te nemen wanneer een hand een obstakel dichtert nadert. Dit betekent dus dat de gevolgen van botsing met een obstakel ook via dit netwerk in het brein gecodeerd worden.

Gegeven deze bevindingen; wat kan er dan nu geconcludeerd worden? Wat we al wisten is dat obstakelvermijding een automatisme is dat sterk leunt op informatieverwerking via de dorsale stroom. Daar kan ik aan toevoegen dat er een samenvloeiing moet zijn van ventrale en dorsale stroom informatie voordat een obstakelvermijdingsbeweging geprogrammeerd wordt. Deze samenvloeiing wordt verder beïnvloed door aandacht. Ik heb ook aangetoond hoe aandacht experimenteel te testen is voor obstakelvermijding. Verder is het niet alleen visuele informatie die samenvloeit; ook tactiele informatie wordt met visuele informatie gecombineerd. Hoe al deze informatie samenvloeit en wat de samenhang van al deze informatiebronnen precies is, moet niet beschouwd worden als een 'black box'. Zoals ik heb aangetoond is het wel degelijk mogelijk om wetmatigheden aan te tonen voor obstakelvermijding. De volgende stap zou moeten bestaan uit het verder uitwerken van deze vergelijking, zodat het gedrag beter voorspeld en dus beter begrepen kan worden. Het moge duidelijk zijn dat er nog steeds veel te leren is wat betreft obstakelvermijding, hoewel er dus al een aantal verkenningen geweest zijn die hopelijk in de toekomst verder uitgewerkt kunnen worden.

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Stefan, speciaal voor jou: **Stop...**

...Hammertime.

Stefan, als er iemand is die ongenaakbaar is, dan ben jij het. De combinatie van tomeloze inzet, enthousiasme voor het vak, scherpe inzichten, ontzettend veel expertise, betrokkenheid, humor (met een randje), en bovenal geduld is bewonderingswaardig. Zonder jou had dit proefschrift er niet in deze vorm gelegen. Toch ben ik ook blij dat ik je zo af en toe weer eens een nieuw woord engels kon leren.

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Fen, elsker deg. Stor og lang klem. Tige tank datst mei my meikaam bist foar dit aventoer.

Fardou, Lútsen, Sybrich. Jim binne dochs it moaiste wat ik oait makke ha.

Curriculum Vitae

Rudmer Menger werd op 15 juli 1983 geboren in Drachten. In 2001 haalde hij zijn gymnasiumdiploma aan het CSG Liudger te Drachten. Hij begon dat najaar aan een opleiding Rechten aan de Rijksuniversiteit Groningen. Na één jaar is hij overgestapt op de bachelor opleiding Bewegingswetenschappen aan dezelfde universiteit. Aansluitend heeft hij de master opleiding Bewegingswetenschappen afgerond met speciale aandacht voor de theorie van bewegingssturing, filosofie in de Neurowetenschappen, en zelf-organiserende systemen. Nadien heeft hij zich ingeschreven voor de masteropleiding Behavioral and Cognitive Neuroscience ook aan de RuG. Tegelijkertijd is hij werkzaam geweest voor de opleiding Bewegingswetenschappen als docent. In 2010 heeft hij deze 2^e master afgerond en is hij begonnen aan zijn promotieonderzoek aan de Universiteit Utrecht onder begeleiding van Dr. Stefan Van der Stigchel en Prof. dr. Chris Dijkerman. Tijdens zijn promotieonderzoek kreeg Rudmer 3 prachtige kinderen. Rudmer is reeds een jaar werkzaam als Lecturer onderzoeksvaardigheden en rapporteren aan Stenden University of Applied sciences te Leeuwarden.

Rudmer Menger was born on July 15th 1983 in Drachten. In 2001 he obtained his gymnasium diploma at the CSG Liudger in Drachten. That fall he started studying law at the University of Groningen(RuG). After one year he switched to Human Movement Sciences at the same university. After obtaining a bachelor's degree he completed the following master's education with special attention for (theories of) movement control, philosophy of neuroscience, and self-organizing systems. Subsequently, he started a 2nd master's degree in Behavioral and Cognitive Neuroscience, also at RuG. At the same time he was a teacher at HMS in Groningen. In 2010 he finished his 2nd master and started his Ph. D. under supervision of Dr. Stefan van der Stigchel and Prof. dr. Chris Dijkerman. During this period he was blessed with 3 wonderful children. Rudmer has been working as a lecturer research skills and reporting at the Stenden University of Applied sciences in Leeuwarden for the last year.

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