

To what extent are functions of the perceptual and the motor system separable?

**An investigation using dual-tasking, the Garner paradigm, and the visual
threshold of size discrimination**

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Abstract

This dissertation investigates the relationship between the perceptual and the motor system as laid out by the Perception-Action Model (PAM) formulated by Milner and Goodale (Milner & Goodale, 1995, 2006). The PAM sees the cortical visual system as consisting of two separate streams, the dorsal stream, running from V1 to the parietal lobe, and the ventral stream, running from V1 to the temporal lobe. The dorsal stream is considered to be responsible for visually-guided action and the ventral stream is seen to be responsible for perception. In a series of three studies we investigated how information processing that can be interpreted to be dominantly in one stream relates to information processing that can be interpreted to be dominantly in the other stream. In the first study we investigated how performing a rapid serial visual presentation (RSVP) task in combination with two motor tasks, a predominantly dorsal motor task and a ventral motor task, changes the performance on the specific tasks. In the second experiment we investigated how a perceptual and a motor variant of a Garner task differ in relation to a concurrent secondary task with either a motor relevant or a motor irrelevant component. In the last experiment we investigated whether the dorsal stream has a higher precision than the ventral stream, which, if true, would argue for two separate visual representations of an object in the two streams. In the first two experiments we consistently found dual-task costs when tasks were combined which the PAM considers to be separate and in the last experiment we found no evidence for a higher precision of the dorsal stream than of the ventral stream.

Zusammenfassung

Diese Dissertation untersucht die Beziehung zwischen dem Wahrnehmungssystem und dem motorischen System, wie sie von Milner und Goodale im Perception-Action Modell (PAM) formuliert wurde (Milner & Goodale, 1995, 2006). Gemäß dem PAM besteht das kortikale visuelle System aus zwei verschiedenen Pfaden, dem dorsalen Pfad, welcher sich von V1 in den parietalen Kortex erstreckt, und den ventralen Pfad, welcher sich von V1 in den temporalen Kortex erstreckt. Die Aufgabe des dorsalen Pfades ist, nach dem PAM, die Verarbeitung von visuellen Informationen in Relation auf visuell gesteuerte Handlungen und die Aufgabe des ventralen Pfades ist, nach dem PAM, die Verarbeitung von visuellen Informationen in Hinblick auf visuelle Wahrnehmung. In dieser Dissertation präsentieren wir drei Studien, in denen wir untersuchen, in welcher Beziehung Informationsverarbeitung, welche primär in dem einen Pfad stattfindet, zu Informationsverarbeitung steht, welche primär in dem anderen Pfad stattfindet. In der ersten Studie untersuchten wir, inwieweit eine visuelle Zweitaufgabe, welche zusammen mit einer primär dorsalen motorischen

Aufgabe oder mit einer ventralen motorischen Aufgabe durchgeführt wurde, die Leistung auf den verschiedenen Aufgaben beeinflusst. In der zweiten Studie untersuchten wir, inwieweit sich eine visuelle Form einer Garner Aufgabe und eine motorische Form einer Garner Aufgabe unterscheiden, wenn sie parallel zu einer visuellen Zweitaufgabe durchgeführt wurden, welche eher eine für die Motorik relevante Komponente hat oder eine für die visuelle Wahrnehmung relevante Komponente. In der letzten Studie untersuchten wir, ob der dorsale Pfad eine höhere Auflösung hat als der ventrale Pfad, was, wenn es stimmen würde, für zwei verschiedene Repräsentationen eines Objektes in den beiden Pfaden sprechen würde. In den ersten beiden Studien fanden wir, dass das parallele Ausführen von zwei Aufgaben, selbst wenn sie nach dem PAM sich nicht überlappen sollten, zu Zweitaufgabenkosten führt und in der letzten Studie fanden wir keine Evidenz dafür, dass die Präzision im dorsalen Pfad höher ist als im ventralen Pfad.

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1. Introduction

1.1 The Perception-Action Model

The Perception-Action Model (PAM) has advanced since its first publication to one of the most influential models in Neuropsychology (Goodale & Milner, 2018; Milner, 2017; Milner & Goodale, 1995, 2006, 2008). It is widely quoted in textbooks (Gazzaniga, Ivry, & Mangun, 2014; Kolb & Whishaw, 2015; Postle, 2015) and has even been seen as causative by one author in making the study of movement seem relevant to questions concerning perception and cognition (Rosenbaum, 2005).

The PAM has its roots in the 'What and Where'-Model by Ungerleider and Mishkin (Mishkin, Ungerleider, & Macko, 1983; Ungerleider, & Mishkin 1982), which itself has its root in a symposium held in 1967 where distinctions between two modes of visual processing, among them locating and identifying, have been first proposed in several animal species (Held, 1968; Ingle, 1967; Ingle, Schneider, Trevarthen, & Held, 1967; Schneider, 1967; Trevarthen, 1968). It should be noted that this is where we first find an approach that does not consider vision to be one single representation that is then used for motor behavior.

The first case of a possible differentiation like this in humans was then reported in Bridgeman, Lewis, Heit, and Nagle (1979). They reported data in which they had participants point to a target with an unseen pointer after a saccade, combined with either a saccade contingent shift or not. While participants were not always able to detect the shift they were always able to point to the target. This was seen by the authors as a case of information being available to the motor system that was not available to the cognitive system thus differentiating between action and perception in humans. In Bridgeman, Kirsh, and Sperling (1981) the authors showed that an illusory shift in a pointing target does not influence the pointing movement towards the target. The authors conclude that this also shows that the motor system uses veridical spatial information. Bridgeman (1991) interpreted these and other results as reflecting two functional systems, the cognitive system, which solves perceptual tasks using symbolic codes for sensory information and a motor system which solves sensorimotor tasks coding sensory information in isomorphic codes.

In a seminal paper Ungerleider, & Mishkin (1982) proposed a distinction founded on anatomically divergent pathways based on ablation studies in macaques. They considered the dorsal pathway from V1 to the parietal cortex to be responsible for where an object is located and the ventral pathway from V1 to the temporal cortex to be responsible for what an object is, resulting in the well-known what and where pathways.

Milner and Goodale (1995) took over the anatomical distinction but interpreted the functions of the two pathways differently. In their model the ventral pathway became the pathway for visual perception and the dorsal pathway the pathway for visually-guided action.

The exact specification of their model is described in Milner and Goodale (2008). There they write that while the ventral stream is responsible for the “identification of possible and actual goal objects – and the selection of an appropriate course of action to deal with those objects”, the dorsal stream “is critical for the detailed specification and online control of the constituent movements that form the action, making use of metrical information that maps directly onto the action in the ‘here and now’” (p. 775). This interpretation seems to be the one Milner and Goodale are still following (Goodale & Milner, 2018).

1.2 Neuropsychological Evidence

While they also included a diverse array of data taken from monkey physiology (Milner & Goodale, 1995), this differentiation was first based on findings in one patient with visual form agnosia, patient D.F., and findings on patients with optic ataxia (M. A. Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). After suffering from carbon monoxide poisoning, patient D.F. was, among other things, unable to recognize common objects (e.g. a knife), unable to recognize standard drawings of common objects or copy them, and unable to recognize letters, while visual acuity, color vision, tactile recognition and intelligence were largely preserved. Even though she was so severely impaired on visual recognition tasks, she retained basic motor function. The authors reported little difficulty in everyday activities (opening doors, shaking hands, walking around furniture, eating meals). They further reported that, using the same setup as Perenin, Vighetto, Maugeiere, & Fischer (1979) with a rotatable slot into which things could be posted (possibly similar to Perenin and Vighetto (1988)), they found no impairment in patient D.F. when she was asked to post a card into the slot, but severe impairment when asked to verbally indicate the orientation of the slot (yet she was not at chance level, having a 55% hit rate, when 25% would have been chance). The authors then considered this to be the relevant double dissociation to the optic ataxia patients reported by Perenin and Vighetto (1988). The optic ataxia patients also had to perform the posting task and a line orientation discrimination task. Performance in the line orientation task was significantly better than in the posting task. It should be noted that Perenin and Vighetto (1988) reported more errors in the line orientation task for the optic ataxia group than the control group. Still this double dissociation combined with the putative damage to the ventral stream in patient D.F. and the dorsal stream in optic ataxia patients, was the foundation for the perception-action distinction.

1.3 Evidence in Healthy Participants

While investigating patients with brain damage was one direct approach to validate the PAM, at the same time differentiations between the two pathways were also searched for in healthy participants.

One approach taken was to use visual illusions to see whether the vision for action system was more robust to visual illusions than the vision for perception system. Aglioti, DeSouza, and Goodale (1995) constructed a graspable version of the Ebbinghaus-Titchener illusion, in which, in one version, two circles of the same size are surrounded either by large or small circles making the central circle either appear smaller or larger and in another version two circles are surrounded by smaller and larger circles so that they look as if they had the same size, but in fact their sizes were different. They found that in both cases participants grasped the smaller disk with a smaller maximum grip aperture (MGA), i.e. the maximum metric distance between thumb and index finger, and the larger disk with a larger MGA, showing no effect of the illusion. The authors interpreted this as possibly reflecting the two processing streams of the visual system as described by Milner and Goodale. Starting with this study the research into the putative stability of the dorsal stream has flourished while of course the actual starting point of this tradition can be seen as the research performed by Bridgeman et al. (1981). For example Brenner and Smeets (1996) showed that, using the Ponzo illusion, the illusory size of an object influences the lift force but not the MGA. Following up on this Ellis, Flanagan, and Lederman (1999) showed that when a beam is presented in an illusory context so that the midline of the beam appears further to the right using either a Müller-Lyer Illusion or a Ponzo illusion, both verbal midline indication and grasping at the center are affected by the illusion, but grasping is less affected than the verbal report. Other studies approached the question more from the direction set by Bridgeman and colleagues (Daprati & Gentilucci, 1997; Gentilucci, Chieffi, Deprati, Saetti, & Toni, 1996; Post & Welch, 1996), who also participated in the debate (Bridgeman, Peery, & Anand, 1997). The ambivalent results and methodological problems quickly created competing explanations for why it looks like grasping is more robust to visual illusions (Franz, Gegenfurtner, Bühlhoff, & Fehle, 2000; Haffenden & Goodale, 1998, 2000; Marotta, DeSouza, Haffenden, & Goodale, 1998; Mon-Williams & Bull, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farne, 1999). And these discussions continue down to the present day (de Haan, Jackson, & Schenk, 2018; Franz & Gegenfurtner, 2008; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016, 2017; Milner & Goodale, 2008; Schenk, Franz, & Bruno, 2011; Schenk & McIntosh, 2010; Smeets, Kleijn, van der Meijden, & Brenner, 2020; Whitwell & Goodale, 2017; Whitwell, Goodale, Merritt, & Enns, 2018). Due to this debate it has become increasingly difficult to argue unambiguously that illusion studies support the PAM and it is not clear that any illusion can be used as supporting the PAM unless we know exactly how the illusion is created in the brain and how this then leads to the given results when this illusion is examined in a verbal and a motor condition.

The problematic results of the illusion studies have led to a search for other approaches to investigate the PAM in healthy participants. One such other approach was to investigate the relation of the vision for action system to standard psychophysical laws, like Weber's law. Weber's law describes the relationship between the just noticeable difference (JND) and the intensity of the stimulus (I) and declares that their quotient is constant, with the constant being the Weber constant k (Billock & Tsou, 2011). Ganel, Chajut, and Algom (2008) found that grip size variability, i.e. the standard deviation of the MGA when grasping an object calculated for different object sizes, does not scale with object size. In effect the standard deviation of the MGA stays the same for objects increasing in size, while the MGA increases linearly with objects increasing in size. The authors then interpreted the variation of the MGA as a measure of the "area of uncertainty", for which the observer is unable to tell the difference between the size of the comparison and the target object" (p. R600), and this they then saw to be the JND. Due to the lack of a linear increase in what they considered to be the JND, Ganel et al. (2008) then argued that this means that grasping violates Weber's law. This would of course mean that while vision is susceptible to standard psychophysical laws, grasping is not and this one could then take as support for the PAM.

An alternative explanation was advanced by Smeets and Brenner (2008), who argued that grasping is based on position information and for that reasons should not follow Weber's law. But Ganel, Freud, and Meiran (2014) do not agree with this explanation since in their view it cannot account for memory-based grasping, for which they presented data which, in their opinion, shows that memory-based grasping does follow Weber's law, since they found a linear increase of the JND in memory-based grasping.

Heath, Mulla, Holmes, and Smuskowitz (2011) then investigated whether the JND is constant over the whole movement or only at the end. They found that after half of the movement has been finished the JND is constant, but before this halfway mark of the movement it is not. They therefore conclude that while the results of Ganel et al. (2008) are correct, it is not sufficient to take as support for the PAM and they rather see it as support for the Planning-Control Model by Glover and Dixon (Glover, 2004). Holmes, Mulla, Binsted, and Heath (2011) further investigated whether this scaling happened both during closed and open-loop grasping and they found no difference in the time-dependent scaling in the open and closed-loop conditions. Therefore they argue that the scaling they found in the previous study occurs also during open-loop grasping. As for the reason why they did not find the adaptation as Ganel et al. (2008), they speculate that possibly their 2000 ms delay was too short in comparison to Ganel et al.'s 5000 ms delay.

Ganel et al. (2014) then argued that the results reported by Heath et al. (2011) and Holmes et al. (2011) can be explained by the different task demands. They argued that when participants would

have to grasp the larger object, they would have to open their fingers faster and therefore looking at the time points of the finger opening would create the data found by Heath et al. (2011). To show that this was the correct explanation they had participants start the movement with their thumb and index finger perpendicular to each other in one experiment, which reversed the adherence to Weber's law. In a second experiment they had participants always grasp a disk 10 mm smaller than the target disk and this led to the same JNDs for all objects over all time points. They concluded that the result that action is immune to Weber's law still stands.

A further alternative explanation was proposed by Utz, Hesse, Aschenneller, and Schenk (2015). They argued that the natural upper limit of the MGA due to the size of the finger spread might be responsible for the observed variation in the standard deviation of the MGA. Since one cannot open the finger farther than the maximum that is biomechanically given, when grasping larger objects, the possible distances for the MGA are actually influenced by this maximum possible spread. And since people prefer not to completely extend their fingers, due to this being perceived as uncomfortable, one would expect a smaller standard deviation of the MGA for larger objects, which is what Utz et al. (2015) found. Therefore, since, according to Weber's law, one would expect a larger standard deviation for larger objects, and due to the biomechanical limit we find a smaller standard deviation for larger objects, these effects could sum to create the observed data and mask the influence of Weber's law (see also Schenk, Utz, and Hesse (2017)). Manzone, Jazi, Whitwell, and Heath (2017) then showed that in a pantomimed grasping task the standard deviation of the MGA actually increases with grip size. But, as Schenk et al. (2017) argued, there was no actual safety margin in the study by Manzone et al. (2017) and since the MGA in their study was smaller than the actual width of the object, considering there was no object to grasp, they just pantomimed the movement. It is very much possible that the biomechanical constraints act mostly on the safety margins and thus they are not relevant for pantomimed grasping. After all the maximum object size in the study by Manzone et al. (2017) was 80% of the maximum hand separation span of the participant and when there is no object to be grasped then 80% of the maximum hand separation span does probably not cause the safety margins to be limited by biomechanical constraints. So the discussion, whether grasping escapes Weber's law, is ongoing (Ayala, Binsted, & Heath, 2018; Bruno, Uccelli, Viviani, & de'Sperati, 2016; Heath, Manzone, Khan, & Jazi, 2017; Ozana, Berman, & Ganel, 2018; Ozana, Namdar, & Ganel, 2019).

1.4 Topic of this Dissertation

As sketched in section 1.2, the PAM was built primarily on evidence from one patient compared with a second patient population. But the results from these comparisons have also been subject to

revisions. First of all, single case studies often have low statistical power and their results need to be interpreted with this in mind (Rossetti, Pisella, & McIntosh, 2017). Furthermore, already in 2003, James, Culham, Humphrey, Milner, and Goodale (2003) showed that D.F. actually had a small lesion in the dorsal stream, which was then dismissed as functionally irrelevant. But later research started to appear that showed that possibly D.F.'s dorsal stream was not working as well as in healthy adults. Himmelbach, Boehme, and Karnath (2012) reported that when analyzed more carefully, D.F. also showed impairments in motor tasks which were previously considered to be spared. Hesse, Ball, and Schenk (2014) showed that D.F. was impaired in pointing tasks with both the left and the right hand in both the right and the left hemifield which also suggests dorsal stream damage and is often interpreted as a sign of optic ataxia. Rossit et al. (2018) then showed that D.F. actually showed visuomotor symptoms of optic ataxia when performing tasks used to diagnose optic ataxia. These results strongly question the possibility of using the original studies as unequivocal support for the PAM.

This, of course, increased the importance of group studies with healthy controls. But, as sketched in the prior section, these approaches have also met with criticism. Yet there remain three areas which have not been subjected to a similar criticism as the approaches mentioned above and. These are the idea that the dorsal stream is not susceptible to multitasking costs, the idea that the dorsal stream does not process irrelevant object properties which create the Garner interference-effect in perception, and the idea that the dorsal stream does not only not follow Weber's law but actually has a higher resolution than the ventral stream.

In this dissertation we wanted to investigate whether these approaches have not been criticized in a similar way due to them being more robust and actually presenting good evidence for the PAM or only due to them not having been scrutinized as closely as the other areas.

2. Overview of the Studies

Göhringer, F., Löhr-Limpens, M., & Schenk, T. (2018). The visual guidance of action is not insulated from cognitive interference: A multitasking study on obstacle-avoidance and bisection. *Consciousness and Cognition*, 64, 72-83. <https://doi.org/10.1016/j.concog.2018.07.007>

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Löhr-Limpens, M., Göhringer, F., Schenk, T., & Hesse, C. (2019). Grasping and perception are both affected by irrelevant information and secondary tasks: new evidence from the Garner paradigm. *Psychological Research*, 84, 1269–1283. <https://doi.org/10.1007/s00426-019-01151-z>

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3. Summary of the Studies

3.1 Experiment 1: The visual guidance of action is not insulated from cognitive interference: A multitasking study on obstacle-avoidance and bisection.

3.1.1 Background

The first approach we wanted to investigate was the question whether the dorsal stream is not susceptible to multitasking costs. Singhal, Culham, Chinellato, and Goodale (2007) investigated this question by using a delayed task combined with a secondary task, making this a multitasking paradigm. Research with patient D.F. has suggested that she has difficulties grasping an object that has just been removed from view (Goodale, Jakobson, & Keillor, 1994). The authors saw this as implying a real time control of grasping, which is working in patient D.F., and also that the dorsal stream does not have memory. This has become part of the PAM (Goodale, Westwood, & Milner, 2004), but see also Schenk & Hesse, 2018). Singhal et al. (2007) now wanted to further investigate the ideas that the dorsal stream has no memory and that the ventral stream is recruited in delayed grasping, as shown in the failure of patient D.F. to grasp an object that has just been removed from view, by using a dual-task design. Creem and Proffitt (2001) had shown that a semantic secondary task interfered with grasping an object by the handle while a spatial secondary task interfered far less. Singhal et al. (2007) combined this idea with the concept of real time control of grasping by having participants perform one visually guided grasping task or a delayed grasping task combined with a semantic shape discrimination task. Their hypothesis was that the semantic task would engage the same system, overlapping with the ventral stream, as in delayed grasping and would thus create interference, while there would be no interference in the visually guided grasping task, since the semantic task would not engage the dorsal stream. In a second experiment they used a memory task as the secondary task, expecting that this task would engage the ventral system even more. In both experiments they found that interference was greater in delayed grasping and concluded that this interference possibly came about due to the overlapping nature of the processing resources required for each task. Unfortunately they only used one question at the beginning of the trial, so it is possible that there were actually two consecutive tasks in this study instead of two parallel tasks, since the answer to the question might have been found before the actual pointing movement started.

In another experiment Liu, Chua, and Enns (2008) used a rapid serial visual presentation (RSVP) task concurrently with a pointing task, which was presented during the whole pointing movement. They found that while the secondary RSVP task caused longer reaction times in the pointing task, it did not interfere with the adaptation of the pointing response to a shift of the target while the hand was in motion. They conclude that this shows that the planning of the pointing response shares resources with a cognitive task but not the online control of the pointing response. Unfortunately, Liu et al.

(2008) only looked at movement time as a dependent measure for the pointing and did not actually track the movement, so any smaller interference of the secondary task with the pointing response could not have been identified.

3.1.2 Experimental study

In order to avoid the difficulties implied by the previous studies, we used a continuous RSVP task, which was presented to participants during their whole movement. The RSVP task consisted of numbers presented consecutively on a screen with most numbers being white but random targets being black and the participants had to remember the black numbers. We also used motion tracking in order to analyze the actual trajectories of the movements. Furthermore we used two movement patterns that have already been found to be specifically affected by dorsal or ventral stream damage. The first movement pattern was bisection, in which participants had to use their index finger to bisect an imaginary line between two obstacles. This movement pattern was found to be affected by damage in the ventral stream (McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; McIntosh, McClements, Schindler, et al., 2004). The other movement pattern was obstacle-avoidance, in which participants had to move their hand through two obstacles without touching the obstacles. This movement pattern was found to be affected by damage in the dorsal stream (Schindler et al., 2004). According to the PAM therefore we would expect bisection, the ventral stream task, to be affected by a secondary RSVP task but not obstacle-avoidance, the dorsal stream task. We used how much their movement was adapted by a shift of one outer obstacle towards the center as the dependent variable for the movement task, that is how much they reacted to a shift of the virtual midpoint of the line by moving their hand towards that virtual midpoint.

We found that participants adapted their movements more to a shift of an outer obstacle in the single task condition than in the dual-task condition, with no significant difference between obstacle-avoidance and bisection. This suggests that, contrary to the PAM, obstacle-avoidance also suffers under dual-task conditions. We also found that performing the movement task concurrent with the secondary task negatively affects the secondary task both in bisection and obstacle-avoidance also contrary to the PAM, which argued for independence between the cognitive task and the motor task.

3.2 Experiment 2: Grasping and perception are both affected by irrelevant information and secondary tasks: new evidence from the Garner paradigm.

3.2.1 Background

The second approach we wanted to investigate was the use of the Garner paradigm in grasping (Ganel & Goodale, 2003, 2014). (Garner, 1974; Garner, 1976, 1978) showed that when stimuli vary only along a relevant dimension, for example if one has to classify an object as either long or short, then classification performance is good, but if the object also varies along an irrelevant dimension, for example thick and thin, so that one has four objects which have to be classified, a long thick one and a long thin one as well as a short thick one and a short thin one, classification performance drops (with performance being measured, for example, in reaction time). In the condition in which an irrelevant dimension also varies, the participant has to “filter” the irrelevant dimension and only focus on the relevant dimension. This condition is therefore called the filter condition, while the condition in which only the relevant dimension varies is called the baseline condition.

Ganel and Goodale (2003) showed that, when using a setup similar to the one described above as example, participants showed increased reaction times in the filter condition, when they had to classify objects as thick or thin that also varied in their length, relative to the baseline condition, when the objects did not vary in their length. But when participants were asked to grasp these objects there was no difference in the MGA between baseline and filter conditions as well as the reaction time, the time to reach the MGA, and the movement time. The authors therefore conclude that the dorsal stream, responsible for grasping, is analytic in its processing, ignoring irrelevant dimensions, while the ventral stream is holistic, which means unable to ignore irrelevant dimensions. It needs to be noted that it is not clear why one would expect a difference in the absolute value of the MGA between baseline and filter conditions, since it is not clear that participants would necessarily have a smaller (or larger) MGA in the filter condition. It is also not clear why the reaction time for movements should show a Garner effect, since the relevant decision in movements does not happen at the start of the movement but possibly at the point of the MGA or later, which creates the following problem, described by Hesse and Schenk (2013).

Hesse and Schenk (2013) argued that the lack of a Garner effect found by Ganel and Goodale (2003) might be the result of this difference in the temporal profile of speeded classification and grasping. After all, a speeded classification task is performed with a button press which has to happen as soon as possible while the time to reach the MGA is more than twice the duration of the reaction time in the speeded classification task, according to the data presented by Ganel and Goodale (2003) (see Figure 2 p. 666). Therefore they created a task in which the speeded classification had a similar time profile to the grasping task by positioning the buttons at the same distance as the object which

needed to be grasped. This manipulation abolished the Garner effect in the speeded classification task, supporting their thesis that the lack of a Garner effect found by Ganel and Goodale (2003) was a result of the temporal profile of the different tasks.

Ganel and Goodale (2014) then revisited their earlier study to show that when analyzing the standard deviation of the MGA in grasping and comparing that to the standard deviation of the MGA in manual estimation, that is indicating by separating thumb and index finger how large the object is, there is a significant difference between baseline and filter conditions in the manual estimation condition but not in the grasping condition. This they also replicated in a second experiment. They conclude that this is more evidence for analytic processing in the dorsal stream and holistic processing in the ventral stream. But one could argue, as also mentioned below, that it is not at all clear what manual estimation actually measures (Schenk, 2012).

3.2.2 Experimental Study

In order to further investigate the differentiation between holistic and analytic processing in the different streams, we combined the Garner task with a secondary task to investigate whether adding a secondary task increases the effect of the Garner task on grasping. As described above, the PAM would not expect a secondary task to influence grasping at all, but only to influence a speeded classification task.

We had participants perform a speeded classification task and a grasping task on the same stimuli, being presented in a mirror apparatus. These stimuli varied only in length (baseline condition) or in length and in width (filter condition). Next to the stimuli was presented a secondary task in which the relevant dimension that varied was either color or object shape. In the color condition the target differed in color from the distractors by being slightly more orange and in the shape condition the target differed from the distractors by being a perfect square while the distractors were rectangles of the same dimensions as in the grasping task.

We found an expected Garner effect in the speeded classification task and we also found the expected dual-task costs when the secondary task was present. We also found, contrary to Ganel and Goodale (2014), a significant difference between baseline and filter in the standard deviation of the MGA, while it needs to be mentioned that, descriptively, this effect seems to be a result of the dual-task shape condition. We also looked at a more common measure used in grasping research, the slope of the function relating object size to MGA, which indicates how well the hand opening adapts to the size of the object. There we found a significant difference between filter and baseline conditions and also a significant difference between single and dual-task conditions, which again

seems to be a result of the secondary shape task. We also found a significant difference between baseline and filter in the adjustment time of the hand, that is the time at which the hand opening for the large object was bigger than half the difference between the lengths of the objects. Lastly we also looked at the reaction times for grasping, where we found no effect of the filter condition, as was expected considering the time profile of the task, but we found a main effect of the secondary task.

In sum, we found that when a secondary task is added grasping performance decreases and Garner effects, which might be hid in a single task condition as in the standard deviation of the MGA, can be discovered, although this needs further research.

3.3 Experiment 3: Grasping discriminates between object sizes less not more accurately than the perceptual system.

3.3.1 Background

The last approach we wanted to investigate was whether grasping actually has a higher resolution than perception. Additionally to the data purporting to show that grasping does not adhere to Weber's law, Ganel, Freud, Chajut, and Algom (2012) suggested an alternative but similar approach to show that grasping is processed differently than perception. For their study they used two circular disks with a diameter of 40 mm and 40.5 mm respectively. They estimated a difference of 0.5 mm to be below the perceptual threshold of size discrimination, since this was a size difference of about 1%.

They then presented participants with both disks, one disk being positioned directly in front of the participants and the other disk being positioned either to the right or to the left of the participant behind the disk in front. The participants had then to verbally report whether the disk in front was larger or smaller than the disk in the back and then grasp the disk in front but not the disk in the back (one group first had to report whether the disk was smaller or larger and then grasp the disk, another group first had to grasp the disk and then report whether the disk was smaller or larger, there was no statistically significant difference between the groups). They also performed a second experiment in which participants had to manually estimate the size of the disks, which was not central to their argument.

The data subsequently showed that participants were correct in assessing the size of the disk in 58.7% of the cases in the first experiment and 62.7% of the cases in the second experiment, which is below the commonly agreed on threshold for the just noticeable difference (JND) of 75%. This showed that participants were not able to consistently verbally indicate which of the two disks was larger or smaller.

But analyzing the grasping data showed that there was a significant difference in the mean MGA for the small and the large disk. Participants had a smaller mean MGA when grasping the small disk and a larger mean MGA when grasping the large disk, irrespective of whether they correctly identified the size of the disk or not. The authors concluded from this that the MGA always reflected the actual size of the object, independent of whether the size of the object was perceived correctly or incorrectly.

In their second experiment they had participants manually estimate the size of the target disk and there they found that the manual estimation followed the perceived size of the target disk. That is the manual estimate, measured as the distance between thumb and index finger held for a total of 150 ms, with which participants intended to indicate the size of the disk, was dependent on how participants perceived the object. If participants perceived the object to be larger, the manual estimate was larger and if participants perceived the object to be smaller, the manual estimate was smaller, regardless of the actual size of the object. The authors considered this to be analog result to their grasping data. It should be mentioned that a discussion exists what is actually being measured with manual estimates (Schenk, 2012) and that the authors never performed a direct statistical comparison between their grasping and their manual estimation data, which would be necessary for the conclusions the authors reached.

Irrespective of what the authors actually measured with the manual estimation data, we intended to investigate whether their conclusion from the first experiment holds that the MGA always reflects the actual size of the object and not the perceived size.

3.3.2 Experimental Study

In order to be able to compare the continuous measure of the MGA with the dichotomous measure of the perceptual decision, we decided not to use another perceptual measure as Ganel et al. (2012) did in the case of their manual estimation task, since even if the results found by Ganel et al. (2012) would have held up a direct statistical comparison, the conclusion could not have been that the MGA always reflects the actual size of the object but only that the average of the MGA is significantly smaller for the small object and significantly larger for the large object, which is not the case in the manual estimation condition.

We were interested in the question whether the MGA is actually always smaller for the small object and larger for the large object. And even if this is not always the case, the PAM would predict that, if grasping is more precise than perception, the MGA should be smaller for the small object and larger

for the large object in more trials than the number of trials in which the participant says that the smaller object is smaller and the larger object is larger.

We therefore decided to instead find the optimal cut-off value that separates the MGAs of the grasping trials (Schenk, 2006; Schenk & Milner, 2006). Starting from the smallest MGA value up to the largest we calculated how many trials would be correctly “classified” if we used a cut-off value at positions between the minimum and the maximum. If one used a cut-off value that is smaller than the smallest MGA, all MGAs to large objects would be correctly classified as large but all MGAs to small objects would incorrectly also be classified as large, therefore one would have only 50% of all MGAs correctly classified. The same would happen if one used a cut-off value larger than the largest value. But if, as Ganel et al. (2012) argued, the MGA would always reflect the actual size of the object, we should have been able to find a cut-off value that would correctly classify all MGAs towards the smaller object as small and all MGAs towards larger objects as large. Or at least find a cut-off value that correctly classifies the MGAs in this case more often than the perception of the participant is correct. For example, if all MGAs towards the 40 mm object were exactly 45 mm, the MGA always being slightly larger than the actual object the movement is directed towards, and all MGAs towards the 40.5 mm object were exactly 45.5 mm, then a cut-off value of 45.25 would perfectly classify all MGAs towards the larger object as larger and towards the smaller object as smaller. Due to noise in the motor system such perfection is not to be expected, but according to the PAM and Ganel et al. (2012), a classification that is at least as good as the verbal identification should be possible. For the optimal cut-off we chose the classification that was the best possible given the grasping data from the participant.

We therefore first tried to replicate the data found by Ganel et al. (2012) and then intended to analyze the replicated data using the optimal cut-off method sketched above. We performed three experiments. In the first experiment we were not able to replicate the data reported by Ganel et al. (2012) In the second experiment we did replicate the findings by Ganel et al. (2012) and in the third experiment we added an open loop condition in order to compare the open loop condition with the closed loop condition used in the previous experiments. In this third experiment we again did not replicate the data from Ganel et al. (2012) for the closed loop condition and found no effect in the open loop condition. In experiments 1 and 3, where we did not replicate Ganel et al. (2012), we found that MGAs were significantly different when participants judged the object sizes correctly but not when they judged them incorrectly. Using the optimal cut-off method we then found that grasping was always less precise than the verbal report, which was also the case in experiment 2, where we directly replicated Ganel et al. (2012). This shows that it is not the case that participants’ MGA always reflects the actual size of the object.

4. Presentation of the Studies

4.1 The visual guidance of action is not insulated from cognitive interference: A multitasking study on obstacle-avoidance and bisection.



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The visual guidance of action is not insulated from cognitive interference: A multitasking study on obstacle-avoidance and bisection

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ABSTRACT

The Perception-Action Model (PAM) considers the visual system to be divided into two streams defined by their specific functions, a ventral stream for vision and a dorsal stream for action. In this study we investigated two behavioral paradigms which according to PAM represent the two contrasting functions of the ventral and dorsal stream, namely bisection and obstacle-avoidance, respectively. It is an assumption of PAM that while ventral stream processing is ultimately linked with processing in other cognitive systems, dorsal stream processing is insulated from cognition. Accordingly it can be expected that a secondary task will interfere with bisection but not with obstacle-avoidance. We tested this prediction using a rapid serial visual presentation task as our secondary task (RSVP). Contrary to expectations we found significant interference for both bisection and obstacle-avoidance. Our findings suggest that dorsal-stream processing is not insulated from cognitive processes.

1. Introduction

Bruce Bridgeman and his colleagues were among the first to suggest a subdivision of the visual system into two functionally and anatomically separate subsystems (Bridgeman, Kirch, & Sperling, 1981; Bridgeman, Lewis, Heit, & Nagle, 1979; Ingle, 1968; Schneider, 1967, 1969). This hypothesis was further developed by Ungerleider and Mishkin (1982) who used the terms ventral and dorsal pathways to refer to occipito-temporal aspects and the occipito-parietal aspects of the visual system, respectively and extended by Livingston and Hubel (Livingstone & Hubel, 1988) who linked the ventral/dorsal subdivision to a similar subdivision in the subcortical visual structures between a parvo-cellular system projecting primarily to the ventral part of the visual cortex and a magno-cellular system projecting primarily to the dorsal pathways. The result was a subdivision that went all the way from the retina to the highest levels of the hierarchy of the visual system in the sensory cortex. It was always assumed that the two systems are not just anatomically but also functionally distinct. Ungerleider and Mishkin assumed that the two systems represent and process different attributes of the visual world. The ventral system deals with colour, shape, pattern and other features that help us to identify an object. In contrast the dorsal system deals with position and motion. Broadly speaking the dorsal system helps to determine where in the world an object is located or in the case of motion where this object will be located in the near future. As a short-hand they introduced the terms “what”-system for the ventral and “where”-system for the dorsal pathway. Milner and Goodale (1995) accepted the anatomical characterization of the two systems but suggested a different functional interpretation. They argued that the key distinction is not between visual attributes but between different behavioral functions. The two relevant functions in this case are

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visual perception and visually guided actions, accordingly Milner and Goodale's proposal became to be known as the what/how distinction. Visual perception in this case means the identification of objects and scenes. For this process a representation is useful that emphasizes features that are mostly unaffected by the specific conditions under which a given object or scene is perceived. The type of invariant representations that had been described for areas in the ventral stream seemed perfect for this task. The task of visually guided action in contrast requires that parts of our body are guided towards objects and this demands that features of the sensory input that provide information about the relationship between observer and object are maintained. This relationship between a given behavioral task and its preferred modus of sensory representation is most obvious in the case of an object's position. To recognize an apple as an apple it is not critical whether that apple is to the left or right of me. However, if I wish to grasp the apple I need to know its position relative to my grasping hand.

This example also shows that Milner and Goodale's functional redefinition of the role of the two visual systems was more than a re-branding of the what/where distinction. Crucially while the what/where distinction assigns all processing of spatial information to the dorsal stream, the what/how distinction assumes distinct visual systems for space representation in the ventral and dorsal pathways. The insight that visual cognition ('what') and visuomotor control ('how') use different spatial representations and different brain processes was supported by a seminal study published by Bridgeman and colleagues in 1997 (Bridgeman, Peery, & Anand, 1997). The illusion used in their study was based on a demonstration by Roelofs (1935). Roelofs observed that when a rectangular frame is presented with one edge directly in front of the observer, the edge is not perceived as directly in front of the observer but in fact as shifted in the direction opposite to the rest of the rectangle. Bridgeman (1991) modified this illusion. He asked participants to judge the location of a dot presented with or without a surrounding rectangular frame. It was found that when the dot was not in the center of the frame, the offset between dot-position and midpoint of the frame induced a mislocalization of the dot. This mislocalization is called the induced Roelofs effect. Bridgeman et al. (1997) demonstrated that this illusion fooled our conscious perceptual judgment but did not affect rapid reaching movements. This and other observations (Aglioti, Desouza, & Goodale, 1995) prompted a rush to find other examples where a perceptual illusion left visually guided action unaffected. Many examples were found and thus the evidence for the what/how distinction became ever more impressive (for reviews see: Bruno, 2001; Carey, 2001). Dassonville and Bala (2004) later proposed an alternative hypothesis which stated that the induced Roelofs effect was actually based on a distortion of the observer's midline. Bridgeman then suggested a further way to test this reinterpretation by using a paradigm which he had already developed in his own lab. In a multi-lab collaboration Dassonville, Bridgeman, Kaur Bala, Thiem, and Sampanes (2004) were able to show that their interpretation based on the assumption of a distorted midline explained the findings better than the what/how distinction. While this reinterpretation of Bridgeman's own earlier findings could not seriously undermine the evidence base for the what/how distinction it provided an impetus for many other researchers who argued that the failure of perceptual illusions to influence visually-guided actions reflected methodological problems and did not support theoretical subdivisions (Franz & Gegenfurtner, 2008; Smeets & Brenner, 2006). While this debate is still on-going it can be concluded that the mechanism underlying the what/how dissociations for perceptual illusions is now sufficiently marred in controversy to prevent the use of perceptual illusions as a compelling tool for examining the validity of the what/how distinction or as we will call it from now on the perception-action model/PAM (Kopiske, Bruno, Hesse, Schenk, & Franz, 2017; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016; Whitwell & Goodale, 2017).

At this stage we might ask ourselves whether such a tool is actually needed. Goodale and his colleagues emphasized that it is the evidence from neurological patients which provides the backbone of support for their model (Westwood & Goodale, 2011). How else could one explain why patients with ventral damage fail to perceive aspects of visual objects while still interacting successfully with those very objects and why patients with dorsal damage fail to produce accurate movements towards visual objects despite having normal perceptual abilities? Neuropsychological evidence for the what/how distinction is certainly intriguing but it is hardly unchallenged and more importantly it is subject to a problem that affects many neuropsychological interpretations. Finding preserved function in a patient with brain damage can indicate that the damaged brain structure is not involved in this function, but it does not have to mean this. Conversely, such preserved capacity could also indicate that this function is served by a redundant brain system. If just one component of the system is affected, the loss can be compensated and the function is preserved. Schenk (2010) argued that this latter explanation provides a more plausible account for the neuropsychological evidence that has been marshalled in defense of the what/how distinction (Schenk, 2010). To sum up neuropsychological evidence does not provide unequivocal evidence that the distinction found in the case of brain-damage also applies to the healthy brain. Findings from research on illusions seemed to provide the required evidence. However, the reliability of this evidence has been questioned. This means we need to find alternative ways to test the claim that in healthy brains vision for perception and vision for action is also processed in separate pathways.

Such an alternative was suggested by Singhal, Culham, Chinellato, and Goodale (2007). The PAM suggests that only the ventral stream feeds into and has access to the cognitive system. Accordingly it can be expected that processing in the cognitive stream might interfere and interact with processing in the ventral stream but the same should not be true for the dorsal stream. This can be tested with a dual-task paradigm. Performance in a task assigned by the model to the ventral stream when carried out on its own should be significantly better than performance for the same task when carried out in conjunction with a second, cognitive task. This should not be the case for a task that is assigned to the dorsal stream. To put it differently, we expect significant multitasking costs for ventral tasks but not for dorsal tasks. We know that multitasking costs are widespread and we also know that these costs vary between tasks. Different tasks have different demands and we can expect that different tasks vary in their susceptibility to multitasking interference. If we want to claim with any confidence that the variation in multitasking costs are due to the fact that one task is processed in the ventral stream and the other in the dorsal stream, we need to ensure that the two tasks are well-matched in most respects. Singhal and colleagues achieved this by exploiting an interesting assumption of the PAM. PAM assumes that the dorsal stream has no visual memory (Westwood & Goodale, 2003). Consequently actions that are based on memorized visual information, even if that

information has been withdrawn for only a few hundred milliseconds, have to rely on information coming from the ventral stream. This means it is possible to compare two almost identical visuomotor tasks that differ only in one respect, namely for one task the visual target information, e.g. the target object to be grasped, is present right up to the time when action starts (immediate action) and in the other case the target object is seen at the beginning of the trial but view of the object is withdrawn a fraction of a second before the movement is started (delayed action). In the former case, the dorsal stream can exclusively handle the task, no multitasking costs are expected. In the latter case the ventral stream is involved and multitasking costs are expected. Singhal and colleagues used an immediate and delayed grasping task to test this prediction in two separate experiments (differing with respect to the secondary task employed) and found - as expected - significant multitasking costs for delayed grasping but not the immediate version. This was taken as specific evidence for the claim that the dorsal system is insulated from the cognitive system. More generally it might also be seen as support for the key assumption that the distinction between vision for perception and action applies to the healthy brain. However, there are difficulties with that interpretation. First and foremost the underlying assumption that the dorsal stream has no visual memory is neither convincingly supported by physiological, neuropsychological or psychophysical evidence (for a recent review, see [Schenk & Hesse, 2017](#)). Consequently, the claim that delayed action must involve the ventral stream is problematic. But without this assumption the increased multitasking costs observed in the delayed condition cannot be used to extend the what/how distinction from damaged brains to healthy brains. Secondly, there is a peculiarity of the study's design that renders the interpretation difficult. The secondary task in both experiments is presented only during the time period between the onset of a signal prompting the beginning of the movement and the actual onset of that movement. Finding different multitasking costs in two primary tasks (e.g. immediate versus delayed grasping) could therefore also indicate that the potential vulnerability for cognitive interference occurs at different time intervals of the two tasks. If true presenting the secondary task only during a short period of the entire task could mean that this task coincides with the vulnerable period of one task but not the other. This account achieves reasonable plausibility when the two tasks in question only differ with respect to the time-course of critical events – as is the case in the comparison between immediate and delayed grasping. More specifically there is potentially a quite simple reason that could account for the increased multitasking costs in the case of delayed grasping. During immediate grasping, sensory conditions remain constant while the secondary task is introduced; during delayed grasping, vision is removed at the exact time when the secondary task is introduced. Thus in delayed grasping there is direct attentional competition between two salient events (e.g. introduction of auditory stimuli and change in visual conditions) that could lead to interference between the two tasks. It is not unreasonable to assume that this effect may have been exacerbated by a second design feature of this study, namely: immediate and delayed grasping conditions were presented in interleaved fashion so that the change in visual conditions in the delayed condition came suddenly and somewhat surprising. Such a correlated change in sensory conditions did not happen during the immediate condition. This difference could explain why in immediate grasping less interference was observed. A final issue relates to the parameters that provided evidence for a different multitasking vulnerability in delayed versus immediate grasping. A consistent difference was only found for movement time. One might expect that cognitive interference with ventral processing affects the time it takes to prepare a movement and thus reaction time but it is not clear why such interference should affect how long it takes to execute that movement.

Some of those problems were avoided in another study on the same topic. [Liu, Chua, and Enns \(2008\)](#) used a rapid serial visual presentation paradigm to serve as the secondary, cognitive task. This cognitive task ran alongside the primary task – pointing task – for the entire duration of the trial. Liu and colleagues thus avoided the problem that compromised the Singhal et al. study, namely that interference could be probed during a specific interval of the trial. Interestingly, the pointing task used in Liu et al.'s study came with a twist. In some trials the pointing target shifted to a new position *after* participants had started to move, requiring an *online adjustment* of the pointing response. The secondary task affected the reaction time for the initial pointing response but not the capacity to make online adjustments in response to late target displacements. [Liu et al. \(2008\)](#) assume that reaction time for the initial movement reflects motor planning while parameters of the late online adjustments can be taken as performance markers for motor programming. They thus argue that dual-task interference affects only planning but not programming. PAM assumes that motor planning but not programming requires input from the ventral stream. Liu et al. results thus seem to support the notion that cognitive interference affects only ventral stream processing and thus provide evidence that the what/how distinction applies also to the healthy brain. There are some difficulties with that conclusion.

Firstly, the hypothesis that all processes prior to movement onset involve the ventral stream and that only online adjustments are under the exclusive control of the dorsal stream is at odds with the assumptions of the PAM and contradicted by numerous neuropsychological findings showing that reaching and grasping movements are spared in patients with ventral stream damage and impaired in patients with dorsal stream damage specifically in conditions where no online adjustments are required (for a review see [Goodale and Milner \(1992\)](#)). Secondly, the absence of multitasking costs for online adjustments might reflect the insensitivity of the measures adopted to probe for these costs. The dual-task effect on reaction time shows that additional load typically only delays an ongoing motor process. Similarly we might expect that for online corrections dual-task interference might delay the onset of that online correction but not prevent its implementation. To detect such delays it is important that pointing movements are recorded throughout its entire course. However, such data were not available to Liu and colleagues. They had only a touch-screen to record the time and location of the end-position and thus used movement time as their only measure to judge whether online corrections had been affected by the secondary task or not. Unless we assume that the implementation of an online correction takes as long as it takes to perform the entire reaching movement there is no reason to assume that a delay in the onset of that correction would lead to an increase of movement time. Put simply, movement time is a fairly insensitive measure to check for interference effects in reaching movements (for an example of this difficulty, see [Hesse, Schenk, and Deubel \(2012\)](#)). One way to avoid this problem is to look for the reverse interference, i.e. to check how aspects of the ongoing motor process affect performance in the secondary, cognitive task. Such reverse interference measures when used in combination with a continuously running secondary task have the advantage that

interference can be probed at any time of the trial. Moreover, since the secondary task remains the same across different motor conditions performance in the secondary task can provide us with a standard measure for interference. We can thereby avoid the use of different measures with different sensitivity profiles for the contrasting motor tasks or motor aspects.

To sum up, the examination of dual- or multitasking costs for different types of visual behavior provides us with a tool to examine the claim that visuomotor behavior is based on processes that are insulated from cognitive processes. This approach thus provides an opportunity to test whether the what/how distinction applies to the healthy brain. A few studies addressed this question directly but could not provide conclusive answers. For this reason we conducted a further study which aimed to rectify some of the methodological difficulties that we identified in the preceding paragraphs. Specifically, we named four issues. Firstly, it is important that we pick two convincing and comparable representatives of a ventral and a dorsal task. We opted for bisection and obstacle-avoidance as representatives of a ventral and dorsal task, respectively. In line with this classification it was found that bisection but not obstacle-avoidance is impaired in patients with damage associated with the ventral system (visual form agnosia and unilateral neglect, see McIntosh, McClements, Dijkerman, Birchall, & Milner, 2004; Rice, McIntosh, Schindler, Démonet, & Milner, 2006) and the opposite pattern was found after dorsal-stream damage (Schindler et al., 2004). Furthermore, obstacle-avoidance has been presented as a behavior that relies on purely, subconscious (McIntosh, McClements, Schindler, et al., 2004; Striemer, Chapman, & Goodale, 2009) visual information. Picking the appropriate pair of tasks to test the prediction of the PAM is not trivial since for many of the possible candidates critical issues have been raised (e.g. grasping versus manual estimation (Franz, 2003; Schenk, 2012); orientation matching versus posting (Hesse, Franz, & Schenk, 2011)). This is also true for bisection versus obstacle avoidance (see Ross, Schenk & Hesse, 2014). While we argued above that neuropsychological evidence can have its own difficulties, it is important to note that our critique related to the difficulty of drawing neurofunctional conclusions on the basis of behaviors that are spared by a brain lesion (preserved behavior). However, this critique does not affect the type of neuropsychological evidence where a specific brain lesion causes a deficit in a specific behavior. In this case the implication that the damaged brain structure plays an important role for the affected behavior is actually quite compelling. Based on this reasoning we decided to use neuropsychological evidence on impaired behavior after selective brain damage to guide our choice and concluded that the neuropsychological evidence is particularly consistent and strong for the claim that bisection and obstacle avoidance are related to the ventral versus dorsal stream, respectively.

Finding dual-task interference in obstacle-avoidance behavior would thus constitute a particularly interesting challenge to the claim that dorsal-stream behavior is insulated from cognitive processes. Secondly, we emphasized the importance of using a secondary, cognitive task whose duration matches the duration of the experimental trial. Using such a task ensures that the vulnerability to cognitive interference can be measured for all phases of the primary task and furthermore avoids the possibility that differences in multitasking costs do not simply reflect variations in timing. For this reason we opted for a rapid serial visual presentation task (RSVP) with multiple possible targets that requires participants in our experiments to attend to the stream of visual stimuli for the entire duration of each trial. Thirdly, we want to avoid the problem of confounding dual-task costs with differences in sensitivity. The findings from Ross et al. (2014) have highlighted the fact that obstacle-avoidance but not bisection performance is affected by variability in the participants' start positions. Start positions are just one potential source of noise. The variability measures obtained in the study by Ross and colleagues showed that movement-end- and midpoint positions are quite generally more scattered than those found for bisection. Looking at reverse interference, i.e. the effect of primary tasks (bisection vs obstacle-avoidance) on the secondary task (RSVP) provides an elegant way to address this problem. The secondary task remains the same for both tasks and this means dual-tasks costs can be measured with the same sensitivity for both primary tasks. In order to do this we also added a RSVP-only condition to the design of our study.

2. Methods

2.1. Participants

Thirty-three undergraduate and graduate students of the University of Munich (11 males; mean age = 23.5 years, age range = 18–34 years) took part in the experiment. Five participants had to be excluded from the experiment, three due to equipment failure, one as an outlier, and one due to lack of compliance. All participants were right-handed by self-report. They had normal or corrected-to-normal vision. They were also naïve with respect to the goals of the experiment. The experiment was approved by the University of Erlangen's ethics committee and conducted in accordance with the Declaration of Helsinki. Every participant gave informed consent for the experiment and was paid 8€ per hour or was given course credit. The testing was done in two sessions of approximately 1.5 h each.

2.2. Apparatus and stimuli

The experimental setup is shown in Fig. 1. Participants sat on a height-adjustable stool in front of a table. The apparatus, consisting of a chin rest, an LCD shutter window, a monitor, and a wooden board with two cylindrical objects, was positioned in front of them. The wooden board (60 cm²) was used to position the objects at 4 or 8 cm to the left or right of its center in horizontal direction. The distance between starting position and the objects was 31 cm. The monitor was positioned 69.5 cm in front of chin rest. The shutter window is a translucent LCD window which is used to quickly block out the view of the objects and the participant's hand. Its angle was individually adjusted so that the participant could see the complete screen of the monitor above the window, but not the objects. The height of the chin rest was 41.4 cm. The stool was individually adjusted so that participants could comfortably position their chin on the chin rest. All participants wore a head-mounted eye tracker to control for fixation. The start position

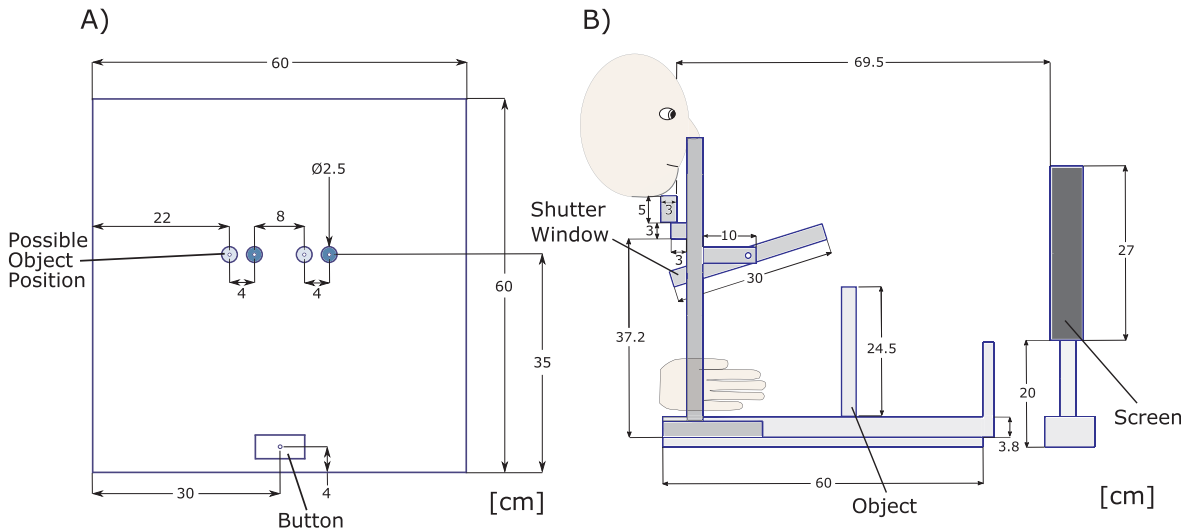


Fig. 1. Setup as seen from above (A) and from the right side (B). (A) Circles in the middle indicate the possible object positions. Both objects positioned outside represents the *Center* condition. Only the right object positioned inside is the *Right Object In* condition and necessitates a movement to the left. Only the left object positioned inside is the *Left Object In* condition and necessitates a movement to the right (this condition is shown in A). It was never the case that both objects were at the inner position at the same time. (B) Experimental setup as seen from the right. The shutter window made it possible to occlude vision of the objects while keeping vision of the computer screen intact. Height of the moveable shutter window was adjusted individually, so that participants were able to see the whole screen but not anything below the screen. All measurements are in cm.

consisted of a button which was positioned centrally on the board. The participants were instructed to keep their hand upright between trials and keep the button pressed with the side of their hand. The objects consisted of two round white cylinders of height 24.5 cm and diameter 3 cm. They could be positioned either 4 cm or 8 cm away from the midline in both directions.

The shutter window was introduced in order to make sure that participants did not see their hands while performing the task (open loop). This ensures that participants only use the information they have gathered at the beginning of the trial. This also makes it impossible to see the repositioning of the objects between trials.

Hand position was recorded with a Vicon Bonita System at a sampling frequency of 100 Hz. Markers were positioned laterally on the index finger, so that they did not disturb the participant in the bisection condition. Further markers were positioned on the interosseous muscle between thumb and index finger and on the wrist. Only the index finger marker was used for further analysis.

Participants were instructed to focus on a grey circle presented on the screen at all times. We checked for breaks of fixation using an Eyelink II to monitor eye movements at a sampling frequency of 100 Hz. Trials with broken fixations were discarded.

Rapid Serial Visual Presentation (RSVP) Task

The RSVP task consisted of participants being presented with 31 numbers (see Fig. 2). The numbers had a size of 2.1 degrees. Every number was presented for 50 ms with 66 ms blank interval between numbers. One to three of those numbers could be black

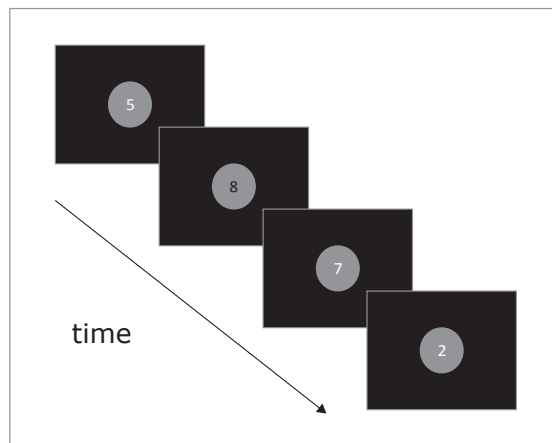


Fig. 2. Four frames of the RSVP task. A number was presented for only 50 ms. The interval between presentations was 66 ms. White numbers were distractors and black numbers were targets. There were 1–3 targets per trials. Participants had to report the target numbers at the end of the trial.

with the remaining numbers being white. Those were the targets and the participants were instructed to verbally report their identity after each trial. In this way we avoided motor or attentional interferences due to reporting the target numbers during the trial. Using this kind of RSVP task had the further advantage that the participants were in this way not able to adopt a strategy which would make it possible for them to perform the tasks in sequence. Since the participants knew that it was possible for one to three targets to occur, in the conditions where there were only one or two targets it was possible up until the last number for that last number to be the target. Therefore they had to start the movement earlier than the last number, since after the last number the shutter window would turn opaque again. This therefore precluded them from adopting a strategy of waiting until all three targets had occurred, since they could not predict whether the current trial would be a trial with three targets or only with two or one. We piloted the task to a difficulty of 80% ($n = 8$).

The participants performed 144 trials, one third of which were no-movement trials, in which they did not have to move their hand but only to perform the RSVP task, one third were single-task trials and one third were dual-task trials, separated into blocks of bisection and obstacle-avoidance. Every block had 12 trials. At every change of blocks the participants were informed about the upcoming task. The objects were positioned either both at the outer position (8 cm from the midline), or either the right one or the left one at the inner position (4 cm from the midline) (see Fig. 1). The position of the objects was randomized and counter-balanced. The participants were instructed to reach as fast and accurately as possible.

2.3. Procedure

At the start of each trial the participants had their hand on the button, their chin in the chin rest and the shutter window was closed. The experimenter initiated the next trial and the shutter window opened and, at the same time, a sound indicated the start of the trial. The participants then had to perform the bisection or obstacle-avoidance task and, in dual-task trials, the RSVP task at the same time. As soon as the participants initiated the movement, the shutter window closed, but the RSVP task, or, in single-task trials, the grey circle, remained visible. After performing the movement, the participants had to return with their hand to the start position. In single-task trials the trial was over when the participant returned to the start position. In dual-task trials the end of the trial was indicated by the end of the number presentation of the RSVP task. The participants then reported what target numbers they had seen.

2.3.1. Obstacle avoidance task

In the obstacle-avoidance task participants were instructed to move their hand into the target zone behind the two objects and not to move around the objects but between them. No further information as to how exactly to move their hands was provided. Participants were not instructed to not collide with the objects but still collisions with the objects never occurred.

2.3.2. Bisection task

In the bisection task the participants were instructed to indicate the midpoint between the two objects (see Fig. 1). That is participants had to imagine a line connecting both objects and then point with their index finger where they would judge the center of this line to be. This pointing movement had to be performed in such a way that their finger would come to rest on the board at the position of the line where they would judge the center to be. As in all conditions, Participants were not able to look down but had to use their peripheral vision.

2.4. Data analysis

The movement data were filtered using a linear filter. In obstacle-avoidance trials we analyzed the position of the marker at the time point when it passed the objects. In bisection trials we analyzed the position of the marker at the end of the movement defined as the first frame in which the speed of the marker was less than 0.02 m/s. We excluded all trials in which the participant performed a saccade downwards towards the objects.

We calculated a *sensitivity index* using the same method as Ross, et al. (2014). We first calculated the average position on the x-axis in the conditions when either the right or the left object was positioned inside, as well as when both objects were positioned outside. We then subtracted the average value for the condition when both objects were positioned outside from the average value for the condition when the left objects was positioned inside and from the average value for the condition when the right objects was positioned inside to get the *sensitivity index* for each object. The *sensitivity index right* related to the objects on the right side and described how much the inward shift of these objects affected the reaching path of the participant. For the left object a corresponding index was calculated (*sensitivity index left*). A *sensitivity index* of 0.02 m means that the hand shifted laterally by 2 cm when the object was shifted inwards by 4 cm. This would in fact be a perfect response since with an inward shift of 4 cm, the midpoint between the two objects is shifted by 2 cm. The *sensitivity indices* were calculated for every participant and then analyzed using a 2 (*task*: obstacle-avoidance vs. bisection) \times 2 (*cognitive load*: single-task vs. dual-task) \times 2 (*side*: *sensitivity index right* vs. *sensitivity index left*) repeated measures ANOVA.

We also analyzed and compared the accuracy data for the RSVP task for the condition without movement, the dual-task condition with obstacle-avoidance, and the dual-task condition with bisection. The data were processed using MATLAB and SPSS.

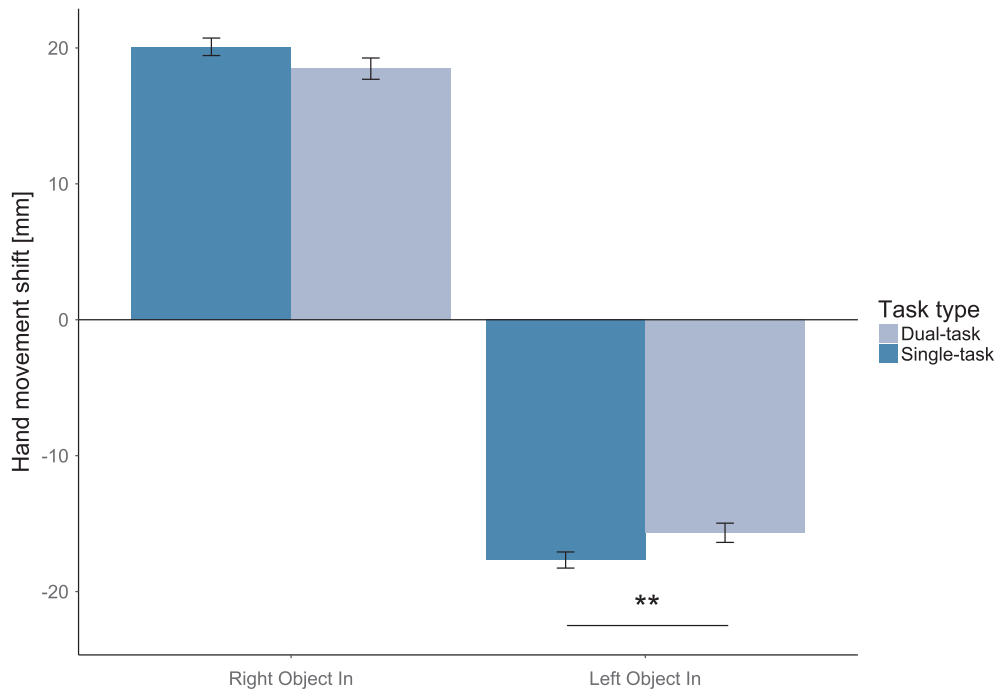


Fig. 3. Sensitivity to a shift of the outer objects. *Right Object In* shows the mean difference in lateral hand position between the condition when only the right object was positioned inside and the condition when both objects remained outside. *Left Object In* presents the same value for the left object at the inner position. Error bars represent one standard error.

3. Results

3.1. Effect of secondary task on primary tasks (sensitivity index)

The distribution of the original data violated the normality assumption. This was due to one outlier (see also Methods Section 2.1). We compared the outcome for the analysis of the original data and of the data without the outlier. With one exception the findings were the same. The one exception was that when the outlier was removed bisection performance proved to be significantly more sensitive to changes in object-position than obstacle avoidance performance. In the following we report the findings from the data without the outlier for which the assumption of a normal distribution could be upheld.

Using the *sensitivity index* described above we calculated a 2 (*task*: obstacle-avoidance vs. bisection) \times 2 (*cognitive load*: single-task vs. dual-task) \times 2 (*side*: *sensitivity index right* vs. *sensitivity index left*) repeated measures ANOVA. The data were normally distributed. As expected we found a main effect for *sensitivity index right* vs. *sensitivity index left* ($F(1,27) = 1682.695$, $p < .001$, $\eta_p^2 = 0.984$; mean *sensitivity index left* = -0.0167 m, mean *sensitivity index right* = 0.0193 m). A positive sign indicates that the hand shifted towards the left and negative sign means that the hand shifted to the right in response to an inward movement of the corresponding objects. In essence the hand always moved inwards in response to an inward movement of the objects (see Fig. 3).

We also found a significant interaction effect between single-task vs. dual-task and *sensitivity index right* vs. left ($F(1,27) = 11.205$, $p < .01$, $\eta_p^2 = 0.293$). This is indicative of dual-task costs, since it means that people did not shift their hand as far in the dual-task condition as in the single-task condition. Noticeably there was no significant difference between bisection and obstacle-avoidance (see Fig. 4). Bonferroni corrected pairwise comparisons then showed that the difference between single and dual-task condition was only significant ($p < 0.01$) in the condition when the left object was positioned inside (see Fig. 3). This means that when the left object was positioned inside there was a significant difference between single and dual-task but when the right object was positioned inside, performance remained the same under single and dual-task conditions.

We furthermore found a significant interaction effect between bisection vs. obstacle avoidance task and *sensitivity index right* vs. left ($F(1,27) = 4.477$, $p = 0.044$, $\eta_p^2 = 0.142$). This indicates that participants reacted less sensitively to a shift of the obstacles in the obstacle avoidance task than in the bisection task. The same trend was already observed in an earlier study (Ross et al., 2014).

3.2. Effect of secondary task on primary tasks (reaction time)

We also calculated a 2 (*task*: obstacle-avoidance vs. bisection) \times 2 (*cognitive load*: single-task vs. dual-task) \times 3 (*side*: both obstacles positioned outside vs. left obstacle positioned outside vs. right obstacle positioned outside) repeated measures ANOVA for the reaction times on the primary tasks. No main effects and no interaction effects were significant.

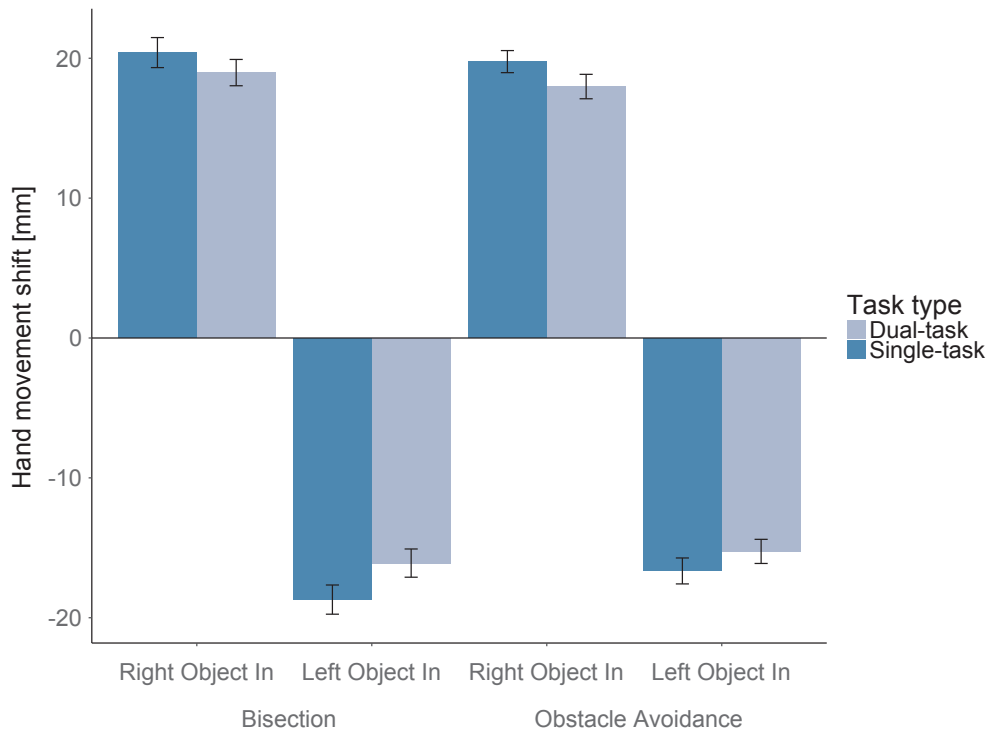


Fig. 4. Sensitivity to a shift of the outer objects by task. The same data as in Fig. 3, also differentiated by bisection task or obstacle avoidance task. There was no significant difference between the two tasks. Error bars represent one standard error.

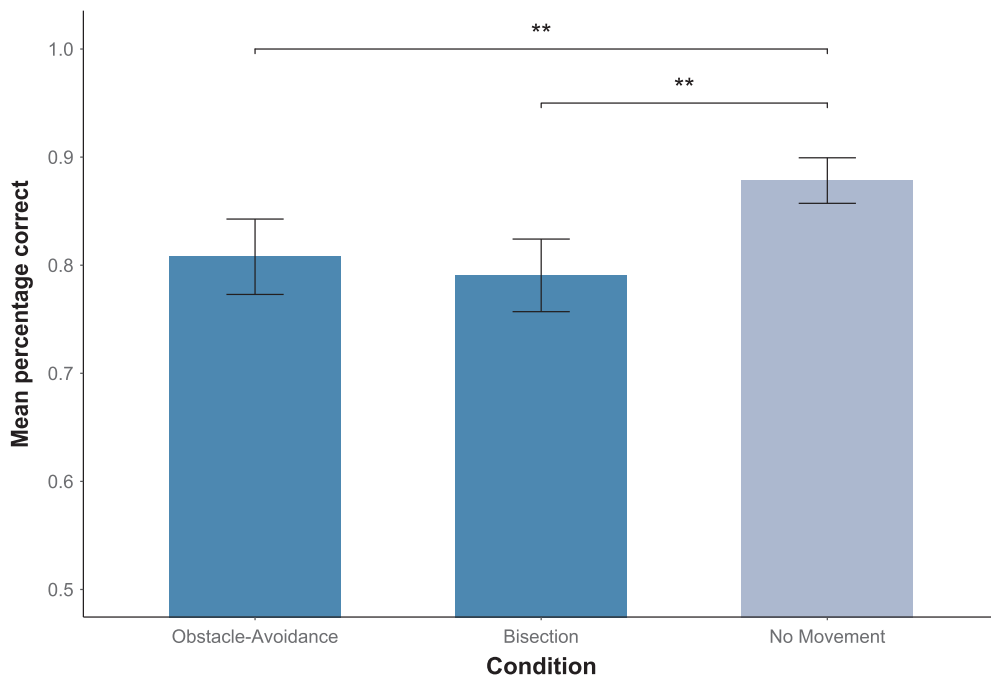


Fig. 5. Results of the RSVP task in the two conditions where a movement was required (Obstacle-avoidance, Bisection) and the condition with no required movement (No Movement). Pairwise comparisons showed significant differences between the No Movement condition and both of the two other conditions. Error bars represent one standard error.

3.3. Effect of primary tasks on secondary task

Furthermore we calculated a repeated measures ANOVA for the accuracy in the RSVP task with the type of trial as condition (see Fig. 5). Here one sees that there is a significant main effect of condition ($F(2,54) = 10.361, p < .001, \eta_p^2 = 0.277$), but Bonferroni corrected pairwise comparisons showed that these effects are only significant between the no-movement and the bisection condition ($p < 0.001$) and the no-movement and the obstacle-avoidance condition ($p < 0.01$). There is no difference between bisection and obstacle-avoidance condition ($p > 0.05$). This means that, irrespective of the motor task, the participants showed reduced accuracy in the dual-task conditions relative to the single-task condition.

4. Discussion

We found a significant effect of a secondary, cognitive task on performance in the primary tasks (bisection and obstacle-avoidance). No significant difference between the two tasks was found. Interestingly, we also found significant effects of the primary tasks on the secondary tasks. Performance in the RSVP task was significantly worse when either a bisection or obstacle-avoidance task had to be performed at the same time as compared to a condition where none of the primary tasks were employed. Statistically, we found no difference in the dual-tasks costs for bisection or obstacle-avoidance. It is in fact surprising that reaction time was not affected by the introduction of a secondary task. Effects on reaction times are quite commonly found in the literature on multitasking (for a review see Koch, Poljac, Müller, & Kiesel, 2018). However, as we argued in a somewhat different context (namely within the context of the Garner paradigm) the meaning of reaction times and their sensitivity to cognitive effects depends on the temporal parameters of the behavioral response that is used to infer the perceptual decision. In most of the cognitive tasks used in multitasking research, the behavioral response is a verbal report or a button-press response. In this case reaction times are presumably temporally quite close to the time of decision and highly correlated with that decision time. In the case of such temporally extended responses as grasping and reaching, it is not so clear that the relevant perceptual decision regarding the target or task configuration must be completed by the time, participants initiate their response. So-called online adjustments to movements (i.e. adjustments taking place while the reaching movement is already ongoing) are possible and provide the participant with an opportunity to defer the perceptual decision to a later time. As a consequence reaction time in tasks with complex and temporally extended behavioral responses are probably less correlated with decision times and thus less sensitive to cognitive effects presumed to act on those perceptual decisions (for a more detailed discussion of this issue, its implications and some findings in support of our analysis of this issue, see Hesse & Schenk, 2013).

While our findings are in conflict with those reported by Singhal et al. (2007) and Liu et al. (2008) – we have already given our reasons why both of these studies may have underestimated the effect of dual-task interference on motor control – they are in alignment with reports that demonstrate dual-task interference in the case of grasping. In two related studies, Kunde and his colleagues employed the *psychological-refractory-period* (PRP) paradigm (Janczyk & Kunde, 2010; Kunde, Landgraf, Paelecke, & Kiesel, 2007) to test the claim that visuomotor behavior, such as grasping, is immune to dual-task interference. The PRP paradigm uses two tasks carried out in sequence. The assumption is that if a central bottleneck is shared between two tasks, then task 2 cannot enter the bottleneck before task 1 has completed the processes dependent on the bottleneck. Task 2 will have to wait for task 1 to pass the bottleneck and this wait period will increase with increasing temporal overlap between task 1 and task 2 processing. In a typical stimulus-response paradigm, the temporal overlap can be manipulated by varying the time interval (SOA) between the onsets of task 1- versus task 2-stimuli. It is expected that the wait period for task 2 and thus the reaction time for task 2 will increase with decreasing SOA. Kunde and colleagues found exactly this pattern even when grasping was used as the second task suggesting that grasping is not immune to dual-task interference. This conclusion was also supported by another study on grasping. Hesse and Deubel (2011), Hesse, Schenk, et al. (2012) used the RSVP (*rapid serial visual presentation*) paradigm and asked participants to grasp objects - in this case rings of different diameters - while at the same time attending to a visual sequence of rapidly presented digits. The added perceptual task affected the grasping performance significantly. Interestingly, the effect was most clearly seen as a delay in adjusting the hand-opening to the ring's diameter. Based on these findings we would argue that there is now enough evidence of dual-task interference in visuomotor tasks to challenge the claim of multitasking immunity in behavior controlled by the dorsal, visual system.

Our findings also inform our concepts of spatial attention and sensorimotor automaticity. Milner and Goodale (1995) suggested not just a what/how distinction for vision but also for attention. They argued that attention-for-perception associated with the ventral stream underlies our ability to select relevant entries for our awareness. The second attention system associated with mechanisms in the dorsal stream selects targets for action and operates independently of awareness (Milner & Goodale, 2006, p. 185). This distinction between an attentional system for perception and one for action sits however uneasily with the wealth of evidence in favor of an intimate link between motor preparation and perceptual attention (for a review of this evidence, see Smith & Schenk, 2012). Findings such as those from our study and the studies by Hesse and Kunde suggest instead that the attentional mechanism involved in perception and action are either identical or at least intimately linked with each other.

The obstacle-avoidance paradigm is of particular interest in this context. Milner and Goodale (2006) based their argument for a second action-related but awareness-divorced attentional system on observations in blindsight patients. Blindsight patients are blind in some part of their visual field and will deny awareness of stimuli presented to that portion of their visual field but may nevertheless point correctly to the location where the stimulus was presented. Milner and Goodale argue that this ability to point to unseen targets suggests the existence of a second attentional system, namely a system that selects targets for action but not for perception. This explains why blindsight patients can successfully point to visual targets for which they have no visual awareness. The fact that blindsight performance for most tasks is clearly subnormal suggests that the mechanisms uncovered in blindsight are most probably not the mechanisms used for performance in the same tasks by healthy people. By extension the attention system uncovered in

blindsight might also not be the one responsible for action control in healthy people. This suggests that in healthy people the distinction between attention for perception and action may not be that clear or relevant. However, obstacle-avoidance might provide an exception. Blindsight performance in obstacle-avoidance is surprisingly good (Striener et al., 2009). Goodale (2011) even speculated that in the case of obstacle-avoidance the mechanism uncovered in blindsight is possibly not just a backup option for the damaged brain but a central part of the mechanism used for this behavior in the healthy brain (Goodale, 2011). To put it more simply the subconscious and automatic avoidance of obstacles found in blindsight patients and patients with visual extinction might be characteristic not just for how brain-damaged patients solve this task but also how neurotypical actors solve it. If true, the distinction between attention for perception and attention for action might be expected to hold at least for the case of obstacle-avoidance. Our findings suggest that this is not the case. We found evidence that obstacle-avoidance induces dual-task costs in a concurrently performed cognitive task. This suggests that perception and action share the same attentional resources and that obstacle-avoidance presents no exception. This does not mean that the visual information used to solve the bisection versus the obstacle task is also coming from the same anatomical source. Our findings, therefore, do not necessarily challenge the neuropsychological evidence suggesting that ventral stream structures are more involved in bisection and dorsal stream structures more important for obstacle avoidance. However, our findings do suggest that even if obstacle avoidance is less reliant on visual information from the ventral stream it is not immune to interference from a secondary task. Such a finding would be compatible with a model that assumes that visual perception and visually-guided action use information from distinct visual streams but also engage shared central resources, but it would also be compatible with a model that dispenses with the assumption of distinct visual streams for perception and action. However, our finding is incompatible with a model that assumes both distinct visual streams and also makes the additional assumption that only one of the two streams interacts with central resources. Consequently, susceptibility to cognitive interference cannot be used as a specific, behavioral signature for one of the two streams and thus multitasking evidence not be used to provide further support for the assumption of distinct streams for perception and action.

Our findings also prompt questions about the concept of automaticity. What is automaticity in motor behavior? Different answers can be given to that question. Automatic behavior is overlearned, the resulting movements are highly replicable and stereotyped and obey certain kinematic rules (Plamondon, 1997). Automaticity has also been associated with subconscious control (Pisella et al., 2000) and is assumed to require little or no attention and therefore to be immune to dual-task costs. Obstacle-avoidance behavior is a good example of automatic behavior. It is overlearned, the velocity profiles of the reaches obey the kinematic rules of automatic behavior and it seems that it can be controlled unconsciously (McIntosh, McClements, Schindler, et al., 2004; Striener et al., 2009; but see also: Hesse, Billino, & Schenk, 2018; Hesse, Lane, Aimola, & Schenk, 2012; Ross, Schenk, Billino, Macleod, & Hesse, 2016; Striener, Chapman, & Goodale, 2018). Nevertheless obstacle-avoidance is not immune to dual-task costs. This suggests that the different features used to describe automaticity in motor behavior do not necessarily align. To put it differently, there seem to be different forms of automaticity in motor behavior.

Before we conclude we need to address an unexpected feature of our results. We found an effect of the secondary task on motor tasks specifically for the object on the left side. The effect for the right-sided object was not significant. This difference was not expected and we have no ready hypothesis to explain this finding but we can speculate.

One possibility is that this is a result of the different constraints the left and the right objects exert on the right hand. Since the right hand is closer to the right object, a shift of the right object might more strongly influence the movement than a shift of the left object. After all not only the hand has to be transported through both obstacles but also part of the forearm and in right handed persons this part of the forearm is oriented more to the right than to the left even when the start position of the hand itself is in the middle between the two obstacles. This interpretation would imply that when participants would use the left hand, this behavior would switch and a shift of the left object would more strongly influence the movement than a shift of the right object. Rice et al. (2008) found a trend in this direction in their control group. They tested obstacle avoidance in right-handed participants both with their right and with their left hand and found that the left obstacle exerts a seemingly greater influence when the left hand is used and the right obstacle exerts a seemingly greater influence when the right hand is used. Under these circumstances it seems plausible to assume that in our study participants' responses to right-object displacements provide a more sensitive measure of the efficiency with which participants take obstacle-positions into account and thus a more likely variable to reveal interference from a secondary task.

4.1. Conclusion

To conclude, the results of our study suggest that obstacle-avoidance is not immune to dual-task costs. This finding neither rejects nor supports Bruce Bridgeman's original suggestion of distinct visuo-spatial representations (and possibly neural structures) for perception and action. In fact our findings challenge only the more specific claim that dorsal-stream behavior is insulated from the cognitive system. We argued for the view of shared attentional resources for perception and action and conclude that seemingly subconsciously controlled and automatic behavior can interfere with performance in a cognitive task. As such our findings are in line with Bridgeman's later and more skeptical view on the perception-action distinction - a view that emphasized the limitations of the perception-action account to explain many of the details of visual behavior in healthy observers (see Dassonville et al., 2004).

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4.2 Grasping and perception are both affected by irrelevant information and secondary tasks: new evidence from the Garner paradigm.

**Grasping and perception are both affected by irrelevant information and secondary tasks:
New evidence from the Garner paradigm**

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Abstract

In their Perception-Action Model (PAM), Goodale and Milner (1992) proposed functionally independent and encapsulated processing of visual information for action and perception. In this context, they postulated that visual input for action is processed in an automatized and analytic manner, which renders visuomotor behaviour immune to perceptual interferences or multitasking costs due to sharing of cognitive resources. Here, we investigate the well-known Garner Interference effect under dual- and single-task conditions in its classic perceptual form as well as in grasping. Garner Interference arises when stimuli are classified along a relevant dimension (e.g., their length), while another irrelevant dimension (e.g., their width) has to be ignored. In the present study, participants were presented with differently sized rectangular objects and either grasped them or classified them as long or short via button-presses. We found classical Garner Interference effects in perception as expressed in prolonged reaction times when variations occurred also in the irrelevant object dimension. While reaction times during grasping were not susceptible to Garner Interference, effects were observed in a number of measures that reflect grasping accuracy (i.e., poorer adjustment of grip aperture to object size, prolonged adjustment times, and increased variability of the maximum hand opening when irrelevant object dimensions were varied). In addition, multitasking costs occurred in both perception and action tasks. Thus, our findings challenge the assumption of automaticity in visuomotor behaviour as proposed by the PAM.

1 Introduction

According to the Perception-Action Model (PAM), the visual system in the primate brain is subdivided into two anatomically and functionally distinct streams (Goodale & Milner, 1992; Milner & Goodale, 1995, 2006). The dorsal stream, extending from the primary visual cortex (V1) to the parietal cortex, is assumed to serve the goal of processing visual information for action, while the ventral stream runs from V1 into the inferior-temporal cortex and is thought to primarily process visual information for perception. According to the PAM, the two streams constitute separate and independent visual systems.

Over the last decades, this very influential model has been criticized (Schenk, 2006, 2012; Schenk, Franz, & Bruno, 2011; Schenk & Hesse, 2018) and many studies originally providing supporting evidence for segregated neurological pathways for perception and action processing (e.g., Aglioti, DeSouza, & Goodale, 1995; Ganel, Chajut, & Algom, 2008; Ganel & Goodale, 2003, 2014; Goodale et al., 1994; Goodale & Milner, 1992) have been challenged (e.g., see Kopiske, Bruno, Hesse, Schenk, & Franz, 2016 for illusions, and Schenk et al., 2017; Utz, Hesse, Aschenneller, & Schenk, 2015 for Weber's law). However, there are two lines of evidence that have received comparably little scrutiny until now: The Garner Interference effect (Ganel & Goodale, 2003, 2014) and dual-task studies (Liu, Chua, & Enns, 2008; Singhal, Culham, Chinellato, & Goodale, 2007). We designed the current study with the aim to re-examine the evidence presented in favour of the PAM from these two behavioural paradigms. In the following, we will briefly summarise the existing literature, deduce the open questions in these fields, and explain the potential advantage of combining research on Garner Interference with research on dual-tasking.

1.1 Garner Interference

Garner Interference is an interesting phenomenon from the field of cognitive psychology (Garner, 1976, 1978). The key of this paradigm is that stimuli are created in such a way, that they either vary only along a relevant dimension (i.e., the dimension participants are asked to judge) or vary along two dimensions: a relevant and an irrelevant one. Reaction times (RT) are determined separately in

blocks in which only the relevant dimension is varied (i.e., baseline blocks) and in blocks in which stimuli vary along both the relevant and the irrelevant dimension (i.e., filter blocks). Depending on the properties that are varied, interference effects occur when variations are present also in an irrelevant dimension of the target as indicated by slower reaction times (RTs) in the filter blocks as compared to the baseline blocks. For example, participants are usually faster to indicate the width of a rectangle (narrow vs. wide) if its length is kept constant or vice versa. If, however, the presented rectangles vary in both dimensions, the RTs for indicating target width increase considerably. This observation has led to the suggestion that the length and width of an object are integral dimensions that cannot be processed independently by the perceptual system. In contrast, other dimensions such as a target's width and its colour were not found to show this kind of interference and can hence be considered to be (perceptually) separable dimensions (Garner, 1976).

Ganel and colleagues applied this paradigm to the domain of visuomotor research (Ganel & Goodale, 2003, 2014). On the basis of the PAM they reasoned that the visuomotor system processes visual information differently. Specifically it was assumed that the visuomotor system focuses on the action-relevant dimension of an object and ignores variations in the action-irrelevant dimensions (analytic processing style). In the case of grasping, the action-relevant dimension might be the length of the object and thus variations in its width should have no effect on the timing or accuracy of the grasping movement. As predicted, Ganel and Goodale (2003) found Garner Interference in a perceptual width-discrimination task but not in the corresponding grasping task. They argued that these findings demonstrate that the perception and the action system process visual information fundamentally differently (holistic vs. analytic processing style), a distinction which was also supported by a more recent study (Janczyk & Kunde, 2012).

However, Hesse and Schenk (2013) proposed that the observed dissociation between perception and action may have resulted from discrepancies in the temporal profile of the two response types (button presses versus grasping). More specifically they suggested that the relatively small Garner Interference effects (20-30 ms) can only be detected in tasks where strict time constraints are

imposed. In speeded perceptual judgements, time constraints are introduced by instructing participants to respond as rapidly as possible resulting in relatively short RTs of around 350 to 450 ms. In contrast, when grasping objects, the time to make a decision is distributed across different phases: the time before the movement is initiated and the time during which the movement is executed. Hence, RTs are likely to be unsuitable to determine interference effects in actions given that the decision about the relevant object dimension may not yet be over by the time the movement is initiated. In other words, the decision time available in the grasping task is usually much longer than in a corresponding perceptual task as the overall time available to make the decision is composed of the time before and the time during the movement. Thus, the time constraints imposed during grasping may be too liberal to provide sufficient sensitivity to detect the relatively small Garner Interference effects. Consequently, Hesse and Schenk (2013) predicted that if time constraints for the perceptual judgement task and the grasping task are equalised, the dissociation disappears. In line with this prediction, they found that when decision times were increased in the perceptual task, Garner Interference disappeared. Conversely, when stricter constraints were imposed during the grasping task, Garner Interference was also evident in visuomotor measures (Hesse & Schenk, 2013).

Further indirect evidence for the suggestion that RTs might be an insensitive measure to reveal Garner Interference in tasks with more liberal time constraints comes from studies that investigated Garner Interference in action tasks that supposedly rely on ventral stream processing (Eloka, Feuerhake, Janczyk, & Franz, 2015; Janczyk, Franz, & Kunde, 2010). According to the PAM, unskilled movements are reliant on ventral stream processing and should hence be affected by irrelevant object features. However, studies testing left-handed and awkward grasping as well as grasping with a pair of pliers (Janczyk et al., 2010; Eloka et al., 2015) were unable to detect Garner Interference in these tasks further challenging the idea that only skilled and automatized grasping mediated by the dorsal stream is immune to variations in irrelevant object features. Furthermore, more recently, Janczyk and Kunde (2016) observed Garner Interference in both a perceptual and a grasping task

when employing a weight manipulation as an irrelevant object manipulation indicating that changes in irrelevant object features other than target size can affect visuomotor measures.

In sum, these findings illustrate that the classical Garner task of measuring RTs while varying object shape may be problematic when comparing Garner Interference effects between perception and action tasks. One way to account for the asymmetry between perception and action tasks would be to use more sensitive temporal measures or to focus on movement accuracy rather than timing. Ganel and Goodale (2014) adopted the latter approach in a recent study. Specifically, they compared the variability of the maximum grip aperture (MGA) during a grasping task (visuomotor condition) with the variability of the hand aperture when participants were asked to pantomime the grasp (perceptual condition). They found Garner Interference, as indicated by an increase in MGA variability in the filter conditions relative to the baseline conditions in the pantomime condition, but not in real grasping. While this is an interesting finding, we feel that there are other (more common) measures of grasping accuracy that should be taken into consideration before making any final conclusions.

A more established and commonly reported measure of grasping accuracy is the slope of the function relating object size to MGA. It is well known that MGA is linearly related to object size and the slope of that linear function expresses the sensitivity with which the grasping hand adjusts to the relevant dimension of the target object (Hesse & Franz, 2009b; Smeets & Brenner, 1999). Moreover, while RT may be an insensitive measure, other temporal measures could potentially be more informative. Specifically, this requires finding a measure that indicates the perceptual decision time in grasping more reliably than RT. During the course of the movement the grip is continuously adapted to the size of the target object and differences in the size of the aperture can already be observed well before MGA is reached (Jeannerod, 1984). Thus, the moment the hand-opening reliably diverges for grasping smaller and larger objects can be considered as an early indicator that participants are taking into account object size. Here we employ such an early adjustment measure

and predict that, if Garner Interference affects grasping, adjustment times should be delayed in the filter condition as compared to the baseline condition.

1.2 Dual-Tasking

The PAM's assumption of dorsal stream automaticity has been addressed using dual-task paradigms (e.g., Liu et al., 2008; Singhal et al., 2007). With respect to dual-tasking, the PAM predicts that dorsal visuomotor processes do not depend on central cognitive resources and should thus not be affected by concurrent demands of other independent (e.g., perceptual or cognitive) tasks. Typically, dual-task costs are demonstrated by deterioration of the performance (such as prolonged RTs and decreased accuracy) in one or both tasks when they are executed concurrently as compared to separately (Pashler, 1989, 1994). Liu and colleagues (2008) were one of the first authors who suggested that visuomotor tasks may be exempt from these dual-tasking costs. They combined a pointing task and a rapid serial visual presentation (RSVP) task and found no difference in movement times between single- and dual-task conditions, but prolonged movement initiation times (i.e., RTs) in dual-task conditions as compared to single-task conditions. They concluded that only action planning which is supposedly mediated by the ventral stream is affected by a secondary task. In contrast, action programming that is assumed to be mediated by the dorsal stream showed no dual-task costs. However, there is a conceptual problem regarding this interpretation and the underlying definition of action programming. The choice to perform a grasping action is a planning act, but the process of adjusting the grasping movement to the location and the size of the target object during the RT-interval is part of the programming process (see Milner & Goodale, 1995; 2008 but also Schenk, 2010 for a more detailed discussion of the distinction between action planning and action programming). Consequently, differences in RT should be considered indicative of movement programming being affected by dual-task requirements. The dissociation between dual-tasking costs for offline (as reflected in RTs) but not online adjustments (as reflected in MTs) as observed by Liu and colleagues can however not easily be mapped onto the distinction between ventral and dorsal processing. Interestingly, in line with this argument, another study that examined dual-task

interference in a visuomotor task using a Psychological Refractory Period (PRP) paradigm found increased RTs in the presence of a secondary task (Kunde, Landgraf, Paelecke, & Kiesel, 2007). Kunde and colleagues (2007) interpreted this finding as evidence against the PAM. In particular, the authors argued that responses based on dorsal and ventral processing were both affected similarly by strains on central resources (see also, Janczyk & Kunde, 2010).

Finally, it is important to note that Liu et al. (2008) were only able to measure the overall duration and the end-position of the movement as they employed a touch screen monitor and did not measure participants' movement kinematics. Thus, any online changes would have been missed. This is particularly problematic as subsequent studies that measured hand movements continuously, suggested that dual-task costs become primarily apparent during the earlier parts of the movement (Hesse & Deubel, 2011; Hesse, Schenk, & Deubel, 2012) or when quick online corrections are required (Sandoval Similä & McIntosh, 2015).

However, there is also evidence for the suggestion that dorsal stream processing is immune to dual-task costs from a study employing a delayed action paradigm (Singhal et al., 2007). Specifically, this study exploited the fact that actions towards memorised targets (delayed actions) are supposed to be guided by the ventral stream while non-delayed or immediate actions are presumed to be served by the dorsal stream (e.g., Hu, Eagleson, & Goodale, 1999; Culham et al., 2003). In line with this argument, Singhal et al. (2007) found larger dual-task interference effects in the delayed action task (ventral processing) than in the visually guided grasping task (dorsal processing) providing further support for the assumption that the dorsal stream may be immune to cognitive interference. Yet, the findings are, in our opinion, not conclusive. Firstly, many recent studies have questioned the underlying assumption that delayed and non-delayed actions are served by distinct visual streams (for a review, see Schenk & Hesse, 2018). Secondly, the timing of the secondary task was problematic as it was presented at the moment the visual target information was withdrawn in the delayed condition. Thus, at the very time participants realised they will have to memorise the target object, they were also given a second cognitive task to solve. This could explain why interference was

enhanced during these delayed-action tasks. Finally, even though the dual-task interferences tended to be larger in the delayed action task, there were still (smaller) interference effects during visually guided grasping with MGAs being larger and MTs being longer in dual-task conditions as compared to single-task conditions.

In summary, we would argue that there is currently no convincing evidence for the idea that dorsal stream tasks are immune to cognitive interference as claimed by the PAM. Instead dual-task costs have been found reliably in the visuomotor domain, in particular in studies employing PRP paradigms (Janczyk & Kunde, 2010; Kunde et al., 2007). With respect to dual-tasking, the aim of the current study was to further clarify whether or not dual-task effects occur reliably in visuomotor tasks also in situations in which the primary and secondary task are executed simultaneously and whether the effects are mediated by the nature of the secondary task.

1.3 Combining Garner Interference with Dual-Tasking

In addition to testing the mere existence of dual-task interference effects during grasping, we were interested in whether, and to which extent, interference between a primary action task and a secondary visuo-attentional or cognitive task may depend on the similarity of the two tasks. Most importantly, we hypothesise that a combination of both paradigms could potentially amplify the effects of Garner Interference and dual-tasking and thus produce more reliable findings. The reasoning for this assumption is simple. If we assume that actions are susceptible to Garner Interference and dual-task costs, both effects may enhance each other. Specifically, the addition of a secondary task might slow down the perceptual decision process and thereby increase the temporal difference between a simple (Garner-baseline condition) versus a complex (Garner-filter condition) decision making process. The result would be a more pronounced Garner effect in dual-tasking conditions as compared to single-task conditions. In other words, by combining both paradigms, one might potentially make the Garner Interference more detectable. Moreover, by using a dual-tasking approach in which the similarity between the primary task and secondary task is manipulated, we can also test if increasing the saliency of distracting information present in the primary task further

increases the Garner Interference effect. In other words, if the secondary task requires participants to attend to object shape (rather than colour) one might not only expect larger dual-task costs in general but also an increased Garner Interference effect in particular.

In summary, we combine the classic perceptual Garner paradigm (judgement of object length) as well as its visuomotor version (grasping objects along their length) with a secondary visuo-attentional task in order to address three questions: (1) Do irrelevant features, as reflected in Garner Interferences, affect perception as well as action? Importantly, we will employ novel measures which, for reasons detailed above, are in our view more appropriate to look for Garner effects in visuomotor tasks. (2) Do dual-task costs depend on the similarity between the primary task (i.e., Garner task) and the secondary task? (3) Does a dual-task context enhance the impact of irrelevant features on a primary perceptual or visuomotor task (i.e., increase the Garner Interference)? We hypothesise that by combining the two tasks we can boost the usually small Garner Interference effects leading to more reliable findings that can potentially settle the question of whether or not actions are immune to stimulus variations in action-irrelevant dimensions.

2 Methods

2.1 Participants

Forty-four (10 males) neurologically healthy undergraduate and postgraduate students and staff members of the University of Aberdeen (UK, Scotland) participated in the study. The data set of one participant, who was unable to perform the task, was excluded from analysis. The age of the remaining participants ranged from 18 to 40 years with a mean age of 23 years (standard deviation of 5 years). Participants were assigned to two conditions with one group (N=24) performing the perceptual task and one group (N=24) performing the grasping task. Five participants completed both the grasping task and the perceptual task. Participants received either course credits or were paid for their participation (£5/hour). All participants were right-handed by self-report, had no neurological or motor impairments and normal or corrected-to-normal visual acuity as well as normal

colour vision. Prior to the study, all participants provided informed consent, and the protocol was approved by the Psychology Research Ethics Committee, University of Aberdeen (PEC/3589/2016/12).

2.2 Set-up

A mirror set-up was used for stimulus presentation in both the perceptual and the grasping task. A computer monitor (EIZO Foris FG2421, 23.5", refresh rate 60 Hz, 1920 x 1080 pixel) was attached to a metal frame with the screen facing downwards. The screen of the monitor reflected onto a semi-transparent mirror (56 cm x 40 cm) positioned at a distance of 34 cm. A wooden board was placed 34 cm beneath the mirror and served as presentation surface for the stimuli. Visual stimuli presented on the screen were reflected by the mirror and consequently perceived by the participant as being placed on the presentation surface. As the compartment above the mirror was lit up by the screen, both the real object present in the grasping task as well as participants' hands remained invisible underneath the mirror. A small felt pad with a diameter of 5 mm was attached to the presentation board and served as the start position of the hand in the grasping task. The distance between the starting position and the midpoint of the grasping object was 24 cm. In the perceptual task, a two-button response box was placed at this location (for details see procedure). Participants sat in a comfortable position in front of the mirror setup on a height-adjustable chair with their head resting on a chinrest looking directly onto the mirror. Prior to the start of the experiment, we calibrated the mirror-setup to compensate for possible visual distortion caused by slight variations in viewing angle. Specifically, we adjusted the presentation location of the virtual stimuli in the grasping task so that they were perceived by participants as overlapping with the real object (this was achieved by switching on lights in the lower compartment of the mirror set-up such that both the real and the virtual stimulus were visible during calibration).

To record hand movements in the grasping task, an infra-red based Optotrak 3020 motion registration system (Northern Digital Incorporation, Waterloo, Ontario, Canada) was used at a sampling rate of 200 Hz. Before starting the measurement, we calibrated the Optotrak system such

that the Cartesian coordinate system was aligned to the presentation surface located underneath the mirror. We attached two IREDs on the nails of each participant's right index finger and thumb. The experiment was programmed in Matlab (The MathWorks Inc., Natick, Massachusetts, United States) using the Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007) and the Optotrak Toolbox (Franz, 2004).

2.3 Stimuli and Procedure

In both the grasping and the perceptual task there were two main experimental variations: the Garner component and the dual-tasking component. Regarding the dual-tasking component, we tested three different conditions (in the following referred to as "dual-tasking conditions" although one of them is in fact a single-task condition): 1) a single-task condition with no secondary task (control condition), 2) a dual-task condition where the secondary task was related to the primary task (i.e., detecting a target stimulus of a certain shape within an RSVP) and 3) a dual-task condition in which the secondary task was unrelated to the primary task (i.e., detecting a target stimulus of a certain colour in an RSVP task). Within each of the three dual-tasking conditions, we introduced a Garner task (primary task) consisting of experimental blocks in which objects varied either only along the relevant dimension (baseline blocks) or in which they varied along both the relevant and an irrelevant dimension (filter blocks). We will first describe the Garner task in more detail (section 2.3.1) and then specify the different dual-tasking conditions (section 2.3.2).

2.3.1 Garner Task

All trials, independent of the current experimental condition, started with a white central fixation cross presented on a black background. After 500 ms, the fixation cross was replaced by one of four differently sized white rectangles. Four different rectangles were created by combining 2 different lengths (40 mm and 60 mm) with two different widths (20 mm and 30 mm), i.e., W20-L40, W20-L60, W30-L40 and W30-L60 mm (see Figure 1). In the baseline blocks, we presented two of the rectangles that varied in the length dimension only while their width remained constant across trials. Hence,

both the objects with a width of 20 mm were presented in one of the baseline blocks and both objects with a width of 30 mm in another separate baseline block. Within each baseline block, both rectangles were presented 12 times each (24 trials per block). In filter blocks, all four rectangle shapes were presented meaning that both dimensions (width and length) could change from trial to trial. Every one of the four rectangles was presented 6 times resulting in 24 trials per block. To match the numbers of presentations of each rectangle shape between baseline and filter blocks, there were two filter blocks in total (i.e., 12 presentations per rectangle size). For all participants filter and baseline blocks were presented interleaved (see section 2.3.3 on counterbalancing for more information).

In the *perceptual task*, participants were asked to respond to the rectangle's length and to indicate as fast as possible, using a left or right button-press on the response box, whether the presented rectangle was short (40 mm) or long (60 mm). In filter conditions, they were instructed to ignore the variations in width. The rectangle disappeared one second after a button-press was registered. Half of the participants in the perceptual task used the left index finger for indicating 'long' and the right index finger for indicating 'short' classifications, while the other half had the opposite assignment.

In the *grasping task*, participants were instructed to grasp a wooden block presented beneath the mirror (matching the virtual presentation of the rectangle in shape) along its length dimension as soon as the virtual object appeared on the screen. Before each grasping trial, the experimenter placed the wooden target object under the mirror at the central position corresponding to the position of the visual stimulus. Each object was positioned accurately on the presentation surface under the mirror with a little pin fitting a matching cut-out in the board. Hence, participants grasped for the virtual stimulus and encountered a real 3D object (thickness of 20 mm) at its position. The virtual object was removed from the screen upon movement onset, which was defined as the moment at which the Euclidean distance between the start position and one of the finger markers exceeded 25 mm. Due to the lighting conditions, participants were unable to see their hand and the real object during grasping (open-loop condition). The experimenter started each trial manually by

pressing a key and participants grasped and lifted the object with a precision grip using index finger and thumb. Participants had 2 seconds to complete their movements after the presentation of the stimulus.

2.3.2 Secondary Tasks

Simultaneously with the Garner task, participants performed one out of two different visual secondary tasks (in addition to a control condition in which no secondary task was employed). Hence the Garner task described in the previous paragraph was completed in three different secondary task conditions: 1) no secondary task (control condition), 2) Garner-relevant secondary task (shape condition) and 3) Garner-irrelevant secondary task (colour condition).

Both secondary tasks were RSVP tasks with the goal of detecting a pre-defined target stimulus. RSVP stimuli were presented on the left side of the mirror, next to the white rectangle relevant for the Garner task. The exact position of the stream of RSVP stimuli was varied randomly between trials either occurring 150 pixels or 300 pixels to the left of the centrally presented Garner stimulus. This spatial variation was introduced in order to prevent participants from adopting facilitating strategies for target detection and to induce a jitter for more generalizable results. The presentation duration of each stimulus within the RSVP was ~50 ms (i.e., 3 frames at 60 Hz monitor refresh rate) and the inter-stimulus blank interval of ~85 ms (i.e., 5 frames at 60 Hz monitor refresh rate). At the beginning of each trial, the program determined randomly whether or not the target stimulus appeared. The target stimulus was defined by its colour in the Garner-irrelevant secondary task and by its shape in the Garner-relevant secondary task. The target could occur at any time during the trial. At the end of each dual-task trial, participants reported verbally whether or not they had seen the target stimulus (two alternative forced choice task), and the experimenter entered their response into the program. Stimuli for the Garner-irrelevant colour task were squares (50 mm x 50 mm) coloured in various shades of purple, which we generated by changing the blue-component within the RGB system. The RGB values for the four distractors were set to [125 50 255], [125 50 102], [125 50 153] and [125 50 204]. The target was perceived as being slightly more orange than the other stimuli (RGB value: [125

50 20]). In the Garner-relevant shape task, distractor stimuli were the same four white rectangles that we used for the Garner task, while the target stimulus was a smaller white square (25 mm x 25 mm). Task difficulty was piloted on N=5 to achieve accuracy rates of about 85% in a single-task condition. In both dual-task conditions, the RSVP tasks started simultaneously with the appearance of the rectangle for the Garner task and lasted for 2s. Participants were instructed to keep fixation during the trial at the central Garner rectangle and to view the RSVP task in visual periphery.

2.3.3 Randomisation and Counterbalancing

In both, the grasping task and the perceptual task, the dual-tasking condition component (control, shape and colour) was blocked and counterbalanced across participants (i.e., 6 possible dual-tasking block orders counterbalanced across N=24 participants in each task). Within each of these dual-tasking blocks participants performed 96 trials of the Garner task which were divided in 4 sub-blocks of two baseline and two filter conditions (consisting of 24 trials each). Baseline and filter conditions were presented in an alternating fashion resulting in four different possible arrangements (B1F1B2F2, B2F2B1F1, F1B1F2B2 or F2B2F1B1). These four arrangements were counterbalanced across participants and dual-tasking blocks. Finally, within each filter and baseline block, stimuli were presented in a randomised fashion and the occurrence of the RSVP target was determined randomly for each trial in the dual-tasking conditions.

2.4 Data Analysis

Data processing and analysis were performed using the commercial software packages MATLAB R2015a (The MathWorks Inc., Natick, Massachusetts, United States) and SPSS (IBM SPSS Statistics for Windows, Version 24.0. Armonk, NY: IBM Corp.).

Grasping Data: Movement data from the IRED markers were filtered offline using a second-order Butterworth filter with a low-pass cut-off frequency of 15 Hz. We were interested in several parameters including reaction time (RT), movement time (MT) and maximum grip aperture (MGA). Movement onset was defined as the first frame in which one of the markers attached to thumb and

index finger exceeded a velocity threshold of 0.05 m/s. RT was defined as the time between stimulus onset and movement onset. The end of the movement was reached when the resultant velocity of one of the markers attached to thumb and index finger dropped below a velocity threshold of 0.075 m/s. MT was defined as the time between movement onset and end of the movement. The grip aperture was calculated as the 3D distance between thumb and index marker. The maximum of this distance between movement onset and end of the movement was defined as the MGA. Trials with substantial data loss, especially around the time of the MGA, or with RTs below 100 ms were discarded offline (2.8 % of all trials).

Perceptual Data: In the perceptual task, we measured RTs as the time interval between stimulus onset and the registered button-press.

For all timing data (i.e., RTs and MTs) we calculated the median time for each condition and participant. We used medians instead of means for our analyses of timing variables in order to enhance robustness against outliers. Note that the qualitative pattern of results remains identical when using means. For the accuracy data (i.e., MGA), we calculated the arithmetic mean and determined the standard deviation for each condition and participant as a measure of variability. Furthermore, we determined the slope of the function relating MGA to object size using linear regression analysis for each participant and condition separately. This measure is commonly used in the literature to determine how well participants adjusted their hand opening to the target size in the grasping task (Freud, Ganel, Avidan, & Gilaie-Dotan, 2016; Hesse & Franz, 2009b; Hesse et al., 2012). Moreover, we also calculated an additional aperture adjustment measure reflecting the point in time by which participants had reliably adjusted their grip apertures to the respective object length. To do so, we computed for every participant and each object length the mean aperture profile for each Garner and dual-tasking condition starting at movement onset and averaging each sample in real-time (every 5 ms) over the course of the movement. Subsequently, we determined the point in time at which the mean aperture size for long objects diverged from the mean aperture size

of short objects by at least half the object size difference (i.e., 10 mm) (see Hesse & Franz, 2009a for a similar procedure).

All data were statistically analysed using 2 (Garner condition: baseline vs. filter) x 3 (dual-task condition: control, dual-task colour, dual-task shape) repeated-measures ANOVAs. If the sphericity assumption was violated, p-values were Greenhouse-Geisser corrected (full degrees of freedom are reported with corresponding ϵ -values). Post-hoc comparisons were corrected for multiple testing using the Bonferroni method and a significance threshold of $\alpha = .05$ was used to determine statistical significance. The datasets analysed during the current study are available at zenodo.org, doi: 10.5281/zenodo.1408787.

3 Results

3.1 Perceptual Task

Figure 2 depicts the median RTs averaged across all participants in baseline and filter tasks for each of the three dual-tasking conditions. The 2 x 3 repeated-measures ANOVA revealed highly significant main effect of Garner condition $F(1,23) = 48.23$, $p < .001$, $\eta_p^2 = .677$, showing that participants were consistently slower to indicate the rectangles' length in the filter condition than in the baseline condition. On average the Garner Interference effect was about 32 ± 5 ms which is similar to that observed in previous studies (Ganel & Goodale, 2003, 2014; Garner, 1976; Hesse & Schenk, 2013). Furthermore, we found a highly significant main effect of dual-tasking condition, $F(2,46) = 178.47$, $p < .001$, $\eta_p^2 = .886$. Pairwise comparisons revealed that participants were significantly faster in the control condition (395 ± 9 ms) as compared to both dual-task conditions (colour: 595 ± 15 ms and shape: 606 ± 17 ms, both $p < .001$). RTs in both dual-task conditions did not differ significantly from each other ($p > .999$). These results indicate that there were, as expected, large dual-tasking costs as a consequence of sharing cognitive capacities between two simultaneous perceptual tasks (Pashler, 1989, 1994). Finally, there was no significant interaction effect, $F(2,46) = 0.20$, $p = .980$, $\eta_p^2 = .001$, suggesting that the Garner Interference effect was not modulated by dual-tasking constraints. The

absence of an interaction effect is in conflict with our hypotheses, since we expected the size of the Garner Interference effect to be modulated by the secondary task. Specifically, we expected that the Garner Interference may increase when the task requirements of the secondary task are similar to those of the primary Garner task (i.e., in the dual-task shape condition). Clearly this was not the case in our data.

3.2 Grasping Task

3.2.1 Timing of the movement: RT, MT and Adjustment times

Figure 3 shows RT data from the grasping task. The analysis revealed no main effect of Garner condition, $F(1,23) = 0.16$, $p = .694$, $\eta_p^2 = .007$, suggesting that participants were equally quick to initiate their grasping movements in baseline and filter conditions. However, there was a significant main effect of dual-tasking condition, $F(2,46) = 7.67$, $p = .001$, $\eta_p^2 = .250$. As in the perceptual experiment, post-hoc comparisons revealed reliable dual-task costs for movement initiation times: RTs in the control condition (239 ± 8 ms) were significantly quicker than in both dual-task conditions (colour: 261 ± 8 ms, $p = .011$, shape: 263 ± 5 ms, $p = .006$), while there was no difference between the two dual-task conditions ($p > .999$). This finding suggests that there is dual-task interference in grasping, affecting the grasp planning process. There was no interaction effect between the Garner and the dual-tasking conditions, $F(2,46) = 0.41$, $\epsilon = .761$, $p = .612$, $\eta_p^2 = .017$.

Concerning the MTs, our analyses did neither yield an effect of Garner condition, $F(1,23) = 0.56$, $p = .461$, $\eta_p^2 = .024$, nor an interaction effect between Garner and dual-tasking condition, $F(2,46) = 1.10$, $p = .343$, $\eta_p^2 = .045$. There was also no significant main effect of dual-tasking condition, $F(2,46) = 1.90$, $\epsilon = .782$, $p = .172$, $\eta_p^2 = .076$. Descriptively MTs were longest in the dual-task shape condition (527 ± 20 ms) and shortest in the single-task condition (496 ± 18 ms), with MTs in the dual-task colour condition falling roughly in-between (510 ± 16 ms). Thus, descriptively MTs slightly increased with enhanced similarity between the primary and the secondary task (i.e., dual-task shape condition), but this effect was not statistically significant.

The adjustment times are depicted in Figure 4. Interestingly, the 2 x 3 repeated measures-ANOVA revealed a significant main effect of the Garner condition, $F(1,23) = 5.39$, $p = .029$, $\eta_p^2 = .190$, with a later adjustment of the hand opening to object length in the filter (340 ± 27 ms) as compared to the baseline conditions (305 ± 22 ms), as well as a significant main effect of dual-tasking condition, $F(2,46) = 4.51$, $p = .016$, $\eta_p^2 = .164$. Post-hoc tests showed that the adjustment of the aperture occurred significantly later in the dual-task shape condition (357 ± 27 ms) than in both, the control condition (302 ± 27 ms, $p = .045$) and the dual-task colour condition (308 ± 23 ms, $p = .022$) which did not differ significantly from each other ($p > .999$). There was no significant interaction effect, $F(2,46) = 0.39$, $p = .681$, $\eta_p^2 = .017$. In summary, this measure specifically addressing the temporal adjustment of the grip aperture profile, illustrates a Garner Interference effect as well as dual-task costs. Importantly, dual-task costs were more pronounced when there was a higher similarity between the primary and secondary task demands (i.e., shape condition). Note that this delayed adjustment in the shape condition was not reflected in an overall increase in MTs.

At a first glance, it might appear that the missing Garner Interference effect in RT and MT, representing two of the main timing measures of the grasp, supports the view that the action system processes information analytically and thus differently to the perceptual system whereby providing evidence for a functional dissociation between the two processes as suggested by Ganel and Goodale (2003). However, as argued in the introduction and also previously by Hesse and Schenk (2013), commonly used timing measures such as RT and MT might not be the most reliable variables to uncover Garner Interference effects in grasping. Remarkably, a timing measure that is more specifically tailored to reflect decision making during the grasping movement – i.e., the early adjustment times of the grip to object size - did show Garner Interference. Note that Ganel and Goodale (2014) put forward a similar argument based on which they suggested that MGA variability might be a more suitable and robust measure than RT to reveal Garner Interference effects in action processes.

3.2.2 Accuracy of the movement: Variability of MGA and slopes

As it has been suggested that Garner Interference during grasping might reveal itself primarily in measures of movement accuracy rather than the timing of the movement, we also analysed MGA variability in line with a recent study by Ganel and Goodale (2014). Interestingly, and in contrast to the findings by Ganel and Goodale (2014), the 2 x 3 repeated-measures ANOVA on the data revealed a highly significant effect of Garner condition $F(1,23) = 18.90$, $p < .001$, $\eta_p^2 = .451$, with a larger variability of the MGA in filter conditions ($6.02 \pm .28$ mm) than in baseline conditions ($5.38 \pm .28$ mm). There was no main effect of dual-tasking condition, $F(2,46) = 0.76$, $p = .472$, $\eta_p^2 = .032$, and no interaction effect, $F(2,46) = 2.49$, $p = .094$, $\eta_p^2 = .098$. Interestingly, even though we did not find a significant interaction effect, and thus evidence for the idea that a Garner-related secondary task (shape task) enhances Garner Interference effects, the interference effects were at least descriptively much larger in the dual-task shape condition than in the single-task and dual-task colour conditions (see Figure 5).

Previous research has established the linear relationship between MGA and object size as a reliable measure for how well participants adjust their hand opening to the object when grasping it (Freud et al., 2016; Goodale et al., 1991; Hesse & Franz, 2009b; Hesse et al., 2012; Karnath, Ruter, Mandler, & Himmelbach, 2009; Westwood, Danckert, Servos, & Goodale, 2002). MGA has been shown to be linearly related to object size over a wide variety of object sizes (Hesse & Franz, 2009b). Thus, the slope of the function relating MGA to object size is considered a robust indicator of the overall accuracy of the grip. Here, we used these slopes as an additional accuracy measure to determine the occurrence of the Garner Interference effect during grasping. Specifically, we hypothesised that if the action system takes into account a secondary (grasp-irrelevant) dimension then the grip calibration to the grasp relevant dimension should be slightly impaired in the filter conditions. Indeed, the 2 x 3 repeated-measures ANOVA on the slopes revealed again a highly significant main effect of Garner condition, $F(1,23) = 10.28$, $p = .004$, $\eta_p^2 = .309$. As we hypothesised, slopes were shallower in the filter ($.56 \pm .049$) than in the baseline condition ($.62 \pm .046$), demonstrating a decreased accuracy in adapting the hand opening to object size (see Figure 6). Furthermore, there was also a main effect of

dual-tasking condition, $F(2,46) = 3.78$, $p = .030$, $\eta_p^2 = .141$. Post-hoc comparisons showed that slopes were significantly steeper in the control condition ($.62 \pm .053$) than in the dual-task shape condition ($.55 \pm .047$, $p = .018$) while there was no difference between the control condition and the dual-task colour condition ($.61 \pm .047$, $p > .999$) and also no significant difference between the two dual-task conditions ($p = .170$). The interaction between both factors was again not significant, $F(2,46) = 0.20$, $\epsilon = .796$, $p = .770$, $\eta_p^2 = .009$. The finding further highlights that action execution is susceptible to dual-task interference effects in particular in situations where properties of the perceptual secondary task are also relevant for the primary visuomotor task (i.e., shape of the stimulus).

4 Discussion

4.1 Garner Interference

The first question we aimed to address in this study was whether or not visuomotor tasks that require dorsal stream processing such as grasping are immune to Garner Interference. Our findings clearly indicate that this is not the case. We found evidence of significant Garner Interference in three out of five measures of grasping. Garner Interference increased the variability of the MGA, reduced the sensitivity with which the hand opening adjusted to the size of the target object (MGA slope), and delayed the time at which the hand aperture reliably reflected the length of the target object (adjustment time). Similar as previous studies, we did not find reliable interference effects in RT and MT (e.g., Ganel & Goodale, 2003, 2014).

It seems surprising that we found a clear Garner Interference effect on MGA variability while Ganel and Goodale (2014) did not. However, based on our findings we are able to offer a possible explanation for this discrepancy: At least descriptively, Garner Interference affecting MGA variability was clearest in dual-task shape conditions in our study. As we had hypothesised, this additional task might have slightly enhanced the Garner Interference effect and thus may have made it easier for us to detect the relatively small effects (see section 4.3). Without inclusion of the dual-task shape condition it is questionable if the effect would have reached significance (see Figure 5). Furthermore,

in addition to using a single-task condition only, Ganel and Goodale (2003, 2014) ran their experiments under closed-loop vision conditions, providing participants with a better opportunity to adapt their hand during the grasping movement.

One reviewer pointed out that a potential alternative explanation for an increase in MGA variability when the Garner effect is tested in the dual-task conditions may be that participants might have not followed our instructions of looking at the Garner target but may instead have looked at the RSVP stimuli. In this case the Garner target would have appeared in their visual periphery, resulting in reduced visual accuracy and thereby potentially enhancing MGA variability. However, previous studies investigating grasping to targets presented in the observer's visual periphery found that the size of MGA tends to increase with increasing visual eccentricity, but both MGA-variability and grip scaling remain stable (Brown, Halpert & Goodale, 2005; Goodale & Murphy, 1997). Note, that this was even the case when grasping was tested at much larger visual eccentricities than in our experiment (i.e., up to 70° of visual angle, see Goodale & Murphy, 1997). Given the fact that MGA usually increases when movements are performed in visual eccentricity and given the assumption that the Garner target may have shifted into the observer's periphery under dual-task conditions, one would predict larger MGA for dual-task conditions. However, such pattern was not found in our results. A repeated-measures ANOVA revealed no main effect of dual-tasking, $F(2,46) = 0.43$, $p = .653$, $\eta_p^2 = .018$, Garner Interference, $F(1,23) = 0.26$, $p = .618$, $\eta_p^2 = .011$, and no interaction effect, $F(2,45) = 0.35$, $p = .354$, $\eta_p^2 = .044$, on MGA. These findings suggest that it is unlikely that our findings on MGA variability are caused by a changed oculomotor strategy.

Finally, regarding the fact that we used an open-loop vision condition, it seems surprising that we did not find a Garner Interference on RTs given that such an effect was found in a previous study that employed an open-loop vision condition to encourage participants to pre-plan their movements during the RT-interval (Hesse & Schenk, 2013). However, in contrast to this previous experiment, we did not vary the position of the target objects on a trial by trial basis. In our opinion, this difference

might be responsible for our failure to replicate Garner Interference effects on RTs during open-loop grasping.

In summary, our findings combined with those of our previous study suggest that neither RTs nor MTs are reliable measures to detect Garner Interference effects during grasping and that instead accuracy measures (such as MGA variability, MGA slope) and timing measures, which are attuned to the time-course of the decision making process in a grasping task, such as adjustment times, provide more reliable measures for identifying Garner Interference in grasping.

4.2 Dual-tasking

Our second question related to dual-tasking and its effect on perception and action. The PAM suggests that the presence of a secondary task may affect perceptual performance but not the performance in visuomotor tasks that are served by the dorsal stream. Here, we found further evidence that contradicts this claim. Similar to previous studies (e.g., Kunde et al., 2007; Singhal et al., 2007) we found that RTs of the grasping response were clearly affected by the presence of a secondary perceptual task. In contrast, we found no clear dual-task effect on MTs. This is in line with other studies investigating grasping movements in the presence of an additional visuo-attentional RSVP task (Liu et al., 2008; Hesse & Deubel, 2011). As argued by Hesse and Deubel (2011) the lack of dual-task interference on MTs may be related to the fact that objects were presented at the very same location throughout the experiment. Hence, participants may quickly learn the required movement path to reach that location and automate that aspect of the movement. Consequently, MTs will become less susceptible to interference effects. The situation for MGA is different. In contrast to target location, the size of the target object changed from trial to trial meaning that observers were required to program and adjust their grip accordingly in every trial. This prevents automation and may thus increase the sensitivity of grip-related variables to dual-task effects.

Interestingly, looking at the accuracy of the grasping response, we found that dual-tasking effects became primarily apparent when the secondary task involved attending to object shape. In other

words, dual-task costs were higher when the secondary task involved similar features as the grasping task (i.e., the processing of object shape). Specifically, in the dual-task shape condition the slopes of the function relating MGA to object size became shallower indicating a less accurate grip adjustment and adjustment times were delayed by about 50 ms in comparison to the baseline and the dual-task colour condition. Only MGA variability did not show any dual-task costs even when there was high similarity between the primary and the secondary task. Again, based on the fact that the size of MGA remained constant in all conditions, we think it is unlikely that the reduced slopes in the dual-task condition and the delayed adjustment times are caused by participants shifting their gaze away from the grasping target toward the RSVP task. This is further supported by the finding that the occurrence and size of dual-task costs seemed to depend on the similarity between the primary and the secondary task. When the secondary task required participants to attend to an object feature that was also relevant for dealing with the primary task (i.e., object shape in our study) as compared to a task-irrelevant object feature (such as object colour), dual-task costs tended to increase and occurred a bit more reliably. In particular, adjustment times were longer and the slopes were shallower in the dual-task shape than in the dual-task colour conditions while there was no difference between the dual-task colour and the single-task conditions. Hence, the failure of previous studies to detect dual-task costs in grasping may, at least partly, be related to their choice of the secondary tasks. Finally, as mentioned above, we cannot fully exclude the possibility that the introduction of a secondary visual task may have altered the gaze behaviour of our observers. However, a recent study by Göhringer, Löhr-Limpens, and Schenk (2018) examined the effects of a secondary task on obstacle-avoidance behaviour and found reliable dual-task effects when fixation was controlled.

There is one further alternative explanation for the finding that the secondary shape task resulted in more reliable dual-task costs than the secondary colour task that needs to be considered: It is possible that shape task was simply more difficult than the colour task. We tried to avoid such differences by piloting both secondary tasks on their own and by adjusting the parameters of the two tasks to achieve a common accuracy level of approximately 85%. Nevertheless, we cannot rule out

that small differences in difficulty persisted. This uncertainty does, however, not affect our main conclusion that grasping is subject to dual-tasks costs. Importantly, for our main question of whether or not actions are susceptible for dual-task interferences it is not crucial whether we attribute the observed dual-task costs to the fact that one of the secondary tasks was more similar to the primary task thus tapping into *the same* processing resources, or to the fact that one of the secondary task was more difficult thus requiring *more* processing resources. Either way, the findings show that a secondary visuo-attentional task can cause reliable dual-task costs for a primary action task.

Based on these findings, we would argue that previous claims of dual-tasking immunity of the action system were a result of a) the analysis of a very small subset of performance measures (e.g., Liu et al., 2008) and/or b) the choice of secondary tasks that were either too distinct from the action task (e.g., Singhal et al., 2007), or potentially too easy. In line with the suggestion that movements need to be analysed in more detail in order to unveil dual-task costs during grasping, Hesse and colleagues (2012) have shown in their previous studies that a secondary visuo-attentional task primarily affects the early adjustment of the grip to object size (i.e., they found that the adjustment of the hand to object size was delayed in dual-task conditions). Finally, another discrepancy between studies that showed clear dual-task interference in action tasks and the study by Singhal et al. (2007) that did not find substantial dual-tasking costs lies in the timing of the secondary task. Singhal and colleagues presented a short auditory stimulus (50 ms) to which participants had to respond at the beginning of the trial. In contrast, we employed a RSVP paradigm with stimuli being presented over the whole duration of the grasp. Targets could occur at any moment in time during action planning and execution meaning that primary and secondary task had to be executed truly simultaneously and could not be performed sequentially. To sum up, the findings from our current study and those from previous studies (Hesse & Deubel, 2011; Hesse et al., 2012; Janczyk & Kunde, 2010) suggest that both, action and perception are susceptible to dual-task costs, but also that effects can be missed if experimental methods and measures are not sensitive enough.

4.3 Interaction between Garner Interference and Dual-Tasking

Our third research question, addressed the issue of whether combining the Garner paradigm with a dual-tasking condition might increase the size of the Garner Interference effect, thereby potentially making it easier to detect. In addition, we aimed to test whether the specific demands of the secondary task condition might also modulate the size of the Garner Interference effect. Specifically we speculated that using a secondary perceptual shape-discrimination task, which requires similar processing strategies as dealing with the Garner task might enhance the Garner Interference effect. If this is true, this should have become apparent in significant interaction effects between the factors Garner Interference and dual-tasking condition in the perceptual task and possibly also for the grasping task. In short, we found no clear evidence for this prediction, as no interaction effects were observed on any of our dependent measures. This finding is in accordance with former studies using the PRP paradigm, suggesting additivity of stimulus onset asynchrony (SOA) and Garner Interference effects in perceptual tasks (Kunde et al., 2007; Janczyk et al., 2010). In these studies, the grasping task did not show any Garner Interference effects, but suffered from a secondary task. In our study, the presence of Garner Interference effects as well as dual-task costs, but a lack of interaction between them, was true for both the perception task as well as the visuomotor grasping task. In other words, even when the dual-task affected RTs reliably indicating that the processing of the primary task was slowed, the size of the Garner Interference effect remained rather stable across all conditions.

The only measure in which the Garner Interference effect was moderated by the dual-task demands, at least descriptively, was MGA-variability. Here, the Garner Interferences seemed indeed increased when a secondary shape discrimination task was employed during grasping. However, at this point, our findings also suggest that the interaction effects between Garner Interference and dual-tasking are subtle and fragile, and that high-powered studies are needed to provide more conclusive evidence for our hypothesis that dual-task demands can moderate Garner effects as reflected in certain kinematic parameters of the grasping movement. Based on our current findings we would

suggest that the idea might still hold some promise but replications are required to get a final answer to this question.

5 Conclusions

The PAM is supported by a wide-range of evidence. Some of the evidence has been reviewed and scrutinised quite heavily. Other sources of support have received far less research attention. In this study, we focussed on two claims of the model. Both claims were tested in the past and positive evidence on those tests has been used to argue for the continued validity of the model. One claim is that the dorsal stream and behaviours relying on visual information from the dorsal stream are immune to Garner Interference. The second claim states that dorsal-stream behaviour is immune to interference from a secondary perceptual or cognitive task. In our study, we obtained evidence that contradicts both claims. We therefore conclude that neither evidence from Garner Interference nor evidence from dual-tasking provides unequivocal support for the claim that visual information for perception and action are processed in functionally independent anatomical streams.

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Fig. 1 Objects for the Garner task

Baseline: Objects vary only in length, the dimension relevant for the Garner task. *Filter:* Objects vary in length and width, i.e. also in the dimension irrelevant for the Garner task

Fig. 2 Perceptual data

a) Mean reaction times from the perceptual experiment. *Control:* Garner paradigm single-task condition; *Colour:* Garner paradigm with additional colour RSVP task (dual-task colour); *Shape:* Garner paradigm with additional shape RSVP task (dual-task shape). Garner baseline conditions are shown in black, filter conditions in white. **b)** Differences in reaction time between baseline and filter conditions of the Garner paradigm. Error bars depict ± 1 SEM

Fig. 3 Reaction times in grasping

a) Mean reaction times from the grasping experiment. *Control:* Garner paradigm single-task condition; *Colour:* Garner paradigm with additional colour RSVP task (dual-task colour); *Shape:* Garner paradigm with additional shape RSVP task (dual-task shape). Garner baseline conditions are shown in black, filter conditions in white. **b)** Differences in reaction time between baseline and filter conditions of the Garner paradigm. Error bars depict ± 1 SEM

Fig. 4 Adjustment times of hand opening to object size

a) Mean adjustment times, i.e. the point in time when the mean hand opening for long objects exceeded that for short objects for at least 10mm (half a difference between the object lengths). *Control:* Garner paradigm single-task condition; *Colour:* Garner paradigm

with additional colour RSVP task (dual-task colour); *Shape*: Garner paradigm with additional shape RSVP task (dual-task shape). Garner baseline conditions are shown in black, filter conditions in white. **b)** Differences in the slopes of the adjustment times between baseline and filter conditions of the Garner paradigm. Error bars depict ± 1 SEM

Fig. 5 Variability of peak hand opening

a) Mean standard deviations (STD) of the maximum grip aperture (MGA). *Control*: Garner paradigm single-task condition; *Colour*: Garner paradigm with additional colour RSVP task (dual-task colour); *Shape*: Garner paradigm with additional shape RSVP task (dual-task shape). Garner baseline conditions are shown in black, filter conditions in white. **b)** Differences in mean STD of the MGA between baseline and filter conditions of the Garner paradigm. Error bars depict ± 1 SEM

Fig. 6 Adjustment of hand opening to object size

a) Mean slopes of the linear regression between maximum grip aperture (MGA) and object size. *Control*: Garner paradigm single-task condition; *Colour*: Garner paradigm with additional colour RSVP task (dual-task colour); *Shape*: Garner paradigm with additional shape RSVP task (dual-task shape). Garner baseline conditions are shown in black, filter conditions in white. **b)** Differences in the slopes of the linear regression between MGA and object size between baseline and filter conditions of the Garner paradigm. Error bars depict ± 1 SEM. N.B.: Higher slopes reflect better adjustment, so negative differences indicate Garner Interference effects

Fig. 1

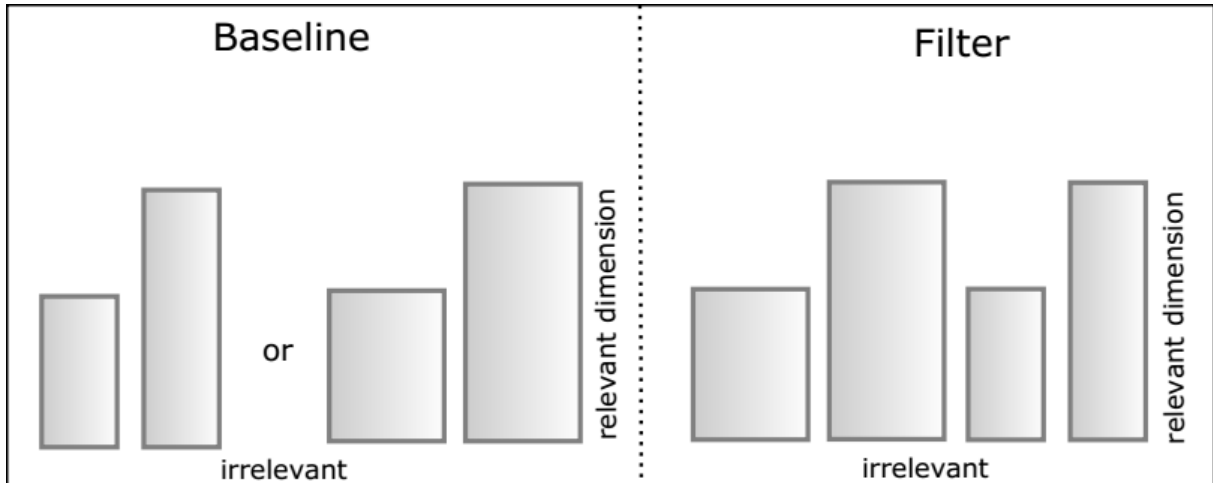


Fig. 2

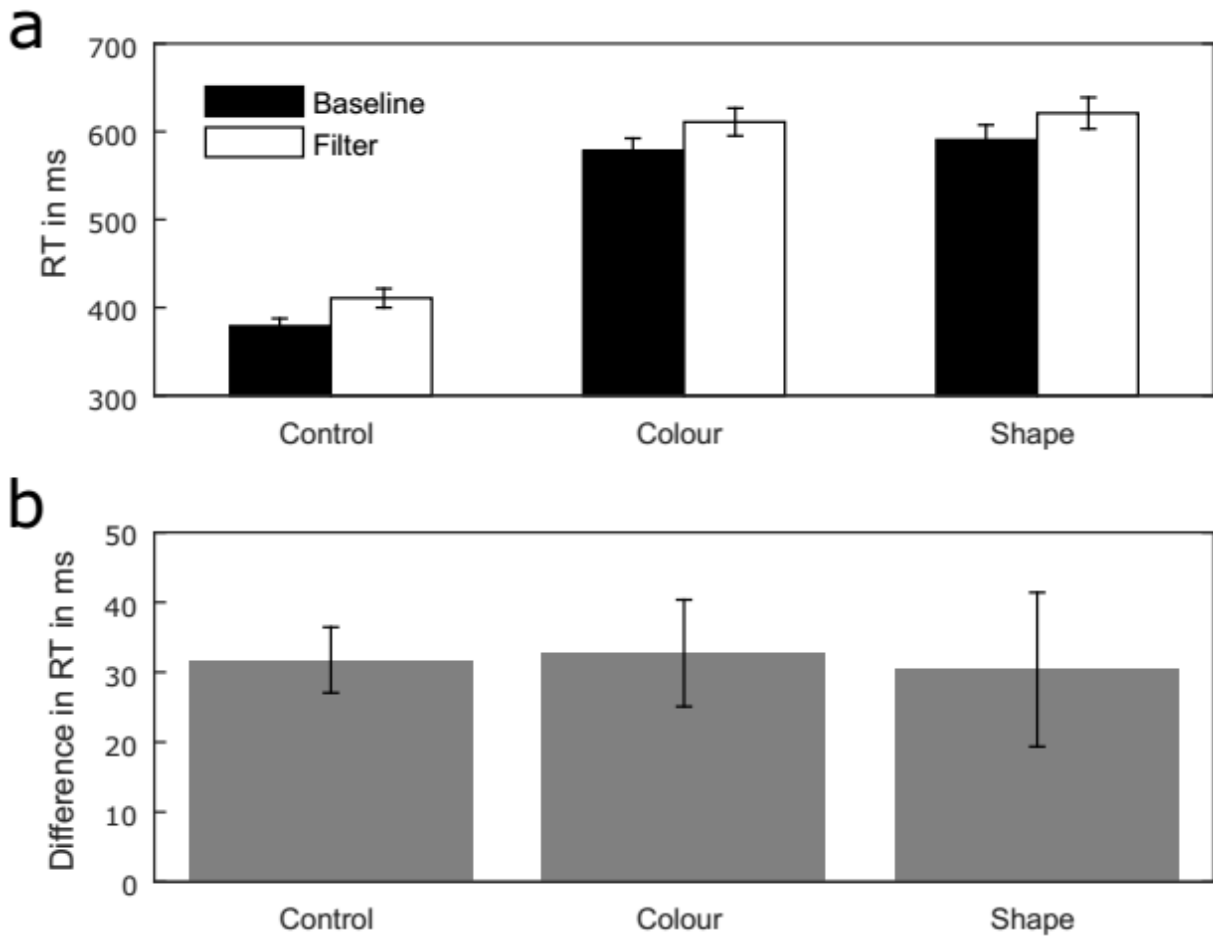
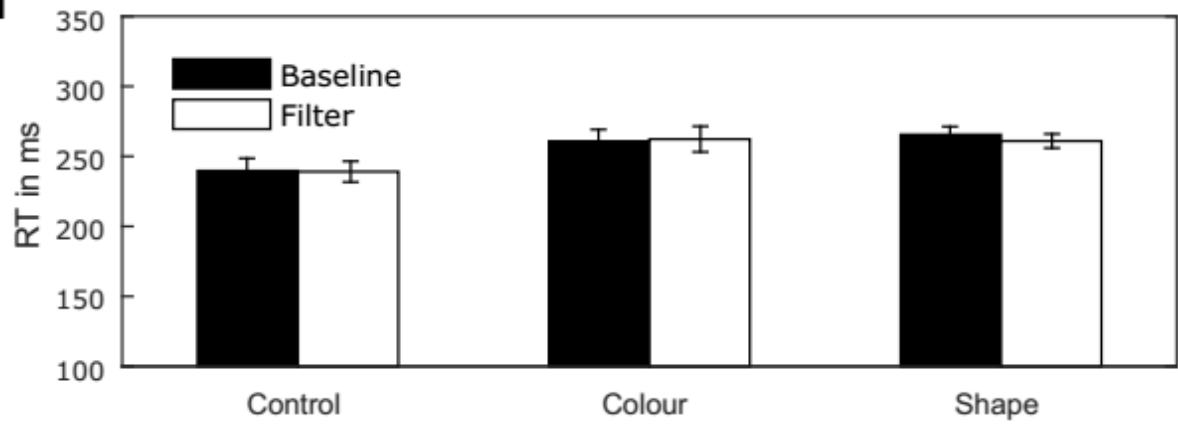


Fig. 3

a



b

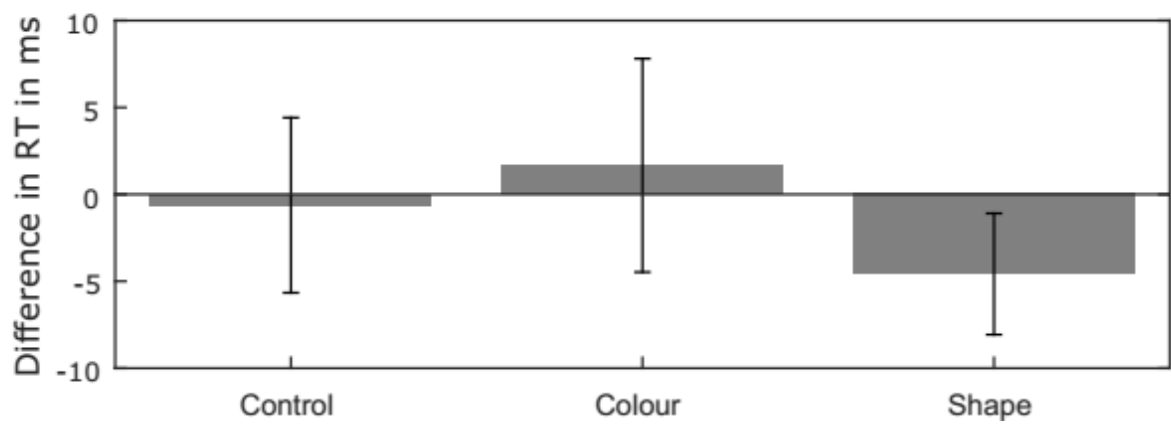
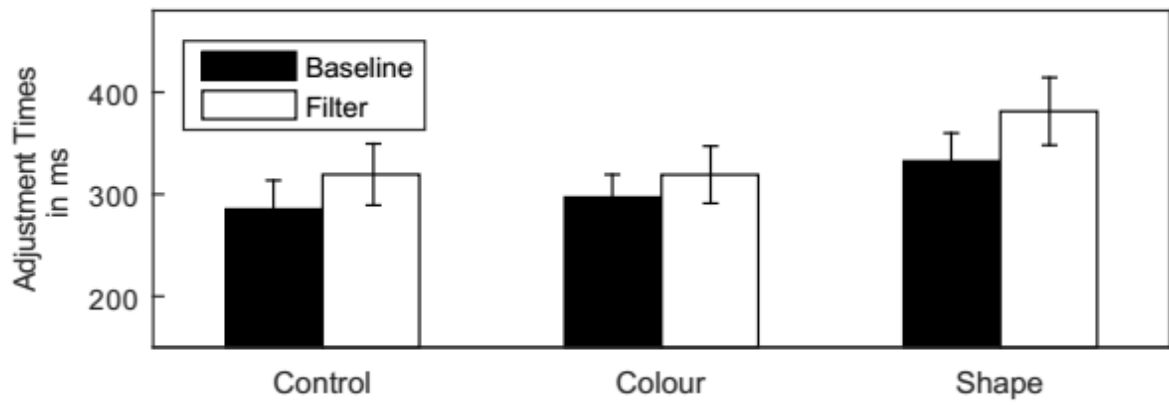


Fig. 4

a



b

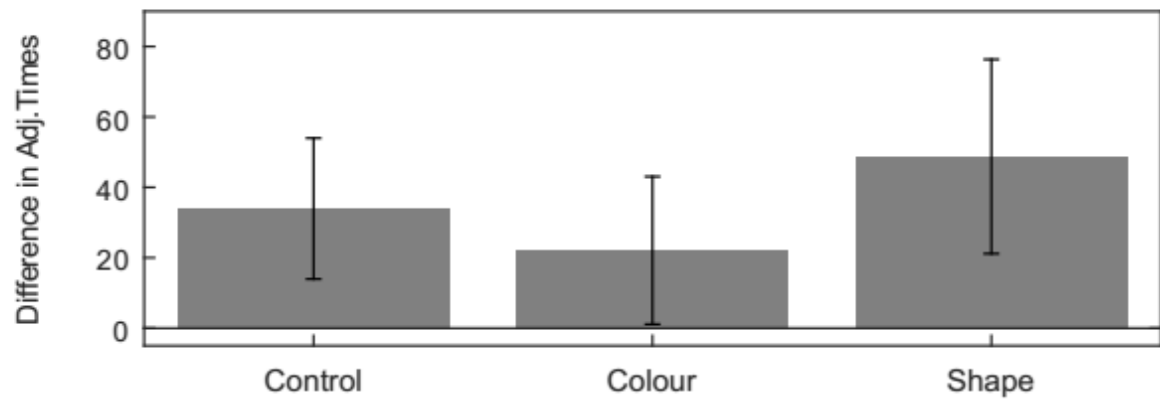
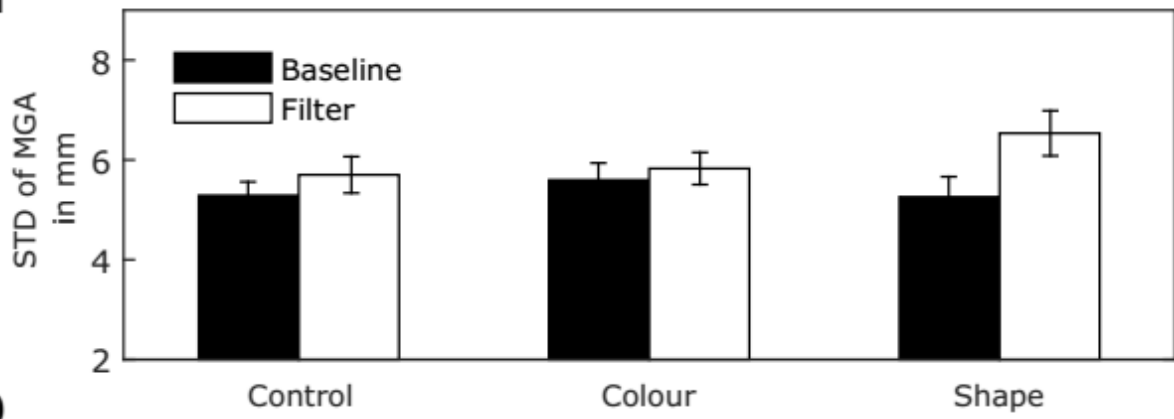


Fig. 5

a



b

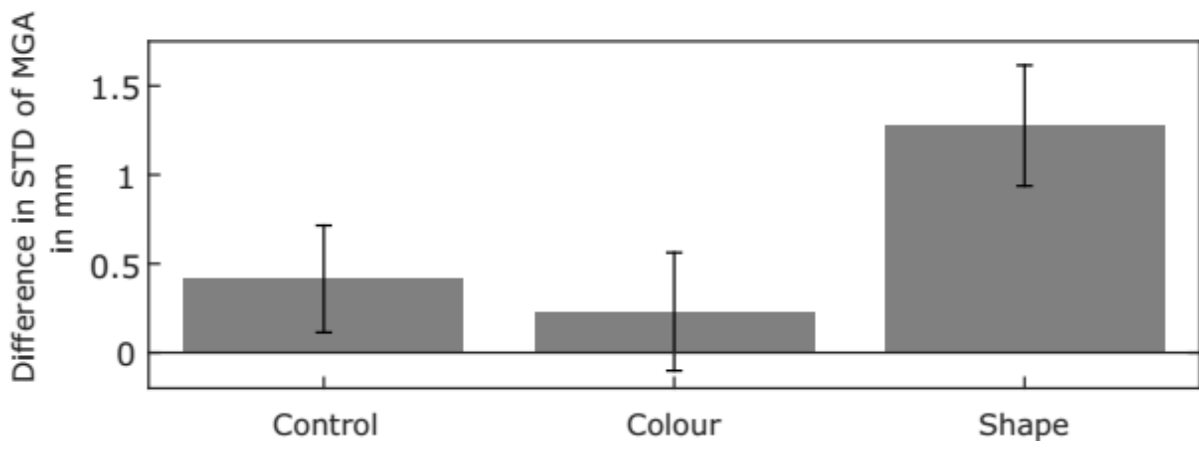
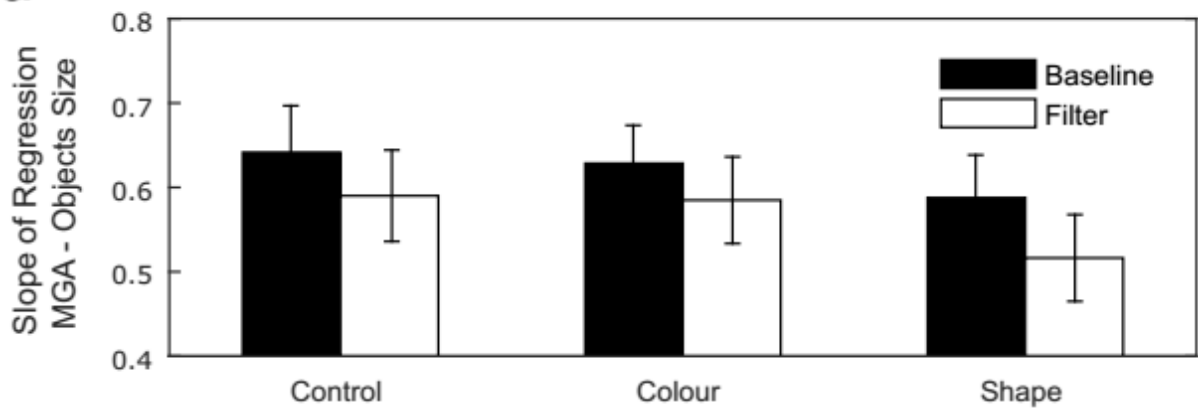
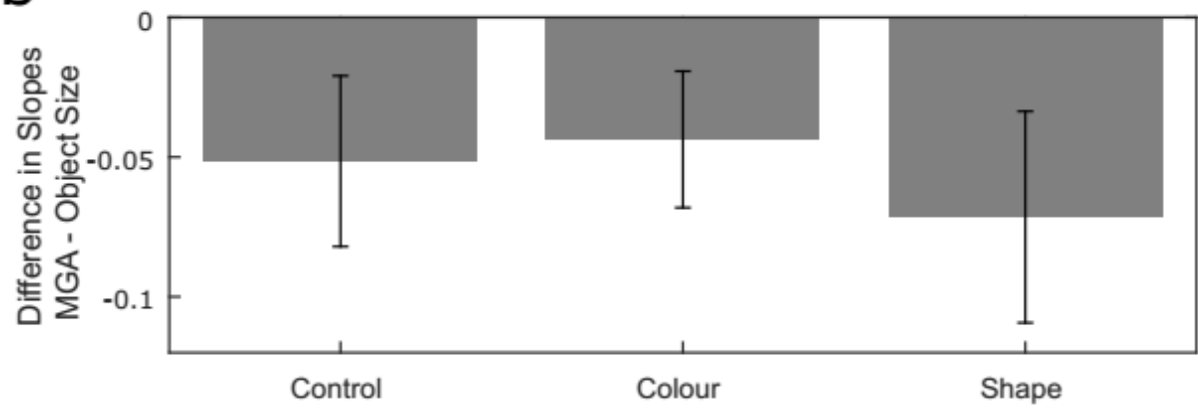


Fig. 6

a




b



4.3 Grasping discriminates between object sizes less not more accurately than the perceptual system.

Article

Grasping Discriminates between Object Sizes Less Not More Accurately than the Perceptual System

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Abstract: Ganel, Freud, Chajut, and Algom (2012) demonstrated that maximum grip apertures (MGAs) differ significantly when grasping perceptually identical objects. From this finding they concluded that the visual size information used by the motor system is more accurate than the visual size information available to the perceptual system. A direct comparison between the accuracy in the perception and the action system is, however, problematic, given that accuracy in the perceptual task is measured using a dichotomous variable, while accuracy in the visuomotor task is determined using a continuous variable. We addressed this problem by dichotomizing the visuomotor measures. Using this approach, our results show that size discrimination in grasping is in fact inferior to perceptual discrimination therefore contradicting the original suggestion put forward by Ganel and colleagues.

Keywords: perception-action model; Two Visual Streams Hypothesis; grasping; object size; Just Noticeable Difference

1. Introduction

According to the Perception-Action Model (PAM), suggested by Milner and Goodale [1,2], the visual system consists of two functionally separated streams, the dorsal stream and the ventral stream. The ventral stream provides vision for perception and the dorsal stream provides vision for action. The model was first formulated to account for deficits observed in patients suffering from ventral or dorsal stream damage. Visual form agnostic patient D.F., who suffered from ventral stream lesions, was found to still have functioning motor control, despite her severely impaired visual perception [3,4]. In contrast, optic ataxia patients suffering from dorsal lesions tend to show impaired motor control, while their visual perception remains largely normal. [5].

The model contains an important assertion. The visual processes taking place in the two distinct streams use different representations and different processing modes [6]. In principle, it is therefore possible to test this two-visual pathway hypothesis also in healthy participants. For example, finding that some processing error (or to put it more neutrally: processing feature) affects only perceptual tasks, but not visuomotor tasks, could be taken as an indication that the two tasks use different visual representations and that only one type of representation is affected by this error. In this context, the most extensively studied error is the susceptibility to perceptual illusions. Many studies have suggested that perceptual illusions affect perceptual but not visuomotor tasks (e.g., [7,8]). However, this evidence has been challenged in numerous studies, and counter-examples and alternative accounts have been provided (for reviews, see Carey [9], Bruno [10], Franz [11], Franz and Gegenfurtner [12], Bruno and Franz [13], Schenk, et al. [14], and Schenk [15]). A recent large-scale, multicenter, preregistered study

showed that for the Ebbinghaus illusion, one of the most commonly studied illusions, the illusion effects are pretty much identical for perception and action [16,17]. Illusions are, however, not the only tool employed to demonstrate the distinctness of representations in the perceptual and the visuomotor system. Ganel and Goodale [18], for example, showed that the Garner-interference effect influences perceptual size-judgements but not the size of the grip apertures in a visuomotor task. Furthermore, Ganel, et al. [19] also reported that a fundamental psychophysical law, Weber's law, is selectively violated in grasping. Finally, Singhal et al. [20] showed that a more general cognitive phenomenon, namely the finding that the concurrent execution of two tasks creates performance costs for at least one of the two tasks, reliably occurs in tasks that can be assigned to the perceptual system but is much less prominent in tasks assigned to the visuomotor system. However, all these approaches have been met with counter-evidence and are currently bogged down in controversy [21–29].

In 2012, Ganel, Freud, Chajut, and Algom [30] proposed another novel approach to test for the existence of distinct processing modes in perception and action. They presented participants with objects that differed in size by only 0.5 mm. Participants were first asked to indicate verbally which of the two objects was the bigger one, and subsequently had to grasp the object directly in front of them. It turned out that participants were at chance level with their verbal judgements. Yet, when their hand-openings during the grasping movements were analyzed, those hand-openings differed significantly for the smaller and bigger objects. Most interestingly, even when observers erroneously labelled the bigger object as the smaller one their hand-opening was still (on average) bigger than when they erroneously labelled the smaller object as being bigger. Thus, it seemed that observers' hand-openings were not affected by their conscious size judgement. Their hands reliably adjusted to the true physical size of the objects, even when they could not perceptually discriminate between those objects. Based on these findings, Ganel and colleagues concluded that perceptual judgement and grasping are based on distinct representations of visual size and that the size representation for grasping is more precise than the one used for explicit perceptual judgements. Furthermore, these findings were interpreted as support for Milner and Goodale's claim that vision for perception and vision for action are served by distinct neural pathways.

This conclusion relies, however, on the assumption that both tasks use visual size as their main input which has been challenged by Smeets and Brenner [31]. They presented a model which could correctly account for most aspects of grasping movements, while assuming that the sensorimotor system does not compute object size but instead determines the optimal contact positions for the grasping digits (typically index finger and thumb) on the target object. They demonstrated that using this assumption, grip apertures still positively correlate with object size, despite this parameter never being explicitly computed. On the basis of this account, it would not be expected that visual requirements for perceptual size-discrimination and grasping are identical and thus, in the context of this model, it is hardly newsworthy that significant differences can be found when grasping objects whose sizes cannot be reliably discriminated.

While we accept the more general point, namely that grasping and size discrimination do not necessarily use the same sensory inputs and that grasping should not be treated as the motor equivalent of a size-judgement task (for a more detailed discussion of this point, see Hesse et al. [32] and Schenk et al. [24]), we do think that there is evidence to suggest that visual size information is commonly used for grasping in healthy participants (albeit possibly not, or to a lesser extent, by patients with agnosia [33,34]). For example, the above discussed finding that grasping and perceptual judgements are impacted very similarly by visual size illusions [16] seems to indicate that object size is used also for grasping (for a slightly different view, see de Grave, et al. [35]). Further evidence comes from studies on grasping familiar objects. For example, McIntosh and Lashley [36] showed that the assumptions that we make about the size of familiar objects have a significant impact on how we grasp those objects. Taken together these findings suggest that size does play an important role in shaping our grasping response. Thus, if we accept that grasping relies on object size information, it is indeed surprising and noteworthy that in grasping we seem to be able to distinguish between object sizes that

are perceptually identical. However, while we do not question the assumption that both grasping and perceptual judgement rely on object size information, we challenge the claim by Ganel, Freud, Chajut, and Algom [30] that there is a dissociation in the accuracy of this information.

So, let us have a closer look at the evidence upon which the claim is based that the representation of size underlying grasping is superior to the representation underlying perceptual judgement. On average observers guessed the correct size of the object only in 58.7% of trials, i.e., barely above chance. In contrast, when the average maximum grip aperture (MGA) was analyzed a reliable and significant difference between the MGAs for the smaller and bigger object emerged. However, is this contrast enough to claim that the hand distinguishes between objects more reliably than the observer? To illustrate the problem with this claim, we can take the example of body height in Scottish and English men. The mean height of adult male Scots is 176 cm, and thus approximately 2 cm less than the mean height of English adult males. Thus, if we took a representative sample of Scottish and English males to compare their average height, we would expect to find that the average Scottish height is significantly below that of the English sample. Nevertheless, would we be asked to assign nationality on the basis of body height we would make frequent errors. The same analogy holds for comparing grasping and perceptual data. MGAs for smaller objects may well be significantly smaller than for bigger objects, but chances are there are many grasping responses directed to the bigger object producing smaller MGAs than those found for grasping responses directed to the smaller object. Thus, the following question arises: if we tried to guess the size of the target on the basis of the observed MGAs, would the number of correct guesses significantly exceed the number of correct guesses achieved by the observers in the perceptual judgement task? To address this question, we replicated the study by Ganel, Freud, Chajut, and Algom [30] and re-analyzed the findings by obtaining measures for size-classification accuracy based on the MGAs of the participants grasping responses.

In total, we performed three experiments. In the first experiment, we aimed to replicate the first experiment from Ganel, Freud, Chajut, and Algom [30]. Surprisingly, our findings differed from those obtained by Ganel, Freud, Chajut, and Algom [30] already prior to the proposed re-analysis of the data. We therefore decided to replicate this experiment (Experiment 2) with a new sample of participants to check whether our original findings were reliable. The second experiment produced a new pattern of findings which (again prior to the proposed re-analysis) were more similar to the results obtained by Ganel and colleagues [30]. In our final experiment (Experiment 3) we examined the role of hand-sight and asked participants to perform the tasks used in Experiments 1 and 2 once under closed-loop conditions (i.e., moving hand remained visible throughout the trial) and again under open-loop conditions (i.e., hand only visible at the start of the movement). In this last experiment we found for the closed loop condition a pattern more similar to Experiment 1.

2. Materials and Methods

2.1. Experimental Setup

We followed Ganel, Freud, Chajut, and Algom [30] in the design of the study. The objects we used had the same sizes of 40 mm and 40.5 mm and a height of 2 mm. The target object was placed 15 cm in front of the starting position of the participant's hand in Experiment 1 and 2, and 8 cm in front of the starting position in Experiment 3. The second object was always placed at a horizontal distance of 12.9 cm and a vertical distance of 9 cm relative to the first object (see Figure 1).

The starting position was marked with a round pole which participants had to hold. The large starting pole, used only in Experiment 1, had a height of 10.9 cm and a diameter of 3 mm and participants were instructed to grasp the starting pole where they could comfortably hold it. The small starting pole, used in Experiments 2 and 3, had a size of 4.5 cm and 3 cm respectively, also with diameters of 3 mm. Participants were instructed to grasp the pole at the very top, so that they would not have to move around it during grasping. When participants held the starting pole, they had to push down a button with the side of their hand. The release of this button sent a signal to the computer

indicating the start of the movement. Participants always had to grasp the near object using index finger and thumb. After grasping it, they had to hold it up for a short time and then place it down on the table again. When estimating the size, they had to report whether the object in front was larger or smaller than the one in the back by saying “größer” (German for larger) or “kleiner” (German for smaller).

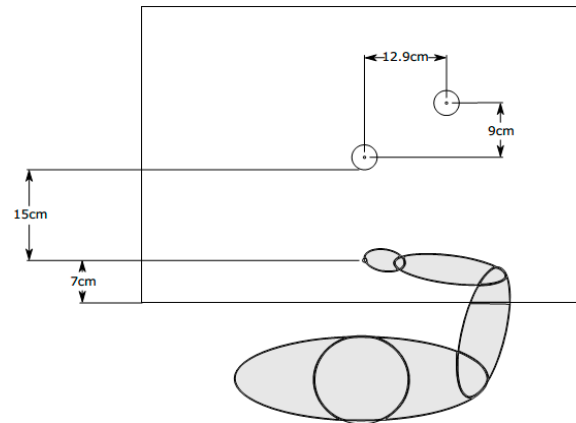


Figure 1. Experimental setup. Shown here is the stimulus arrangement of one exemplary trial. At the beginning of each trial, participants grasped the starting pole. Participants were then asked to grasp the object positioned straight ahead, seen here as the larger disk. The second disk was always positioned either to the right and back, as shown here, or to the left and back. Participants then had to indicate whether the object in front was larger or smaller than the object in the back. In half of the blocks the order was reversed with participants first indicating the size and then grasping the disk.

In Experiment 1 hand movements were recorded using an acoustic 3D movement registration system (Fa. Zebris, Tuebingen, Germany) with a sampling rate of 50 Hz. Two circular markers were attached to the most right lateral part of the thumb nail and the most left lateral part of the index finger nail, having the midpoint of the markers also be the midpoint of the nail-finger border. The markers were attached with medical tape. The cables connecting the markers to the Zebris system were attached to their upper arms giving them complete freedom of movement. In Experiments 2 and 3, we used the Vicon Motion Tracking System with Bonita Cameras and a sampling frequency of 100 Hz. This infrared optical 3D motion tracking system uses passive reflecting round markers, two of which were positioned, the same as in Experiment 1.

The aspects in which the experiments differed will be explained in the following sections.

2.2. Experimental Procedure

2.2.1. Experiment 1

In this experiment, half of the participants first had to grasp the object closest to them and the other half first had to indicate whether the object was larger or smaller than the object placed further away from them. The white target objects were placed on a black surface. Participants were asked to close their eyes, grasp the starting pole and wait until they heard a sound indicating the start of the trial. They then had to open their eyes and begin with the first task. After 2.5 s, another two sounds were heard in quick succession, indicating the start of the second task. After another 2.5 s, a quick sequence of two tones indicated the end of the trial. The participants had to close their eyes again and wait until the next trial.

Object sizes and object positions were counterbalanced and randomized across trials. Participants performed a total of 96 trials. After blocks of 32 trials, participants could have a break. The experimental session started with 12 practice trials.

2.2.2. Experiment 2

In Experiment 1, we did not replicate the original results reported by Ganel, Freud, Chajut, and Algom [30]. We therefore decided to perform another experiment to determine if we could replicate our own findings in a new sample of participants. Unfortunately, after we had already collected data of 10 participants (mean age = 28, range 20–40, 3 male), we noted that the large starting pole used in this experiment forced participants to first circumvent the top half of the starting pole before they could move their hand towards the target object. This resulted in a quite unusual grasping trajectory (see [37] for similar observations) and prompted us to tweak that aspect of our experiment by shortening the length of the starting pole. Consequently, we did not include the data of those first ten participants in our analyses and instead opted for recruiting 30 new participants. The experimental procedures in Experiment 2 were nearly identical to those employed in Experiment 1. The only differences were that the starting pole was shortened (as described above) and that participants now wore shutter glasses that controlled their vision.

2.2.3. Experiment 3

In this last experiment we compared a closed-loop (full vision) condition, used also in Experiments 1 and 2, with an open-loop vision condition where vision was occluded during grasping. We wondered whether in the closed-loop condition, the potential influence of the perceived size might be reduced in its effect on MGA due to the availability of visual feedback (i.e., due to the fact that participants could observe their grasping hand and compare its aperture to the diameter of the target object, see Glover and Dixon [38] for a similar argument). To address this question, we introduced a condition where visual feedback was withdrawn at the start of the movement. To do so, we used an LCD shutter window which, when switched to its opaque status, occluded participants' view of the target object and their own hand. In the closed loop condition, the shutter window turned transparent at the beginning of the trial and remained transparent until participants had completed their grasping movement. White objects were placed on a white surface. This ensured that the objects were clearly visible when the shutter window was transparent but were invisible when the window was switched to opaque. As we found in Experiments 1 and 2 that the task order was irrelevant, participants now always started with reporting the target's size before grasping it. In all other respects the general procedure was identical to that employed in Experiment 1 and 2. In the open loop condition, the shutter window switched to transparent (open) at the beginning of the trial to allow participants to view the target objects. The window switched to opaque as soon as participants released the start button.

There were a total of 144 trials divided into 6 blocks with 24 trials per block. Size and position of the objects were randomized within the blocks. There were three closed loop blocks and three open loop blocks. For each participant, a new randomized sequence of closed and open-loop blocks was used. At the beginning of the experiment, participants were given 18 practice trials. After every two blocks, the participants were offered a break.

2.3. Participants

Participants in all experiments were right-handed by self-report and had normal or corrected-to-normal vision. Written consent of all participants was obtained prior to the studies. All experiments complied with the Code of Ethics of the World Medical Association Declaration of Helsinki [39] and were approved by the ethics committee of the University of Erlangen (Re.-No. 91_12 B). Participants were reimbursed with course credit or 8€ per hour. Each experiment lasted about 1.5 h.

2.3.1. Experiment 1

Thirty participants (18 female) were tested for this experiment with an average age of 27 years (range 19–48). One participant had to be excluded due to technical problems with the motion tracker. Four further participants had to be excluded from the ANOVA analysis who had insufficient data in

one of the data cells (e.g., one participant never judged a small object erroneously to be large in the third experimental block).

2.3.2. Experiment 2

Thirty participants (16 female) were tested for this experiment with an average age of 27 years (range 19–53). In four participants, the kinematic data was corrupted and the participants had to be excluded. Five additional participants had to be excluded from the ANOVA analysis due to insufficient data in one of the data cells.

2.3.3. Experiment 3

Thirty-three participants were tested with a mean age of 26 years (range 18–35). In three participants, the kinematic data was corrupted and the participants had to be excluded. Again, a further two participants had to be excluded from the ANOVA analysis since they had insufficient data in one of the cells. Of the remaining 28 participants, 17 were female.

2.4. Data Analysis

Ganel Freud, Chajut, and Algom [30] calculated the means of the MGAs for every participant and compared these means employing an ANOVA using *experimental block*, *object size*, and *verbal report* as within-subject variables. The variable *experimental block* indicates from which of the three experimental blocks the data originates, the variable *object size* denotes whether the target object was the smaller or the bigger one, and the variable *verbal report* (called *perceptual judgement accuracy* in the original report) indicates whether the data comes from the set of trials where the verbal judgement was correct (i.e., a small object was identified as small or the bigger object identified as the bigger one) or from the set of trials where the judgement was incorrect (e.g., the smaller object identified as the bigger one). In Reference [30] they found a significant main effect of *object size* that was, however, independent of the verbal report relating to the object's size. All other effects were not significant. We analyzed the data the same way in Experiments 1 and 2 and without the variable experimental block in Experiment 3, since we found no effect of experimental block in Experiments 1 and 2.

We also carried out an additional analysis to examine whether the participants' visuomotor system was truly better in discriminating between small and bigger objects than the participants' perceptual system. To obtain measures of discrimination or classification accuracy on the basis of the MGA data we used an approach that has been employed in two previous studies [40,41]. The aim of this analysis was to use MGA values to determine whether the associated grasping movement was directed towards the smaller or the bigger object. In order to do so, we first had to decide on a cut-off value that best separates the MGAs for the small object and the big object. For any MGA values above the cut-off, one would assume that the target object was the bigger one, for any MGA values below the cut-off, one would guess that the target object was the smaller one. Clearly, some cut-off values are better than others in the sense that they produce more correct assignments. We decided to use the best cut-off value possible to give the claim by Ganel, Freud, Chajut, and Algom [30] the highest chance to be confirmed. In other words, we used the cut-off value that maximized the number of correct choices. We will call this measure optimal cut-off proportion or OC%.

For the subsequent ANOVA grasping trials were separated based on the size of the object, the experimental block, and based on the accuracy of the observer's judgement. This caused the issue that in some cases data cells remained empty when, for example, a participant never perceived the small object as big. As the OC% analysis could still be computed, participants with empty data cells were excluded from the ANOVA but not from the OC% analysis.

All data is publicly available and can be accessed at www.zenodo.org, doi: 10.5281/zenodo.2577955.

3. Results

3.1. Maximum Grip Apertures (MGA) Analysis

3.1.1. Experiment 1

The results of the repeated-measures ANOVA with the factors *experimental block*, *object size*, and *verbal report* are shown in Figure 2 (upper left panel). We found that the only significant effect was the interaction effect between object size and *verbal report* ($F(1,24) = 11.799, p < 0.01, \eta_p^2 = 0.33$). Bonferroni corrected pairwise comparisons showed that MGAs for small and large objects differed significantly when participants' judgement of the object's size was correct ($p < 0.001$; small object: mean = 82.6 mm, CI [0.95] = 80.4 mm, 84.9 mm, versus large object: mean = 83.5 mm, CI [0.95] = 81.2 mm, 85.8 mm), but not when it was incorrect. Put differently, participants' perceptual judgement about the size of the target object determined, at least to some extent, whether their grip aperture was correctly adjusted to the object's size.

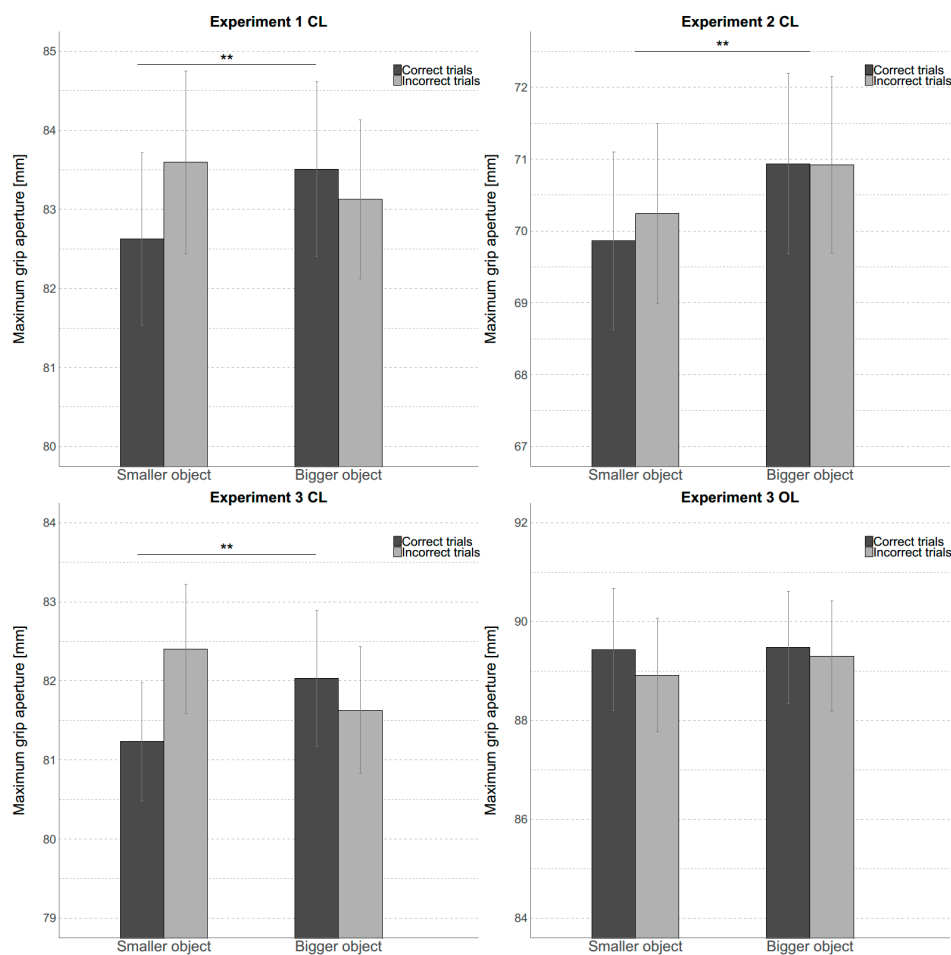


Figure 2. MGA Analysis Results of the Maximum Grip Apertures (MGA) analysis for the three experiments. CL: Closed Loop, OL: Open Loop. Error bars indicate one standard error of the mean. In Experiments 1 and 3 CL interaction effects between *object size* and *verbal report* were significant with pairwise comparisons showing that when participants judged correctly they grasped the small object with a smaller MGA and the large object with a larger MGA on average. In Experiment 2 there was a main effect of *object size*. No main or interaction effects were significant for Experiment 3 OL. ** indicates $p < 0.01$.

3.1.2. Experiment 2

The results were analyzed identically to Experiment 1 and are shown in Figure 2 (upper right panel). In this experiment, we replicated the results of Ganel, Freud, Chajut and Algom [30]. The only significant effect was the main effect of *object size* ($F(1,20) = 11.954, p < 0.01, \eta_p^2 = 0.374$), with MGAs being smaller (mean = 70.1 mm, CI [0.95] = 67.5 mm, 72.6 mm) when the small object was the target and being bigger (mean = 70.9 mm, CI [0.95] = 68.4 mm, 73.5 mm) when the big object was the target, independent of the correctness of the perceptual judgement (i.e., no interaction effect).

3.1.3. Experiment 3

We calculated a repeated-measures ANOVA using *vision* (open-loop versus closed-loop), *object size*, and *verbal report* as within-subject variables. The results are shown in Figure 2 (lower panels). We found a main effect of *vision*, ($F(1,27) = 81.751, p < 0.001, \eta_p^2 = 0.752$), a two-way interaction effect between *vision* and *verbal report* ($F(1,27) = 4.828, p = 0.037, \eta_p^2 = 0.152$), and a three-way interaction effect between *vision*, *object size*, and *verbal report* ($F(1,27) = 5.479, p = 0.027, \eta_p^2 = 0.169$).

To follow-up the 3-way interaction effect, we calculated two separate repeated-measures ANOVAs for each vision condition separately with the factors *object size* and *verbal report*. For the closed loop condition, we found a significant interaction effect between *object size* and *verbal report* ($F(1,27) = 12.781, p < 0.01, \eta_p^2 = 0.321$). Bonferroni corrected pairwise comparisons showed that the difference in MGA when grasping larger and smaller objects was significant only when participants judged their sizes correctly ($p < 0.01$). That is, participants showed smaller MGAs when the small object was presented which they correctly judged to be small (mean = 81.2 mm, CI [0.95] = 79.7 mm, 82.8 mm) and larger MGAs when the larger object was grasped which they correctly judged as being larger (mean = 82.0 mm, CI [0.95] = 80.3 mm, 83.8 mm). When participants incorrectly judged the object size the resulting difference in MGA between small and large object just failed to reach significance ($p = 0.058$). The same ANOVA for the open-loop vision condition revealed no significant main or interaction effects suggesting that MGAs were unaffected by any of the experimental variations.

To sum up, the findings obtained for Experiment 3 in the closed-loop condition closely resembled those obtained in Experiment 1. In particular, we found that perceived size significantly influenced the MGAs.

3.2. Cut-Off Based Analysis

3.2.1. Experiment 1

Ganel, Freud, Chajut, and Algom [30] argued that the visual information available to the visuomotor system guiding the grasping movements is more accurate than the information available to the perceptual system on which the verbal reports of participants is presumably based. To directly test this claim, we compared participants' verbal accuracy with their motor accuracy. The verbal accuracy (i.e., the percentage of trials where participants correctly called the small object small and the bigger object big) was 69%. This percentage is higher than the verbal accuracy reported by Ganel, Freud, Chajut, and Algom [30] but within the conventional range of uncertainty for psychophysical measures (25%–75%). To obtain a measure of how accurately the grasping performance predicted the real size of the target object, we used the procedure described above (General methods; data analysis).

We then compared verbal accuracy with motor accuracy (based on the threshold-technique) using paired-samples *t*-tests. The results are shown in Figure 3 (left panel). A Shapiro–Wilk test confirmed that the sampling distribution was normally distributed. The difference was highly significant with the mean of the perceptual task being higher (mean = 0.69, SD = 0.076) than the mean of the criterion-based values, OC% (mean = 0.58, SD = 0.032; $t(28) = 7.408, p < 0.001$). The findings suggest that grasping performance predicts the correct target size less reliably than the participants' verbal report. Thus, if there is a difference in visual-size related information quality for the visuomotor (dorsal) and

perceptual (ventral) system, the difference is exactly opposite to the one claimed by Ganel, Freud, Chajut, and Algom [30].

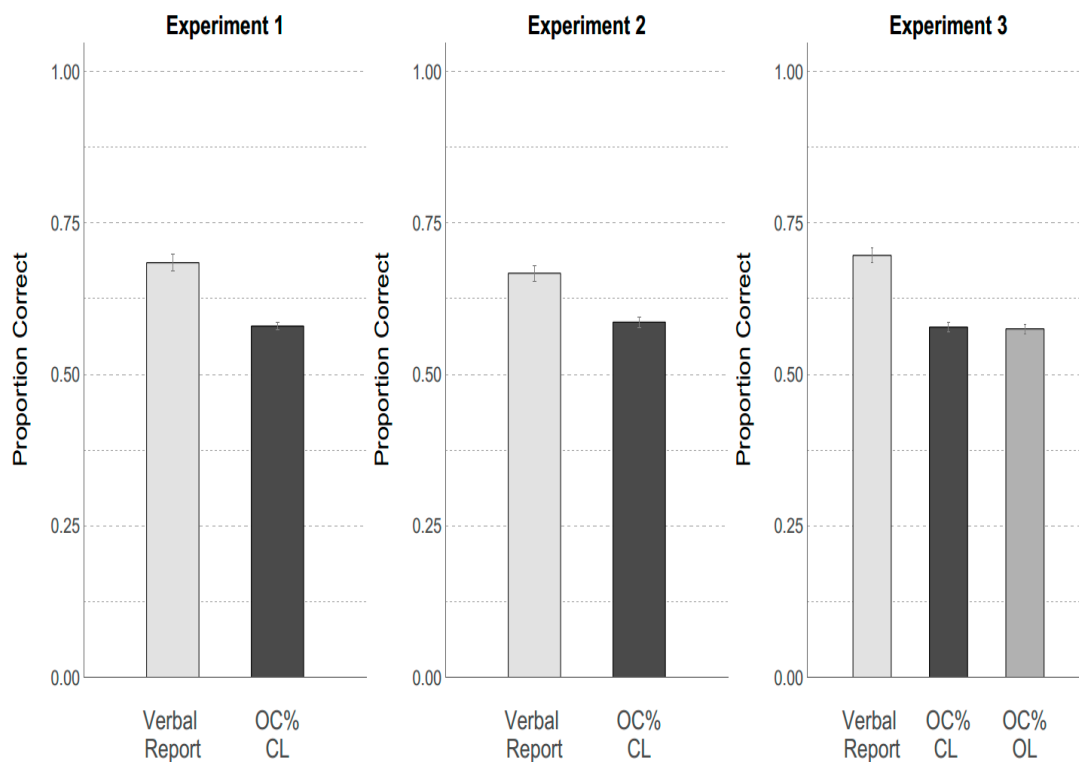


Figure 3. Proportion correct values for Experiments 1–3. Size-classification was consistently superior when based on participants’ verbal reports than when based on participants’ grasping performance (OC%: optimal cut-off proportion). Notably this was also the case in Experiment 2, where we directly replicated the findings of Ganel, Freud, Chajut, and Algom [30]. Error bars indicate one standard error of the mean. CL: Closed Loop, OL: Open Loop.

3.2.2. Experiment 2

As in Experiment 1, we calculated the OC%. The results are shown in Figure 3 (middle panel). The average percentage of correct visual identifications in this experiment was 66.7%. Again, the sampling distribution was not significantly different from normal as assessed by a Shapiro–Wilk test. We then calculated a paired-samples t-test comparing the percentage of correct trials as reported by the participants with OC%. The difference was highly significant with participants again being more accurate in their verbal report values (mean = 0.67, SD = 0.068) than in the OC% values (mean = 0.59, SD = 0.044; $t(25) = 4.942$, $p < 0.001$).

To sum up, we found a clear effect of object size on MGA. This effect was not modulated by the perceived size, i.e., independent of the observer’s verbal judgement. Nevertheless, OC% again confirmed as before (see Experiment 1) that classification accuracy based on MGA is in fact worse than that obtained for the verbal report.

3.2.3. Experiment 3

We used the same measure as described before to estimate classification accuracy (small versus larger object) for the verbal and motor measures, but this time we calculated this measure separately for open- and closed-loop vision conditions. The results are shown in Figure 3 (right panel). The sampling distributions were not significantly different from normal as assessed with a Shapiro–Wilk Test. In the closed-loop condition, the percentage of correct trials in the perceptual condition (mean = 0.70, SD = 0.066) was significantly larger than the percentage of correct values as assessed by criterion values,

OC%, (mean = 0.58, SD = 0.42; $t(29) = 7.810$, $p < 0.001$). In the open-loop condition the results were similar, with the perceptual identification of object size (mean = 0.70, SD = 0.066) being significantly larger than the OC% values (mean = 0.58, SD = 0.042; $t(29) = 9.072$, $p < 0.001$). Thus, as before, our findings suggest that, if anything, the classification based on the participants' verbal report is better than classification based on their grasping.

4. Discussion

Ganel, Freud, Chajut, and Algom [30] presented participants with two very similarly sized target objects. The diameter of the smaller object was just 0.5 mm less than that of the bigger object. When asked to tell whether a given object was the smaller or the bigger one, their performance was at chance level. However, when asked to grasp one of the two objects, the average grip aperture for the smaller object was significantly smaller than that found for the bigger object. It was concluded that the visual information available for motor performance is more precise than that available to conscious perception – which has been presented as a further piece of evidence in favor of the hypothesis that vision for action and perception are based on distinct visual representations and are served by different anatomical systems [1,2]. In a series of three experiments, we aimed to replicate and extend the results presented by Ganel, Freud, Chajut, and Algom [30]. We aimed to answer two questions. Firstly, can we replicate the original results, i.e., the finding that participants' grasping movements distinguish between object sizes that participants are unable to discriminate verbally. The second, more important, question was, however, whether such a difference really implies that the visual information available to the visuomotor system is more precise than the information available to the perceptual system. Such a claim would lead us to expect that the classification of objects into smaller and bigger objects can be done more reliably on the basis of measures derived from motor performance than from verbal performance.

Let us look at the first question of whether we can replicate the main finding from the Ganel, Freud, Chajut, and Algom [30] study. The answer is no, not consistently. Ganel, Freud, Chajut, and Algom [30] found that MGA was determined by the actual size of the object irrespective of whether participants identified the size of the object correctly or not. In contrast, we found that in two out of three experiments, participants' beliefs about the object's size influenced their MGAs. What about the second claim that the precision of the size-information reflected in the grasping performance is superior to the size-information used for the perceptual report? We found consistently (in all three experiments) the opposite pattern. When using classification accuracy, we found that motor-based classification is worse than classification based on participants' verbal reports. Taken together, the findings from our three experiments suggest that visual information used for grasping is not better than information available to the perceptual system. While Ganel, Freud, Chajut, and Algom [30] used their findings to support the PAM our analysis suggests that their results do not actually demonstrate the superiority of visuomotor classification as compared to perceptual classification.

In this context it is interesting to note that in the second experiment, where our data followed the same pattern as observed by Ganel and colleagues, the re-analysis of the data using the motor-classification approach nevertheless showed that classification based on perception is better than classification based on action. This demonstrates the potential of the motor-classification approach to allow a direct comparison of information used in motor tasks and non-motor tasks. It also means that our study coming to a different conclusion than Ganel and colleague's is primarily due to our use of a different type of analysis and does not just present a failure to replicate.

In the following we will explore the implications of our findings and discuss some open questions and limitations of our study.

4.1. The Role of Knowledge in Visuomotor Performance

The role of knowledge in visuomotor performance is a contentious issue. According to the division of labor within the visual system as suggested by Milner, Goodale, and colleagues [1,2], vision in the

ventral system is used to identify objects. Object identification allows the cognitive system to retrieve stored information about an object. The dorsal system, in charge of using vision for guiding actions, does not have direct access to such memorized information. Consequently, visuomotor responses are expected to remain unaffected by our knowledge about objects. This prediction was tested by McIntosh and Lashley [36] and found to be wrong. When participants were presented with objects whose actual size did not correspond to their familiar and expected size, they made errors in their grasping responses. This demonstrates that participants' knowledge determines, at least in part, their visuomotor response. Similar findings were obtained by others [41–44]. Ganel, Freud, Chajut, and Algom's [30] study addressed a similar question in a somewhat different way. Presenting target objects that appeared to the observer to be near-identical led to numerous instances where the observer's judgement about the object's size and its true size were at odds. This provided an opportunity to test whether it is the perceived size or the actual size of the object that drives the grasping response. Ganel, Freud, Chajut, and Algom [30] argued that the perceived size was irrelevant and only the actual size affected the grip aperture. However, our findings are in conflict with this conclusion. Two out of three experiments demonstrated a significant influence of the perceived size on grasping. On the basis of our findings, we conclude that beliefs or knowledge about objects affect object-oriented actions, a finding that undermines the hypothesis that the visual processes in the ventral and dorsal systems are independent of each other.

4.2. Classification Versus Comparing Means

Our results show that the type of analysis used will determine what conclusions are drawn from the data. Ganel, Freud, Chajut, and Algom [30] focused on the significant MGA difference between trials with small versus big objects and concluded that the grasping hand can distinguish more reliably between small and big objects than the perceptual system of the observer. More importantly, however, they did not test how good classification performance would actually be, were they to use MGAs to guess whether the target was the big or the small object. Here, we computed this classification performance and found that classification based on the grip aperture size is less reliable than classification based on observers' verbal reports.

It is easy to be fooled into the belief that finding a significant difference indicates above chance discrimination performance. This potential fallacy is not restricted to the field of motor control. Franz and von Luxburg [45] recently demonstrated that the same problem also occurs in a very different cognitive domain. They re-examined data from a study on lie-detection [46]. ten Brinke, Stimson, and Carney [46] asked volunteers to judge whether people on videos were lying or telling the truth (i.e., dichotomous measure). It turned out that most observers were poor at that task and their guesses were hardly better than chance. However, the researchers speculated that observers' *implicit* ability to distinguish between liars and truth-tellers might be superior. They tested this idea in a priming experiment. Static images of liars and non-liars were presented shortly before words relating to lying or truthfulness were flashed onto the screen. Observers had to classify those words and it was found that response times (i.e., continuous measure) were faster whenever the meaning of the word and the truthfulness of the presented face were congruent, i.e., observers were quicker to classify a word related to lying when this word was preceded by a face belonging to a liar than when it was preceded by a face belonging to an honest person. Franz and von Luxburg [45] took the response times and applied various classification procedures. They found that the accuracy of the classification based on the response times in the priming task was no better than the classification accuracy based on observers' verbal responses. This example and our own findings in this study illustrate why we should be wary of any dissociation that contrasts a significant mean difference of a continuous measure in one task with a non-significant classification ability in a different task.

4.3. Is Size-Information for Motor Control Inferior to Size-Information in the Perceptual System?

We did not just find that size-classification based on motor performance is not better than perceptual size-classification. In fact, we found that motor-based size-classification is worse. One might argue that this also implies the existence of distinct representations of visual size in dorsal and ventral pathways. Thus, proponents of the perception-action model might be tempted to conclude that, while our findings may prompt some minor adjustments to the model, this finding still provides support for the PAM's core claim of distinct visual representations for perception and action. However, this conclusion assumes that the trial-by-trial distribution of grip aperture values is entirely driven and shaped by the trial-by-trial distribution of the represented sizes in the visual system. This assumption is, however, implausible. The value of the grip aperture in any given trial is likely to be the result of many factors: the estimated size of the object, the current noise in the motor system, and the intended approach angle to name just a few possible factors that can influence the maximum grip aperture. As we have argued elsewhere [23,24,32], it is in our view a mistake to treat the MGA as a perfect read-out of the motor system's estimate of the target object's size. Other constraints and sources of noise will contaminate this measure. Given these considerations, it should perhaps not surprise that classification based on grasping is worse than classification based on verbal report. In addition, it is important to point out that we also found a direct influence of perceptual judgement on grip aperture in two of our experiments. This finding suggests that the visual information used in perception is also used in action.

4.4. Manual Estimation

Someone familiar with the original study by Ganel, Freud, Chajut, and Algom [30] might wonder why we did not use a so-called manual-estimation (ME) condition in our study and whether this limits or compromises the conclusions we can draw from our findings in any way. In the ME condition of the original study participants were asked to indicate the size of the target object using their index finger and thumb. Their results for the manual-estimation condition followed the findings for the perceptual (verbal report) task. However, there are several reasons why we think the absence of a manual estimation condition is not a critical issue for our study and does not affect its main conclusions.

Firstly, it should be noted that Ganel and colleagues primarily based their conclusions on the findings from their verbal report and not on those from the ME condition. For example, when they emphasize that the hand seems to distinguish between objects that are perceptually indiscriminable, they refer to a perceptual threshold based on observers' verbal report. Furthermore, the key statistical finding reported and used in support of the PAM is the significant difference in hand-opening between the two differently sized objects that is found irrespective of the observers' verbal judgements. In contrast, the findings from the ME condition are only compared in a qualitative manner to those obtained in the grasping condition. It is remarked that while ME mirrors observers' verbal assessments, the same is not true for the grasping condition. However, no statistical comparison between the ME condition and the grasping condition is reported, and thus we do not know whether this difference is reliable (for a more detailed discussion of this problem, see [47]).

Secondly, the absence of the ME condition does not affect our main argument, which is that comparisons between continuous and dichotomous performance measures can be highly misleading. We demonstrated that even if statistical tests suggest that the task with the continuous measure is more sensitive than the task with the dichotomous measure, a comparison of the two tasks based on a mapping of both measures onto a dichotomous level can negate, or even contradict, this conclusion. Given that such comparisons are frequently used in the discussion of the PAM, our conclusions remain valid and relevant to this specific scientific debate regardless of whether or not a ME condition is included.

Thirdly, a little thought experiment illustrates that the addition of a ME condition would not substantially affect the implications of our study. We demonstrated that grasping when probed for its ability to discriminate between the small and the big object does no better job than observers' verbal

report. Now, let us assume we added a ME condition and analyzed it the same way as the grasping condition. Two outcomes are possible: It turns out that discrimination is not worse or potentially even better for ME than for grasping. In this case the findings from ME provide further support for our conclusion that accuracy of vision for perception is not worse than accuracy of vision for action. Alternatively, we might find that ME is in fact worse than grasping (as would be hypothesized by the proponents of the PAM). In this case, we would have conflicting results. One measure for perception shows accuracy that is superior to grasping, while the other perceptual measure suggests that accuracy is inferior to grasping. What would we learn from this result? Most likely, we would conclude that grasping is not in general better than perception (but that it depends on the exact perceptual measure used) and that thus one could not use the findings to support the PAM (for examples of such data constellations, see [48]).

Thus, if someone intended to derive PAM-supporting evidence from such a data-pattern, they would have to resort to the assumption that ME is a truer measure of perception than verbal reports. We think such an assumption is not necessarily justified. As we have argued before [24,33], ME is not an unproblematic task. Its direct comparison with grasping is made difficult by confounds. In grasping, participants can use direct visual and haptic feedback to improve their performance over time. The same is not true for ME where they receive either no, or only indirect or delayed visual and haptic feedback. As we have reported elsewhere [49], feedback where the endpoint of the action cannot be directly related to the target positions is not very useful.

To conclude, our study refutes the claim by Ganel, Freud, Chajut, and Algom [30] that the visuomotor system can discriminate between object sizes more reliably than the perceptual system. In fact, our results suggest that the opposite is true. Moreover, we found that the perceptual judgement has a direct effect on the grasping performance. Taken together, our findings further undermine the claim of distinct representations of visual size for perception and action.

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5. General Discussion

We presented three studies that were all concerned with investigating the connection between perception and action using different approaches to the question. In the first study we presented further evidence that challenges the claim of multitasking immunity of the dorsal stream. Kunde, Landgraf, Paelecke, and Kiesel (2007) and Janczyk and Kunde (2010) had already shown that response times in grasping were subject to the psychological refractory period (PRP) effect. In these studies they had participants grasp an object after a first ventral task while the time between the two tasks, the stimulus onset asynchrony (SOA), varied. They showed that response times in the grasping task increased the more the two tasks overlapped. They argued that this spoke against the PAM, since this showed that interference between a ventral task and grasping was possible. But, since only reaction times were measured, it is possible that only part of the action planning component, a ventral component of the task, was influenced by the ventral primary task, while the grasping performance itself was not analyzed in both studies. Hesse and Deubel (2011) and Hesse, Schenk, and Deubel (2012) showed that when a concurrent secondary task was presented in parallel to grasping an object, the grasping performance itself decreased. We have now shown that not only is grasping influenced by a secondary task but also obstacle-avoidance, which further argues against the possibility of multitasking immunity in the dorsal stream.

Our results also speak against the possibility of there being two separate attention systems, one attention system for action and one attention system for perception. Hesse and Deubel (2011) and Hesse et al. (2012) already interpreted their results as speaking against separate attentional systems for the dorsal and the ventral stream, which Milner and Goodale (2006) argued for. The obstacle-avoidance task was specifically useful to address this question, since obstacle-avoidance in blindsight patients is rather stable (Striemer, Chapman, & Goodale, 2009) and Goodale (2011) argued that this mechanism might be responsible for object avoidance even in the healthy brain. Our results show that in healthy participants the obstacle-avoidance task does suffer under dual-task conditions, as well as the RSVP task, and therefore they are probably both connected to one attentional system and if the mechanism responsible for obstacle-avoidance is the same as in blindsight patients, then this mechanism also suffers from dual-task costs.

In this experiment we did not find an effect on reaction times (similar to Hesse and Deubel, 2011). We used an open loop setup and so participants would have to finish the decision where to point by the time the movement was initiated. Therefore, when a second task has to be performed at the same time it would be expected that reaction times should go up since the decision where to point has to be made at the same time as the secondary task but this was not the case. And since it was an open loop setup, there was no chance to adapt the pointing response while the hand was in motion,

at least not to the currently seen objects. But this would only be problematic if the dorsal stream has strictly no memory. If the dorsal stream is also able to access memories, as has been argued (Schenk & Hesse, 2018), then possibly the participants were still able to adapt their movements while the hand is in motion to a memory representation of the objects. This would explain why reaction times were similar, since the programming of the movement is not finished when the movement is initiated but continues while the hand is in motion.

While we focused on multitasking in the first study, in the second study we showed that a Garner interference effect can also be found on a variety of grasping measures and we presented further evidence that a secondary task interferes with visuomotor performance. This shows that grasping is not immune to Garner interference and provides further evidence that dorsal tasks do suffer under dual-task conditions. Specifically we also found Garner interference on MGA variability, while Ganel and Goodale (2014) did not. This can be attributed to us also using a secondary task which might have slightly enhanced the Garner interference effect.

A similar difficulty to the first experiment was that, while we did find an effect of multitasking on grasping reaction times in this experiment, we did not find a Garner effect on grasping reaction times, even though a prior study had found this (Hesse & Schenk, 2013). A possible explanation for this is that in the prior study the position of the object varied and in this study it remained the same. This means one further aspect did not need to be accounted for by the participant and thus it is possible that, as in the first experiment, the programming of the action was not finished by the time the movement was initiated.

In the last study we did not focus on multitasking but investigated whether two different size representations of one object exist in the two streams and whether the dorsal representation is more precise. While prior studies had found that knowledge about an object does have an influence on how that object is grasped (Borchers & Himmelbach, 2012; McIntosh & Lashley, 2008; Schenk, 2006), Ganel et al. (2012) argued that when participants are presented with objects that look the same, therefore influencing the prior knowledge of the participants, this had no influence on how the object is grasped. But we were not able to consistently replicate that the mean MGA was larger when grasping the large object and smaller when grasping the small object. Instead we found that in two experiments the belief of the participants did influence the mean MGA. We then further showed that, when analyzing the data in a way that really tests whether the conclusions of Ganel et al. (2012) are correct, the opposite pattern emerges. Ganel et al. (2012) interpreted their differences in mean MGAs as supporting the assumption that the MGA consistently reflects the actual size of the object. This cannot be concluded, since the mean does not inform one about the distribution of the data around that mean. A similar problem has been shown by Franz and von Luxburg (2015) in the area of

unconscious lie detection, where ten Brinke, Stimson, and Carney (2014) argued similarly to Ganel et al. (2012) that unconscious lie detection was superior to conscious lie detection.

We therefore were not able to confirm that the MGA consistently reflects the size of the object but found instead that, when using classification accuracy, the motor-based classification is worse than the verbal reports. We therefore conclude that their results cannot be seen as unequivocal support for the PAM.

In this experiment the biggest limitation is probably the instability of the results. This limitation might be connected with the smaller limitation that our objects induced higher precision in the participants than the objects used by Ganel et al. (2012). In their study participants correctly identified the objects in 58.7% and 62.7% of trials respectively. In our experiment participants correctly identified the objects in 69%, 66.7%, and 70% of trials respectively. While this is still below the often used limit for the JND of 75%, it is still larger than in the experiments of Ganel et al. (2012). We have no explanation for this divergence, since we used disks designed in exactly the way described by Ganel et al. (2012). But having so many more trials in which the participants were correct implies that we have far fewer trials in which participants were incorrect. While for Ganel et al. (2012) about 40% of trials were incorrect, for us it was only about 30% which is a difference of 25%. They therefore had far more incorrect movement trials to analyze. This might contribute to us finding three different results in three experiments, since this decreased the power of our experiments. But still, even when we were able to directly replicate Ganel et al. (2012), as we did in the second experiment of our study, the classification was not better in the motor condition, but far worse. Our findings therefore refute the claims of Ganel et al. (2012) that precision in the dorsal stream is higher than in the ventral stream and suggest that precision in the ventral stream is at least as high as precision in the dorsal stream.

6. Conclusion

In this dissertation we evaluated evidence for the perception-action model (PAM). We wanted to investigate three experimental findings which were frequently cited as compelling evidence for the model. None of these findings received much attention in the research literature. This lack of evidence either in support or against the original findings could reflect lack of interest or unpublished failures to replicate and confirm earlier findings. We reexamined all three effects and found that none of them could hold up to detailed scrutiny. Multitasking affects dorsal tasks as much as ventral tasks. Garner interference, if properly measured, can be found just as reliably in motor tasks as in perceptual tasks. And there is no evidence that the spatial resolution in the dorsal stream is superior to that found in the ventral stream. Together these three findings cast further doubt on the validity and usefulness of the perception-action distinction. Our findings suggest that there is more evidence for integration than separation between putative visual systems. Given this amount of interaction and integration it is unlikely that evidence of task-specific differences can be traced back to the engagement of just of one of the two visual systems. Consequently, many of the behavioral dissociations reviewed in the introduction are in need of new explanations.

7. References

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