

Visual information about object size and object position are
retained differently in the visual brain:

Evidence from grasping studies.

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Abstract

Many experiments have examined how the visual information used for action control is represented in our brain, and whether or not visually-guided and memory-guided hand movements rely on dissociable visual representations that are processed in different brain areas (dorsal vs. ventral). However, little is known about how these representations decay over longer time periods and whether or not different visual properties are retained in a similar fashion. In three experiments we investigated how information about object size and object position affect grasping as visual memory demands increase. We found that position information decayed rapidly with increasing delays between viewing the object and initiating subsequent actions – impacting both the accuracy of the transport component (lower end-point accuracy) and the grasp component (larger grip apertures) of the movement. In contrast, grip apertures and fingertip forces remained well-adjusted to target size in conditions in which positional information was either irrelevant or provided, regardless of delay, indicating that object size is encoded in a more stable manner than object position. The findings provide evidence that different grasp-relevant properties are encoded differently by the visual system. Furthermore, we argue that caution is required when making inferences about object size representations based on alterations in the grip component as these variations are confounded with the accuracy with which object position is represented. Instead fingertip forces seem to provide a reliable and confound-free measure to assess internal size estimations in conditions of increased visual uncertainty.

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1. Introduction

It is well-known that the planning, execution, and control of goal-directed hand movements relies on the availability of visual information (Jeannerod, 1984; Jeannerod, Long, & Baddeley, 1981; Milner & Goodale, 1995; Winges, Weber, & Santello, 2003; Woodworth, 1899). In order to successfully grasp an object, visual information about the object's position in the workspace, as well as its orientation, size, and shape must be processed and subsequently transformed into motor coordinates to perform the intended movement. Yet, successful reaching and grasping is obviously not limited to situations in which we are able to see the target object. In many everyday situations we are able to safely grasp objects without looking at them. When object vision is absent, motor programming has to rely on stored visual representations of the target object. To date, there is a vast amount of research examining how visually-guided movements differ from their memory-guided counterparts (for review see, Heath, Neely, Krigolson, & Binsted, 2010). Most studies report relatively consistent alterations in movement kinematics when vision of the object is prevented, with memory-guided movements typically being slower, less accurate, and more variable than their visually-guided counterparts (e.g., Elliott & Lee, 1995; Hesse & Franz, 2010; Wing, Turton, & Fraser, 1986). There is, however, far less consensus about a) how long accurate visual representations persist (e.g., Elliott, Carson, Goodman, & Chua, 1991; Elliott & Madalena, 1987; Goodale, Kroliczak, & Westwood, 2005; Hesse & Franz, 2009; Westwood, Heath, & Roy, 2003) and b) if dissociable neural substrates underpin visually-guided and memory-guided hand movements (e.g., Connolly, Andersen, & Goodale, 2003; Fiehler et al., 2011; Himmelbach et al., 2009; Lacquaniti et al., 1997; Singhal, Monaco, Kaufman, & Culham, 2013).

Regarding a possible functional dissociation between visually-guided and memory-guided grasping movements, Milner and Goodale (1995, 2006) suggested that interposing even brief delays between viewing an object and performing an action on this object causes a shift from direct visuomotor control (executed by dorsal stream areas) to a perceptual control mode primarily relying on ventral stream processing (see also, Westwood & Goodale, 2003; Westwood et al., 2003). To date, the question of whether or not visually-guided and memory-guided movements rely on dissociable visual representations that are processed in anatomically different brain areas (i.e., dorsal vs. ventral stream) is still controversial (for discussion see Franz, Hesse, & Kollath, 2009; Heath et al., 2010; Hesse & Franz, 2009; Himmelbach & Karnath, 2005; Milner & Goodale, 2008). Within this debate, however, very little attention has been paid to the question of whether decay functions differ for different relevant visual features. This question is

particularly intriguing as previous studies have clearly shown that the relevant visual representations guiding our actions decay over time (Binsted, Rolheiser, & Chua, 2006; Elliott & Madalena, 1987; Hesse & Franz, 2009; Rolheiser, Binsted, & Brownell, 2006). In this study, we were interested in examining how information about object size and object position is retained over longer delays.

There are good theoretical reasons to assume that decay functions may differ for size and position information. According to Jeannerod's (1984; 1995) seminal investigations, grasping movements consist of two independent visuomotor components: Firstly, the transport component that carries the hand to the location of the object relies on extrinsic object features such as the object's position in space. Secondly, the manipulation component that shapes the hand in anticipation of the grasp is based on the intrinsic object features such as the object's size and shape. The suggestion that there are dedicated visuomotor modules for reaching and grasping has also been supported by recent imaging research using functional MRI on human participants. These studies demonstrated that there are distinct activation patterns for grasping (Binkofski et al., 1998; Cavina-Pratesi, Monaco, et al., 2010; Culham, 2004) which are different from those observed in reaching (Connolly et al., 2003). Based on the theoretical and empirical evidence that object position and object size are two distinct characteristics, which are dealt with by separate neural substrates (Culham & Valyear, 2006; Monaco, Sedda, Cavina-Pratesi, & Culham, 2015), it is reasonable to assume that these target characteristics might be affected differently by the introduction of a pre-response delay.

Here, we hypothesised that the representation of target size (an intrinsic feature) is more long-lived than the representation of object position (an extrinsic feature) in the visuomotor system. Previous studies have often implicitly assumed that memory of size is much more precise than memory of position (e.g., Jakobson & Goodale, 1991; Schlicht & Schrater, 2007; Smeets & Brenner, 2008; Wing et al., 1986). This seems a natural assumption to make as the relative positions between observer and target constantly change as we move through our environment, and there would thus be no merit in storing these positions over longer time periods. In contrast, object size remains relatively stable from one interaction to the next, and is unaffected by our own movements (see Milner & Goodale, 2006 for a similar argument). If intrinsic properties are stored for longer time periods then the grasp component that is primarily based on these intrinsic object properties (i.e. target size) should be less affected by the introduction of a pre-response delay than the transport component that is based on extrinsic information about the object's position. Support for this idea comes from a range of studies on both reaching and grasping

movements that consistently show that humans tend to misestimate the position of a target when a pre-movement delay is introduced (e.g., Bradshaw & Watt, 2002; Elliott et al., 1991; Heath & Binsted, 2007). In contrast, findings regarding the grip scaling after delay are less consistent. While generally the hand opens wider after delay, several studies have shown that the hand opening remains well-scaled to the object's size (e.g., Hesse & Franz, 2009; Hu, Eagleson, & Goodale, 1999; Hu & Goodale, 2000), suggesting that size information is much less affected by the introduction of a delay than position information. Unfortunately, in standard grasping tasks that require participants to reach out for an object placed some distance away from their hand's starting position, spatial errors in reaching are usually confounded with postural errors in grip formation (Wing et al., 1986). Indeed, Cavina-Pratesi, Ietswaart, Humphreys, Lestou, and Milner (2010) have shown that the failure of optic ataxia patients to scale their hand accurately to object size is a consequence of making inaccurate reaching movements, rather than an intrinsic visuomotor impairment. This finding further supports the notion that the observed increases in grip apertures after delay are likely to be a direct consequence of the fact that the sensorimotor system adjusts for uncertainty about the object's position by increasing the safety margin between hand and object. On the other hand, Bradshaw and Watt (2002), who found that both the transport component (decreased reaching accuracy) as well as the grasp component (increased maximum grip aperture) are affected similarly by the introduction of pre-response delays, interpreted their data as evidence that the extrinsic and intrinsic object features (i.e. position and size) show similar temporal constraints. As the observed changes in transport accuracy did not directly correspond to the observed changes in grasp accuracy they questioned the conclusion that changes in grip aperture are a mere consequence of the decreased movement accuracy.

The fact that, in a standard grasping task, alterations in transport accuracy (such as misreaching) usually also generate alterations in the grasp aperture (i.e. wider hand opening) is likely the reason why it is still unclear whether or not different object properties are retained differently in the visual brain. In three experiments, we investigated whether the observed kinematic changes in the grip component are a secondary consequence of an increased tendency to misreach (i.e. misjudge the object's position) after delay or can at least partly be attributed to a decay in the object size representation. In Experiment 1 we adopted a paradigm similar to that implemented by Cavina-Pratesi and colleagues (2010) to measure how the introduction of a delay affected grip pre-shaping and scaling depending on whether a long transport phase or no transport phase was required to reach the target. If grasp pre-shaping is affected by the length of the pre-movement delay in conditions in which the hand needs to be transported to the object, but not in conditions

in which no transport movement is involved, then this would suggest that position information and size information are subject to different decay characteristics. In Experiment 2 we dissociated size and position information by a) keeping the object's location visible at all times while varying memory demands on only the size information and b) keeping the object's size constant and varying the memory demands on the position information only. Finally, in Experiment 3, we measured the finger-tip forces used to grip and lift the objects as an alternative measure for remembered object size. It is well-established that visual information about object size is used to estimate the object's weight (Brenner & Smeets, 1996; Flanagan, Merritt, & Johansson, 2009), and that changes in the estimated size are reflected in the grip and lift forces applied to objects when picking them up (Buckingham & Goodale, 2010; Gordon, Forssberg, Johansson, Eliasson, & Westling, 1992). However, to our knowledge, no study has yet investigated how size information, as reflected by grip forces, varies across different pre-response delays. We predicted that, if size information is stored in a more enduring form than position information, fingertip forces should remain tuned to object size regardless of the pre lift-off delay, and even when hand transport is required.

2. Experiment 1

2.1. Methods

2.1.1. Participants:

Thirty-four volunteers (12 male, mean age 25 years, age-range 18–40 years) were recruited from the University of Aberdeen staff and student population, via posters and an online advert. All participants were right-handed by self-report, had normal or corrected-to-normal vision, and no known motor deficits. Participants were reimbursed with £5 per hour of participation. The experiment was approved by the ethics committee of the School of Psychology at the University of Aberdeen, and all participants provided informed consent before participating.

2.1.2. Setup and Stimuli:

Participants were seated comfortably on a height-adjustable chair in front of a table within a lit room. In front of them, a wooden board was secured to the table top at which the target objects were placed. Small wooden dowels (height: 10 mm, diameter 5 mm) served as anchoring pegs for

the targets and as the start position for the hand. The target objects were black wooden blocks with a constant width and depth of 20 mm and three varying lengths (40 mm; 50 mm; 60 mm).

Depending on the experimental condition (far hand transport vs. no hand transport) the targets were placed at different positions on the board. In the far transport condition, the target was placed at a distance of 300 mm from the start position. To ensure a comfortable grasp in the no transport condition, targets were placed on a small platform on the table top (height: 40 mm, length 160 mm, width 120 mm). Participants rested their hand next to the platform on the table and pinched the starting pin located on the platform with their index finger and thumb. The target object was aligned centrally with the starting pin and placed 30 mm to the left of it (corresponding to a 20 mm distance between the edge of the target and the starting pin, see Figure 1A). With the hand in this position, the target object could be grasped comfortably without moving the wrist away from its resting position. To make it easier for participants to keep their hand stationary during the grasp, they were instructed to maintain contact with a Velcro strip that was attached to the side of the platform until the target was grasped. In addition, the experimenter visually monitored their movements.

An infra-red based Optotrak 3020 system (Northern Digital Incorporation, Waterloo, Ontario, Canada) was used to record participants' hand movements. Two small infrared light-emitting diodes (IRED) were attached to the nails of the right thumb and the right index finger. One additional IRED was placed on the table next to the target object. Each target block had one reflective side which faced an Optotrak marker secured to the table, providing a small signal when the block was moved (see Franz, Scharnowski, & Gegenfurtner, 2005 ; Figure 3f for illustration of this procedure). Prior to the experiment, the system was calibrated such that the Cartesian coordinate system was aligned with the top surface of the table. The position of all markers was recorded with a sampling rate of 200 Hz. Liquid-crystal shutter goggles (PLATO Translucent Technologies, Toronto, Ontario; Milgram (1987)) were used to control participants' vision during the experiment. The experiment was programmed in Matlab using the Optotrak Toolbox (Franz, 2004).

2.1.3. Procedure:

This experiment followed a mixed design, with half the participants (N=17) participating in the far transport condition and the other half undertaking the no transport condition. All participants completed five different visual conditions within each transport condition (explained below).

In all tasks, each trial began with the participant pinching the start position between index finger and thumb and the hand resting on the table. The shutter glasses occluded vision until the start of each trial. The experimenter placed one of the target blocks at its designated position and initiated the trial manually with a key press. Subsequently the shutter glasses would open for a preview period of 1 s. Participants were instructed to view the target during this preview period but to wait until an auditory start signal was presented (1000 Hz, 100 ms) before moving towards the target. As soon as they heard the signal, they had to grasp the target along its length (the only dimension that varied between trials) using their thumb and index finger (precision grip). Participants were instructed to lift the object off the pin and place it back on the table next to the pin. Each trial lasted for 4 seconds. After this, the Optotrak stopped measuring and the experimenter prepared the next trial. If participants failed to grasp the object within this time limit the trial was marked as an error and repeated at a random position later in the experiment. The only difference between the far transport condition (standard grasping task) and the no-transport condition was the distance at which the target was placed (see Figure 1A) – in the far transport condition the hand needed to cover a distance of about 300 mm to reach the target object, whereas no hand movement was required in the no transport condition and participants only moved their index finger and thumb for grasping.

Five different vision conditions were implemented to successively increase memory demands in both grasping tasks. In the *full-vision condition (FV)*, the shutter glasses remained open after the go-signal providing participants with full-vision of their hand and the target object during grasping. In the *open-loop after movement initiation condition (OLM)*, the shutter glasses closed as soon as participants had moved one of their fingers more than 15 mm away from the start position in either x or z dimension and/or more than 20 mm away in y-dimension (the larger margin for the y-dimension was used as, depending on participants finger thickness, a 15 mm distance between marker and start position pin could be exceeded with a resting hand). In the *open-loop after start signal condition (OLS)*, the shutter glasses closed simultaneously with the start signal. Hence, the only difference between the OLM and the OLS condition was whether vision was available during the reaction-time interval. Finally, two delay conditions were tested implementing either a 2 second (2s-D) or a 5 second delay (5s-D) between the preview period and the start signal. In both conditions, the shutter glasses closed after the preview interval and remained closed during the delay period after which the start signal was presented. Again, in these delay conditions participants performed their movements without vision of the hand or target (for a graphical illustration of the different vision conditions see Hesse and Franz (2010), Figure 1a).

Vision conditions were blocked and partially counterbalanced across participants. Within each block, the three target sizes were presented eight times in a randomised fashion resulting in 24 trials per block. Each block was preceded by three practice trials (one per stimulus size) to familiarise participants with the task.

2.1.4. Data analysis

From the 3D position data of the markers we calculated the resultant velocity. Movement onset was defined as the first frame in which one of the markers exceeded a velocity of 0.025 m/s. Contact with the object was defined as the point at which the velocity of one of the finger markers dropped below 0.05 m/s in far transport task and 0.025 m/s in the no transport task, or if the velocity signal recorded by the object marker exceeded 0.05 m/s (whichever occurred first). Maximum Grip Aperture (MGA) was calculated as the maximum 3D-distance between thumb and index finger during movement time, which was defined as time between movement onset and object contact. To calculate the hand position at the end of the movement (independent of object size), we determined the midpoint between index finger and thumb. From these midpoints, endpoint variability (variable error) was calculated by determining the surface area of the 95% endpoint confidence ellipses (see Messier & Kalaska, 1997; 1999 for similar procedure). Endpoint variability was determined in the x and y dimension only, as height of the objects was constant throughout the experiment.

Trials were excluded if data were missing around the point of MGA, or if our procedure was unable to determine the point of contact with the object correctly. Applying these criteria resulted in the exclusion of 4% of all trials.

Data were analysed using analysis of variance (ANOVA). When the sphericity assumption was violated, alpha values were adjusted using Greenhouse-Geisser correction (Greenhouse & Geisser, 1959) and eta (ϵ) is provided. Bonferroni-Holmes corrections were used for post hoc comparisons. A significance level of $\alpha = .05$ was used for all statistical analyses.

2.2. Results and Discussion

Our main interest was in the question of whether the previously-observed increase in MGA when vision is occluded prior to movement onset can primarily be attributed to an increased uncertainty about the object's position, or if this parameter also reflects some uncertainty about the object's size. If MGA is increased solely in order to obtain a larger safety margin to compensate for increased uncertainty about the object's position, then MGA should be larger in the far transport

conditions and the effect of removing visual feedback should be more pronounced in this condition. The data were analysed with a 2 (transport: far vs. no) x 3 (object size: 40/50/60 mm) x 5 (vision condition: FV/OLM/OLS/2s-D/5s-D) mixed ANOVA. The analysis revealed a significant main effect of the between group factor transport, $F(1,32)=17.0$, $p<.001$, $\eta_p^2=0.35$. On average, participants opened their hand $11.9 \text{ mm} \pm 2.9 \text{ mm}$ wider in the far transport condition than in the no transport condition (see Figure 2A). Furthermore, there was a significant main effect of object size, $F(2,64) = 327.08$, $p<.001$, $\epsilon=0.62$, $\eta_p^2=0.91$, as well as of vision condition, $F(4,128) = 19.56$, $p<.001$, $\epsilon=0.69$, $\eta_p^2=0.38$. These main effects indicate that, as expected, MGA increased with increasing object size and increasing memory demands. Importantly, however, both effects were mediated by respective transport condition as confirmed by significant interaction effects between vision condition and transport, $F(4,128) = 6.03$, $p=.001$, $\eta_p^2=0.16$, as well as between object size and transport, $F(2,64) = 5.19$, $p=.022$, $\eta_p^2=0.14$. These interaction effects indicate a) that increasing memory demands resulted in larger increases in the MGA in the far transport condition (FV-5s-D difference: $12.3 \text{ mm} \pm 2.3 \text{ mm}$) than in the no transport condition (FV-5s-D difference: $4.2 \text{ mm} \pm 1.3 \text{ mm}$) and b) that MGA was more sensitive to increases in object size in the no transport conditions than in the far transport conditions (see Figure 2). Finally, there was also an interaction effect between vision condition and object size, $F(8,256) = 3.35$, $p=.005$, $\epsilon=0.68$, $\eta_p^2=0.10$, suggesting that participants were less sensitive to changes in object size after increased delay periods. The three-way interaction did not reach significance ($p=.055$, $\eta_p^2=0.06$).

To better understand these interaction effects, and how the availability of vision affected the responsiveness of the MGA to object size changes in the two different transport conditions, we also calculated the slopes of the linear regression function relating the MGA to the three different object sizes. The slopes of these functions were calculated separately for each participant in each of the different vision conditions. Previous studies have shown that, when they have full vision, humans usually scale their grip to object size with an average slope of 0.82 (Smeets & Brenner, 1999). That is, an increase in object size of 10 mm would result in an increase of MGA of about 8 mm. Thus, the closer the slope is to zero the more poorly the grip is scaled to object size. As these slopes are considered to represent an internal size estimate, we hypothesised that if size is encoded in a stable fashion, the slopes should be equivalently steep across all vision conditions. A 2 (transport: far vs. no) x 5 (vision condition: FV, OLM, OLS, 2s-D, 5s-D) mixed model ANOVA was computed on the slope data. This analysis revealed a significant main effect of vision condition, $F(4,128)=5.01$, $p=.004$, $\epsilon=0.67$, $\eta_p^2=0.13$. More importantly, however, there was

also a significant interaction effect between vision and transport, $F(4,128)=3.39$, $p=.026$, $\epsilon=0.67$, $\eta_p^2=0.10$, suggesting that the effect of memory demands on grip scaling depended on the required transport movement (see Figure 2B). Post-hoc comparisons confirmed that there was no effect of vision condition on grip scaling in the no transport condition ($p=.32$, $\eta_p^2=0.06$). In contrast, in the far transport condition, vision condition had a strong effect on the slope of the scaling function, $F(4,64)=6.88$, $p<.001$, $\eta_p^2=0.30$, with the slopes becoming shallower with increased memory demands (see Figure 2B). Furthermore, there was a significant main effect of transport condition, $F(1,32)=8.91$, $p=.005$, $\eta_p^2=0.22$. Overall, slopes were steeper in the no transport condition (0.72 ± 0.04) than in the far transport condition (0.54 ± 0.04).

The finding that slopes decreased in the far transport condition with increased memory demands seems to contradict the notion that object size representations remain stable over time. Furthermore, it contrasts a previous study that reported relatively stable grip scaling after similarly long delay periods (Hesse & Franz, 2009). Two questions arise from these findings: firstly, whether the reduced scaling after delay in the far transport condition is indeed indicative for a decay of the target size information; and secondly why this finding is limited to the far transport condition. The poorer grip scaling could indicate a range effect due to perceptual and/or motor averaging (i.e. overestimation of small object sizes and underestimation of larger object sizes) occurring after long delays. Similar observations have been made for reaching movements where responses to different target distances have been found to decay toward a central (or average) response thus indicating a decay of the relevant visual information over time (Brown, Knauff, & Rosenbaum, 1948; Elliott & Lee, 1995; Hesse, Franz, & Schenk, 2016; McIntyre, Stratta, & Lacquaniti, 1998). However, if this is true, and grip scaling becomes less sensitive to physical changes in object size after delay, then a similar effect should also be observed in the no transport condition. This was however not the case. One could argue that the effects of delay are more pronounced in the far condition as it took participants about twice as much time to complete the movements as compared to the no transport condition (e.g., MTs in far condition: FV: 720 ms \pm 34 ms; OLM: 773 ms \pm 40 ms; OLS: 812 ms \pm 42 ms; 2s-D: 899 ms \pm 49 ms; 5s-D 931 ms \pm 55 ms vs. MTs in the no transport condition: FV: 362 ms \pm 18 ms; OLM: 373 ms \pm 20 ms; OLS: 386 ms \pm 24 ms; 2s-D: 398 ms \pm 22 ms; 5s-D: 396 ms \pm 23 ms). Yet, this explanation seems unlikely as slopes in the no transport condition are still higher after 2s delay than in the far transport condition when vision is occluded at movement onset (OLM). Instead, we propose that the reduced grip scaling after longer delays in the far transport condition reflects a biomechanical limit in the comfortable hand opening span (i.e., a ceiling effect). That is, as the MGA is already over

a 100 mm for the smallest object size in the delay conditions it is physically impossible for many participants to open the hand much wider for larger object sizes (see Figure 2A). Hence, the reduced grip scaling may in fact be a consequence of an increased safety margin in the delay conditions (which may in turn result from a higher uncertainty about the object's position). This explanation could also explain the discrepancy with our previous study which did not find an effect of delay on grip scaling when smaller object sizes were used than in the current study (Hesse & Franz, 2009, largest object 43 mm).

To more explicitly test if increases in MGA can be linked to an increased uncertainty about object position in the far transport conditions, we calculated end-point variability of the grasping movements and correlated this measure with the increase in MGA relative to the FV-condition observed across all other vision conditions. We only performed this correlational analysis for the far transport conditions, as both the increase in end-point variability and the increase in MGA with increasing delay were minimal in the no-transport conditions (endpoint variability: FV: 54 ± 8 mm², OLM: 104 ± 25 mm², OLS: 86 ± 11 mm², 2s-D: 110 ± 13 mm², 5s-D: 148 ± 17 mm²). Even though there was a significant main effect of vision condition on end-point variability in the no-transport conditions, $F(4,64)=5.66$, $p=.004$, $\eta_p^2=0.26$., post-hoc analysis revealed that only the differences between the FV-condition and the two delay conditions were statistically reliable (both $p \leq .007$). In contrast, for the far transport condition the one-way ANOVA with the factor vision condition revealed a much stronger effect on endpoint-variability, $F(4,64)=34.53$, $p<.001$, $\eta_p^2=0.88$. On average variability was 130 ± 12 mm² in the FV-condition, 754 ± 89 mm² in the OLM-condition, 1089 ± 143 mm² in the OLS-condition, 1529 ± 172 mm² after 2s delay and 2171 ± 256 mm² after 5s delay (all paired comparisons $p<.05$). For each participant, we calculated the average MGA across all three target sizes in each of the vision conditions. We then determined the relative increase in MGA relative to the closed-loop condition by subtracting the MGA in the FV-condition from the average MGA determined in the other four vision conditions. Similarly, we determined the increase in end-point variability relative to the FV-condition for each participant. Significant positive correlations between the increase in MGA and the increase in end-point variability were found for all vision conditions (all $p<.05$, see Figure 3) indicating that higher end-point variability was related to larger MGAs in the far transport conditions. This result is consistent with findings from Schlicht and Schrater (2007) who varied levels of visual uncertainty by presenting targets in visual eccentricity and also found that the size of MGA correlated significantly with the contact location variance. Similarly, Chieffi and Gentilucci (1993) reported

wider MGAs (and poorer grip scaling) for targets placed further away from participants indicating that transport variability affects the grasp component in more demanding conditions.

In summary, this experiment provides further supporting evidence that hand pre-shaping as determined by MGA varies with the required transport movement (Cavina-Pratesi, Ietswaart, et al., 2010) when visual uncertainty is increased. The finding that variations in target distance affect grasp pre-shaping not only after delay, but also in closed-loop vision conditions, is in contrast to Jeannerod's (1984; 1981) initial suggestion that changes in object location leave the grasp component relatively unaffected. However, similar findings have also been reported by other researchers (Chieffi & Gentilucci, 1993; Jakobson & Goodale, 1991) who argued that this may indicate that the transport component and grasp pre-shaping are affected by similar task constraints. Specifically, we were interested in examining whether the increases in MGA reflect an increased uncertainty about the object's position or may also (at least partly) be attributed to an increased uncertainty about the object's size. Although we observed a relatively accurate and invariant grip scaling even after 5 seconds of delay in the no transport conditions, suggesting that object size is encoded quite stably, we found a continuous decrease of the scaling slopes in the far transport condition with increased memory demands. Even though this finding could potentially indicate a reduced precision of the internal size estimates after delay, we think that it is more likely to be the consequence of a biomechanical ceiling effect (large MGAs for the small object after delay). However, one could also argue that due to the different locations of the target objects in the workspace in the far and no transport conditions (and relative to the head position), participants received different size information based on depth cues such as binocular disparity that has been found to be crucial for efficient grasp control (Watt & Bradshaw, 2003). Indeed, a recent study by Bozzacchi and Domini (2015) has suggested that depth constancy in grasping is quite poor and affects the size of the grip aperture. To account for this possible confound, we designed a second study in which we dissociated information about target size and target position using a mirror setup. This allowed us to provide a constant visual cue about the target's position while manipulating the size information (Exp. 2A) and to vary the object position while keeping its size constant (Exp. 2B).

3. Experiments 2A and 2B

3.1. Methods

3.1.1. Participants:

Forty participants were recruited from the University of Aberdeen staff and student population, via posters and an online advert. Twenty participants (7 male, age range: 20-36 years, mean age: 25 years) took part in Experiment 2A in which we tested the memory for size information in a grasping task; and twenty participants (10 male, age range: 19-34 years, mean age: 25 years) took part in Experiment 2B in which we tested the memory for object position information in a reaching task. Five of these participants had also taken part in Experiment 1. All self-reported being right-handed with normal or corrected-to-normal vision and no known motor deficits. All participants were reimbursed with £5 per hour for their participation. The ethics committee of the School of Psychology at the University of Aberdeen granted approval for the experiments, and all participants provided informed consent before participating.

3.1.2. Setup and Stimuli:

A mirror-setup was employed in this study. A computer monitor (EIZO Foris FG2421, 23.5", 100 Hz, 1920 pixel x 1080 pixel) was mounted on top of a metal frame in portrait mode, with the screen facing down towards a two-way (semi-transparent) mirror (56 cm x 40 cm) that was placed halfway (34 cm) between the monitor and the work surface. Participants looked into the mirror and perceived the virtual targets shown on the monitor as if positioned on the work surface below the mirror (for description of a similar setup see also Eloka & Franz, 2011).

Experiment 2A: Grasping: The target objects were the same three wooden bars as used in Experiment 1. These target objects were placed in the workspace in which participants performed their grasping movements (below the mirror) at a distance of 250 mm from the start position of the hand. The area beneath the mirror could be illuminated such that participants were able to view the work space and the real target object through the semi-transparent mirror. This was done for calibration purposes only (see below). During the experiments all lights were turned off such that the real target (black) placed on the grasp surface was hidden and not visible to the participants. On the monitor two visual cues were provided on a uniform grey background: First, an object location marker indicating the centre of the real-target placed beneath the mirror with a black cross (+) that was 5 mm in size; and second the target size cue. The size cues were displayed as white rectangles corresponding to the size of the surface of the real target objects (width of 20 mm and varying lengths of 40 mm, 50 mm and 60 mm). The location of the size cue was 7 cm to the left and 10 cm below the centre of the real target object (see Figure 1B for illustration).

Experiment 2B: Reaching: The targets were displayed as white rectangles with a width of 20 mm and a length of 50 mm (corresponding to the medium sized object in the grasping task) at three different locations. The target positions were 180 mm (near), 250 mm (mid) and 320 mm (far) from the start position of the hand and only varied in the vertical (y) dimension (see Figure 1B for illustration).

Again participants' hand movements were measured with an Optotrak 3020 system (Northern Digital Incorporation, Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. Two IREDs were attached to the nails of the right thumb and the right index finger in the grasping task and one IRED on the nail of the index finger in the reaching task. Prior to the experiment, the Optotrak was calibrated such that the Cartesian coordinate system was aligned with the plane of the reaching and grasping surface.

3.1.3. Procedure and Data Analysis:

Participants sat on a height adjustable chair in front of the mirror setup. They were asked to place their head in a chin rest to ensure a constant viewing position and to look down into the mirror.

Experiment 2A: Grasping: Participants' task was to grasp the hidden rectangular block, which varied in size, but whose location remained constant throughout the experiment. The position of the block was indicated by the object location marker and its size was indicated by the size cue presented at a grasp-irrelevant location.

Prior to the start of the experiment, the setup was calibrated. For this the lights underneath the mirror were switched on making the real target under the mirror visible. A white cross was projected from the monitor on top of the target. Participants were instructed to adjust the position of the cross (using the keyboard) such that they perceived it as being displayed in the centre of the target object. This perceived centre point was subsequently stored and used as the position of the object location marker throughout the experiment. During the experiment all lights were turned off. Participants began each trial with their thumb and index finger resting on the start position. When the experimenter started the trial, the object location marker as well as the object size cue were displayed for a preview period of 1 s. Participants were asked to wait for the auditory start-signal (100 ms, 1000 Hz) before initiating their grasping movement.

Experiment 2B: Reaching: Participants' task was to reach and point to the centre of the presented virtual block as accurately as possible. As in Experiment 2A, they had a preview period of 1s after which they performed their reaching movements signalled by an auditory start signal.

In both experiments, the same five viewing conditions as used in Experiment 1 were employed. In the FV-condition the size cue (grasping) or the virtual target (reaching) remained present throughout the trial but, in contrast to Experiment 1, participants could not see their hand. In the OLM-condition the size cue/virtual target was removed as soon as participants' hand had left the start position (same criteria as in Experiment 1) and in the OLS-condition the size cue/virtual target disappeared simultaneously with the start signal. In both the 2s-D and 5s-D condition, the size cue/virtual target was removed after the preview period and a delay was introduced before the go-signal was presented. In the grasping task the object location marker remained visible in all viewing conditions while no visual cues were present during the reaching task. Participants performed all reaching and grasping movements without seeing their hand.

Each target size (grasping) or target position (reaching) was presented 8 times throughout each vision condition in random order (resulting in 24 trials per block). Each block was preceded by three practice trials to familiarise participants with the task and respective vision condition and ten practice trials preceded the experiment to familiar participants with the mirror setup.

Data analysis was similar to Experiment 1 for the grasping data except for how the end of movement was determined (no object marker was used, due to occlusion from the mirror setup). The end of movement was defined as the point at which the velocity of one marker dropped below 0.05 m/s. In the grasping task, 1.7% of all trials had to be removed due to missing data either around the time of MGA or object contact and in the reaching task 0.25% of the trials were excluded due to missing data.

3.2. Results and Discussion

Experiment 2A: Grasping: As in Experiment 1, we were primarily interested in how increasing memory demands affected the maximum hand opening and the scaling of the grip to object size. The 3 (object size: 40, 50, 60 mm) x 5 (vision condition: FV, OLM, OLS, 2s-D, 5s-D) repeated-measures ANOVA on the MGA data confirmed, as expected, a significant main effect of object size, $F(2, 38)=100.1$, $p<.001$, $\epsilon=0.60$, $\eta_p^2=0.84$ (see Figure 4). Interestingly, there was no main effect of vision condition on MGA ($p=.38$, $\eta_p^2=0.05$) as well as no interaction effect between object size and vision ($p=.61$, $\eta_p^2=0.04$). This finding seems to suggest that longer delays do not affect the size of the hand opening when a visual cue about the object's position is provided. Similarly, we found that the slopes of the function relating MGA to object size remained constant across all five vision conditions tested ($p=.68$, $\eta_p^2=0.03$, see Figure 4B) suggesting that grip

scaling remains accurate in the absence of object size information when spatial uncertainty is removed. To test directly if the presence of the target location marker nullified an increase in endpoint-variability across the vision conditions, we calculated again the surface area of the 95% confidence interval ellipses containing the movement endpoints (determined as the midpoint between the two fingers) across all trials for each vision condition. Even-though movement endpoints tended to be slightly less variable in the FV ($603 \pm 48 \text{ mm}^2$) and OLS-conditions ($595 \pm 54 \text{ mm}^2$) as compared to the other three conditions (OLM: $671 \pm 54 \text{ mm}^2$; 2s-D: $705 \pm 53 \text{ mm}^2$; 5s-D: $700 \pm 85 \text{ mm}^2$) these differences did not reach significance, $F(4,76)=2.3$, $p=.06$, $\eta_p^2=0.11$. Overall, these findings indicate that key variables related to movement accuracy, i.e. the maximum hand opening, the scaling of the hand object size, and end-point variability all remain relatively constant when information about the object position is provided. Furthermore, the finding that the slopes of the function relating object size to maximum hand opening are unaffected by the removal of object size information up to delays of 5 s prior to movement initiation seems to suggest that object size is encoded relatively stably.

However, when comparing the data from Experiment 2 with those obtained in Experiment 1 (i.e. Figure 2 vs. Figure 4) it also becomes obvious that the MGA is larger and the scaling to object size reduced compared to both the condition without hand transport and the FV-condition requiring far hand transport. In fact, the kinematic data obtained in Experiment 2A is very similar to that observed in the OLM-condition in the far transport condition of Experiment 1 (i.e. slopes of about 0.6, MGAs between 95-108 mm, end-point variability of 600-700 mm^2). Hence, one could argue that, if object size information is dissociated from the object's position, participants' movements start to resemble delayed movements in natural grasping tasks meaning that the introduction of further delays would have no additional effects on the movements. While we cannot completely dismiss this argument at this point, we would like to point out that the major difference between Experiment 1 and 2 was in whether or not the hand was visible during movement execution in the full-vision condition. Whereas participants were able to see their hand and use visual feedback to adjust their movements in the FV-condition in Experiment 1, vision of the hand was unavailable in this condition in Experiment 2. The finding that hand visibility strongly affects movement accuracy, usually resulting in larger apertures and slower movement times, has been reported in numerous previous studies (e.g., Berthier, Clifton, Gullapalli, McCall, & Robin, 1996; Churchill, Hopkins, Ronnqvist, & Vogt, 2000; Schettino, Adamovich, & Poizner, 2003) and indicates that visual feedback plays an important role in the control and coordination of grasping movements (for different findings see, Connolly & Goodale, 1999). In other words, visual feedback from the hand seems to be used continuously to accurately guide and control the

grasp (Saunders & Knill, 2003; Saunders & Knill, 2005). Therefore, we suggest that the larger MGAs in the FV-condition are primarily a result of participants' inability to see their hand (which at the same time causes a small reduction in the slopes due to the biomechanical limits of the hand), and that the constant MGAs across all memory conditions likely indicate that participants use the positional information provided. The suggestion that object size information is represented with invariable accuracy across all memory conditions is further supported by the relatively consistent slopes that are considerably steeper than those observed in the delay conditions of Experiment 1.

In addition, our pointing task (Experiment 2B) directly examined the extent to which memory of position information affects end-point variability in situations in which the hand is not visible. The 3 (object distance: near, mid, far) x 5 (vision condition: FV, OLM, OLS, 2s-D, 5s-D) repeated-measures ANOVA on end-point variability revealed a main effect of vision condition, $F(4, 76)=34.1$, $p<.001$, $\epsilon=0.60$, $\eta_p^2=0.64$ (see Figure 5A). Post-hoc tests confirmed that end-point variability increased with increasing memory demands and that all differences, except for the difference between the 2s and 5s delay conditions ($p=.94$), were significant (all other $p <.05$). There was no main effect of target distance on the variable end-point error ($p=.88$, $\eta_p^2=0.007$) and no interaction effect ($p=.38$, $\eta_p^2=0.05$). The same analysis applied on the 2-D distance error (Euclidean distance between endpoint and target centre) also yielded a main effect of vision, $F(4, 76)= 22.9$, $p<.001$, $\epsilon=0.51$, $\eta_p^2=0.55$ (see Figure 5B) in addition to a main effect of target distance, $F(2, 38)= 4.90$, $p=.031$, $\epsilon=0.61$, $\eta_p^2=0.21$, and a significant interaction effect $F(8, 152)=2.83$, $p=.03$, $\epsilon=0.50$, $\eta_p^2=0.13$. These results indicate that the distance error increased with increasing memory demands as well as with increasing distance of the target. Post-hoc analysis indicated that the distance error was smaller in the near condition than in the mid and far conditions (both $p<.05$). Moreover, the effect of distance was more pronounced in conditions with reduced visual information (see Figure 5B). In sum, these findings show that even when participants cannot see their hand during movement execution, both the end-point error and the end-point variability continue to increase with growing memory demands. This observation is in line with previous studies reporting increased pointing errors after longer delays (e.g., Hay & Redon, 2006; Heath & Binsted, 2007). Importantly, these findings also suggest that participants used the positional information provided in Experiment 2A very efficiently, as endpoint variability remained constant across all vision conditions in the grasping task.

Yet, there is one potential issue with this notion. In both Experiment 1 and 2 we have made the assumption (in concordance with most studies in the field) that MGA is a measure that relates to

participants' internal estimates of object size. However, it has previously been argued that visual information about object size may not necessarily be the primary factor that determines the hand opening during grasping (Smeets & Brenner, 1999). According to this theory, the grip aperture is in fact formed by guiding the two fingers to the respective contact positions on the object (Smeets & Brenner, 1999, 2001; Smeets, Brenner, & Biegstraaten, 2002), which inevitably results in a scaling of the hand to object size in order to ensure an approach angle which is approximately normal to the object's surfaces. Thus, for normal immediate grasps, the relevant variables that control grip formation are finger position and contact position rather than object size.

While Smeets and Brenner (2008) also suggest that for *remembered* targets, object size information is more likely to be used for grasp control than position information, it could well be the case that in the presence of an object position cue, participants rely again on position information for grasp formation, rather than size information, as it becomes the more reliable cue. If this were the case, the stable MGAs and scaling functions we measured across the different vision conditions may no longer provide evidence for a long-lasting object size representation. However, a movement parameter that is well-established to be directly related to an object's size is the associated lifting force. That is, object size is usually used to estimate the weight of an object which in turn determines the force we apply to lift it. Thus, we conducted a third experiment in which we measured fingertip forces across different vision conditions that successively increased memory demands to determine the stability of participants' internal object size estimate. This approach has a couple of advantages: First, it tests our predictions using another sample, a different method, and a new dependent variable (i.e. fingertip forces) and second, even more importantly, using fingertip forces as dependent variable avoids the problem of the scaling issues that we faced in our previous experiments (i.e. the fact that due to biomechanical constraints the slopes depend on the overall size of the MGA). As all objects, independent of their size, were grasped on a handle the same hand opening was required for grasping them in all conditions.

4. Experiment 3

4.1. Methods

4.1.1. Participants:

Sixteen participants (8 male, age range: 19-35 years, mean age: 23 years) were recruited from the Heriot-Watt University staff and student population in Edinburgh, via posters and an online advert. All participants were self-reported right-handed with normal or corrected-to-normal vision

and no known motor deficits. All participants were reimbursed with £5 per hour of participation. The study was approved by the ethics committee of the School of Psychology at Heriot-Watt University, and all participants provided informed consent before taking part.

4.1.2. Setup and Stimuli:

Three black rectangular blocks with a constant width and depth of 30 mm and varying length of 50, 70 and 90 mm made out of plastic served as target objects. The objects were filled with lead shot introducing weight differences of 100 g between two successive target sizes (small object: 195 g, medium object: 295 g, and large object 395 g). Centrally and on top of each of the objects there was a handle attached (size of the circular grip surfaces: 25 mm in diameter) that contained a 6-axis ATI Nano17 force transducer (for a similar setup, see Figure 1B in Buckingham, Michelakakis, & Rajendran, 2016).

A small plastic peg attached to the left button of a computer mouse that was fixed on the table served as start position of the hand. Objects were placed on the table in front of the participant (and slightly to the left of the participants' midline) at a distance of 30 cm from the start position of the hand (same as Experiment 1). To control vision, participants wore PLATO liquid crystal shutter glasses (Milgram, 1987).

4.1.3. Procedure and Data Analysis:

Participants sat on a chair in front of a table in a well-lit room. The experimental procedure was similar to Experiment 1 and 2. Again we varied the amount of visual feedback as well as the memory demands of the task. As we previously did not observe any difference between introducing a 2 s vs. a 5 s delay between viewing the object and the required movement execution, we only used the 2 second delay condition in the current experiment. Furthermore, vision in the OLM condition was occluded as soon as participants lifted their hand off the mouse-button that served as the start position. In all vision conditions a preview period of 1 s was provided. After the presentation of the go-signal, participants were instructed to reach out and grasp the object on the handle and lift it off the table. Note that independent of object size, the same grip was required for all objects as the same handle was used for all lifts. Each object size was presented eight times within each vision condition in a random order. Vision conditions were blocked and partially counterbalanced across participants. Each vision condition was preceded by three practice trials.

Movement onset was defined as the point at which the mouse button was released. The transducers in the handle recorded the forces applied to the handles in Newtons at a rate of 1000 Hz. Load force (LF) is defined as the vector sum of the forces parallel to the handle and grip force (GF) is defined as the force applied perpendicular to the handle. Pre-lift-off fingertip force rate changes (determined in N/s) were computed after smoothing the data with a 14 Hz dual-pass Butterworth filter, by applying a 5-point central difference equation. The peak values of the grip force rates (GFR) and load force rates (LFR) were determined as an index of sensorimotor prediction of object weight based on visual size cues (Buckingham & Goodale, 2010; Buckingham, Goodale, White, & Westwood, 2016). Only one trial had to be excluded from the whole data set due to missing force data during the lifting movement. Data was analysed in an equivalent fashion to Experiment 1 and 2.

4.2. Results and Discussion

In this experiment our main interest was in how peak grip force rate and peak load force rate vary across visual condition. Both of these variables have been shown to relate to participants' prediction of object weight based on apparent size (Buckingham & Goodale, 2010; Flanagan et al., 2009). A 3 (object size: 50, 70, 90 mm) x 4 (vision condition: FV, OLM, OLS, 2s-D) repeated measures ANOVA was used to analyse the data. As expected, both grip force rates, $F(2, 30)=29.6$, $p<.001$, $\eta_p^2=0.66$ and load force rates, $F(2, 30)=37.2$, $p<.001$, $\eta_p^2=0.71$ were higher for the larger objects (see Figure 6A). Interestingly, however, both measures were unaffected by the removal of visual feedback and the introduction of a memory delay (main effect of vision condition: GFR: $p=.99$, $\eta_p^2=0.001$ and LFR: $p=.56$, $\eta_p^2=0.04$). These findings suggest that grip forces were similar and independent of the availability of visual information about the object. There were also no interaction effects between vision condition and target size for both variables (GFR: $p=.64$, $\eta_p^2=0.04$ and LFR: $p=.08$, $\eta_p^2=0.12$). To further confirm the finding that the applied fingertip forces are scaled according to the object size independent of the visual feedback available, we also computed the slopes of the scaling functions that relate object size to GFR and LFR for each of the participants separately. Here we regressed object size (measured in mm) against the measured changes in the peak force rates (determined in N/s). Thus, a slope of 0.4 indicates that an increase in object size by 1 mm resulted in a peak force rate change of about 0.4 N/s. Note that, as we relate object size to fingertip forces, these slopes cannot be meaningfully compared to those reported in Experiment 1 and 2. A one-way repeated-measures ANOVA applied to this data revealed no effect of vision condition on GFR-scaling, $p=.98$, $\eta_p^2=0.004$ (see Figure 6B). For the LFR-scaling, the

same analysis did, however, indicate a main effect of vision condition, $F(3,45)=2.95$, $p=.043$, $\eta_p^2=0.16$. Post-hoc tests confirmed that only the difference between the slopes in the OLS-condition and the 2s-D condition was significant ($p=.018$). However, neither the OLS-condition nor the 2s-D condition differed significantly from the FV-condition. Thus, we found no evidence that slopes continuously decreased with increased memory demands as would be predicted by a decay of the object size representation.

In summary, these findings suggest that delay and visual occlusion do not significantly affect the grip forces associated with the predictions of the object's weight when lifting objects. Previous studies have suggested that grip forces may provide a better and more reliable measure for participants' internal estimate of object size as it is not confounded with position information (Brenner & Smeets, 1996; Smeets, Brenner, de Grave, & Cuijpers, 2002). Hence, the finding that fingertip forces are independent of the availability of visual information at movement onset (FV vs. OLM condition), and remain constant even after longer memory delays (2s), provides further evidence that the representation of object size used for grasp control is encoded and stored in a stable manner.

5. General Discussion

In a series of studies, we aimed to directly test the assumption that information about target size is encoded in a more stable manner than information about target position. To date, no studies have explicitly tested whether and how visual size representations change with increased visual uncertainty. In the first experiment, we found that when participants had to transport their hand to the object they showed larger grip apertures and progressively poorer grip scaling as well as higher endpoint variability as visual information was reduced. However, if the positional demands were minimised (i.e. no hand transport), both the size of MGA and the grip scaling remained constant across all vision conditions. This finding indicates that the kinematic changes observed in the far transport condition were largely due to the decay of relevant positional information, whereas size information was encoded more stably. This suggestion received further support from Experiment 2: When the demands of object localisation were made redundant during grasping MGA and grip scaling were unaffected by memory demands. In contrast, memory for object position, as tested in a reaching task, decayed rapidly with the reduction of the available visual information. Finally, when we measured participants' fingertip forces as an unbiased indication of encoded object size (Experiment 3), we found constant grip/load force scaling in all vision conditions. Together, these

findings provide compelling evidence for the notion that object size for grasping is encoded in a long-lived and static manner which stands in stark contrast to the rapid decay of the encoded positional information.

We shall first discuss what our findings mean in the context of the two-visual-streams hypothesis (Milner & Goodale, 2006). To briefly reiterate: according to the perception-action model it would be assumed that both object size and object location are computed in real-time within the dorsal stream when vision is available during movement programming (i.e. in the FV and OLM-conditions). In contrast, if visual information is suppressed at the moment movement initiation is required, or any time before that, the visuomotor system has to rely on stored representations mediated via the ventral stream. These ventral stream representations are supposedly less accurate than their dorsal stream counterparts, and subject to memory decay. Our finding that position information decays rapidly is consistent with the general idea that information in the dorsal stream is only available for a very limited amount of time (Milner & Goodale, 1995). However, in its strictest interpretation the real-time view would predict similar localisation accuracy in FV and OLM conditions (as both are assumed to rely on real-time dorsal stream information), followed by a sharp drop in accuracy between the OLM and OLS conditions as a consequence of a switch from dorsal to ventral stream control (Hu et al., 1999; Westwood & Goodale, 2003) – neither of which we observed in our results. Instead, our findings are more consistent with the assumption of a continuous, rather than discrete, decay process of the relevant visual representations (Hesse & Franz, 2009, 2010; Himmelbach & Karnath, 2005). Moreover, given that the movement parameters related to object size (grip aperture scaling and grip force scaling) were unaffected by memory demands, our data provide no evidence that qualitatively different *size* representations are employed across different levels of visual feedback and delay. Obviously, based on our data, we cannot say where the different visual representations are stored or originate from (i.e., dorsal vs. ventral regions). However, what we can say is that, given the fact that movement kinematics related to object size do not change with increased memory demands, it is unlikely that the underlying processing mode changes from dorsal to ventral with memory delay. This interpretation is in line with the more recent notion that similar functional areas are responsible for task-processing when the task context remains identical (e.g., grasping vs. object recognition; Monaco et al., 2014).

From a neurophysiological perspective, the finding that visual information is retained differently for object size and object position is consistent with the recent observation that each of these

properties are encoded in distinct cortical areas (Monaco et al., 2015). Specifically, the anterior intraparietal sulcus (aIPS, part of the dorsal stream) was found to be crucial for the processing of intrinsic object properties relevant for hand pre-shaping and force scaling (such as size and shape) independent of object location, whereas a number of different areas including the superior parietal occipital sulcus (SPOC) showed sensitivity to both object size and location. Note that the SPOC has been associated with processing the transport component of the grasp and aIPS with processing the manipulation component of the grasp (Cavina-Pratesi, Monaco, et al., 2010; Tunik, Frey, & Grafton, 2005). Furthermore, recent studies show that these critical dorsal stream areas also show activation when movements are performed after delay (Fiehler et al., 2011; Singhal et al., 2013). Thus, if we assume that both object position as well as the grasp-relevant object size are computed in the dorsal stream, our findings would suggest that different visual properties show different decay characteristics within dorsal stream areas, with some of them (contrary to previous assumptions) being encoded in a relatively stable fashion.

However, this interpretation is difficult to reconcile with data from neuropsychological patients suffering from dorsal stream damage (i.e. optic ataxia). For example, at least some optic ataxia patients appear to be able to use object size for grasping (Cavina-Pratesi, Ietswaart, et al., 2010), suggesting that ventral stream mechanisms might underpin object size processing. In fact, recent studies found indeed an involvement of the lateral occipital cortex (LOC) in the processing of grasp relevant object properties such as object size, shape, and weight (Cavina-Pratesi, Goodale, & Culham, 2007; Gallivan, Cant, Goodale, & Flanagan, 2014; Monaco et al., 2014), potentially suggesting that both ventral and dorsal areas contribute to the processing of object features relevant to grasping. Therefore, it is possible that object size is not actually calculated in the aIPS, but is projected to this area via connections with the ventral stream (Borra et al., 2008; Grafton, 2010). If object size is mediated through the ventral stream this could also explain why this visual feature is less prone to memory decay. Indeed, the fact that patient DF, who suffers from ventral stream damage with a lesion focus in area LOC (James, Culham, Humphrey, Milner, & Goodale, 2003), performs poorly in tasks in which she has to rely explicitly on object size information, such as pantomiming (Goodale, Jakobson, & Keillor, 1994) and grasping objects in conditions with dissociated size and position information (Schenk, 2012, Task 6) further indicates that the calculation of object size may rely critically on ventral stream processing. However, in this case the question arises of why patient DF still shows normal performance (i.e. hand opening and grip scaling) in natural grasping tasks. Until now, this dissociation in performance between visuomotor and perceptual tasks was taken as evidence that object size is represented in both the ventral and the dorsal stream concurrently, with the dorsal stream representation being used only in natural

visually-guided grasping tasks (Goodale et al., 1994; Whitwell & Buckingham, 2013). However, one could alternatively suggest that in natural grasping tasks DF does not rely on the calculation of object size at all, but can instead base her hand movements on (egocentric) position information alone (Schenk, 2010; Smeets & Brenner, 1999, 2001; Smeets, Brenner, & Biegstraaten, 2002). If this was true then DF's poor grasping performance after delay may indicate that in these tasks she relies on the (rapidly-decaying) position information and that hence her increased hand opening could be attributed to an increased visual uncertainty about relevant positional information. Furthermore, it is important to point out that the assumption that object size is calculated by the ventral stream and transferred into parietal areas crucial for movement execution is easily reconcilable with the recent suggestion that the dorsal and the ventral pathway interact closely to subserve adaptive behaviour and that the ventral stream may in fact play a crucial role in controlling our movements (Buckingham, Cant, & Goodale, 2009; Goodale & Cant, 2007; Schenk & McIntosh, 2010; Valyear & Culham, 2010).

Finally, regardless of the neural loci underpinning object size processing, the current study generally highlights the issue of using grip aperture as an implicit measure of the visual processing of object size. As pointed out above, even though it has been known for a while that grip aperture size is directly linked to transport accuracy (Bootsma, Marteniuk, MacKenzie, & Zaal, 1994; Chieffi & Gentilucci, 1993; Schlicht & Schrater, 2007; Wing et al., 1986), grip aperture is often used in the literature as a standard measure to assess and compare participants' internal representations of object size across tasks with varying localisation requirements (e.g., standard grasping, pantomiming and manual size estimations) in neuropsychological studies (e.g., Goodale et al., 1994; Goodale, Milner, Jakobson, & Carey, 1991; Schenk, 2012) as well as in psychophysical studies on healthy adults (e.g., Brown, Halpert, & Goodale, 2005; Ganel, Chajut, & Algom, 2008; Goodale & Murphy, 1997; Hu et al., 1999). Our findings clearly demonstrate the difficulties associated with using grip aperture size as a variable to measure and compare internal size estimates across tasks with different localisation demands. Specifically we showed that MGA does not provide an unbiased indicator for object size representations underlying grasp control in conditions of visual uncertainty - as despite participants accurately remembering the size of the target, the size of their hand opening will change due to an increased uncertainty about the object's position. This is especially critical when relatively large targets are grasped as it can compromise the usually quite accurate scaling of the grip to object size (i.e. reduced slopes) due to the related biomechanical constraints. A similar argument was put forward by Cavina-Pratesi, Ietswaart, et al. (2010) showing that the impaired grip scaling of an optic ataxia patient is largely caused by his

increased reaching error. If the localisation demands were minimal, the patient showed similar hand openings as healthy control subjects that were correctly scaled to object size. In other words, in tasks where positional information is irrelevant, the hand opening is solely determined by the size of the object. Importantly, the latter is also typically the case in pantomimed grasping tasks and manual estimation tasks in which the measured hand opening only relates to object size while object location (as well as hand location) can be ignored. Hence it is not clear if differences observed in grip openings between these tasks indicate differential processing of object size for perception (ventral) and action (dorsal) as suggested by the perception-action model (Milner & Goodale, 1995) or can be related to the fact that position information is needed for action task but not for the corresponding perceptual task.

6. Conclusion

In summary, we have shown in a series of experiments that alterations in the manipulation component of the grasp (i.e. grip aperture) when reaching without vision and after a delay can primarily be attributed to an increased uncertainty about the object's position. In contrast, visual representations of grasp-relevant object size seem to be represented accurately over longer time periods. This provides the first direct evidence that different grasp-relevant visual properties show distinct decay characteristics. Furthermore, our findings highlight that we have to be cautious when measuring changes in grip scaling to infer how object size is represented or processed in the visual brain, as both positional and biomechanical factors can affect grasp pre-shaping (see Utz, Hesse, Aschenneller, & Schenk, 2015 for related argument). Instead, anticipatory scaling of fingertip forces might provide a more reliable measure to assess internal object size representations used for object interaction.

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Figure Legends

Figure 1: **A:** Illustration of hand position and object position in the far and no transport conditions of Experiment 1. Note that participants did not need to move their hand in order to reach the object in the no transport condition. **B:** Illustration of the stimuli seen by the participants in Experiments 2A and 2B. In Experiment 2A, participants grasped the (hidden) object placed at the object location marker (+) and were provided an object size cue at a different location (see Methods for more information). In Experiment 2B, participants were asked to point to the perceived middle of the target object that could be placed at three different distances from the hand. Note that participants were not able to see their hand in all vision conditions of Experiment 2A and 2B.

Figure 2: Experiment 1: **A:** MGA as a function of object size and transport distance. In the far transport condition participants had to cover a distance of 30 cm between start position and target position while in the no transport condition only a movement of the fingers but not the hand was required (see methods section for more information). Each panel depicts a different vision condition with memory demands increasing from left to right. **B:** Slopes of the functions relating MGA to object size in all five vision conditions and each of the transport conditions. All error bars depict ± 1 SEM between subjects.

Figure 3: Experiment 1: Relative increase in end-point variability (as compared to the FV-condition) plotted as a function of the relative increase in the size of MGA (as compared to the FV-condition) for each of the five vision conditions. Each symbol represents the data of one participant in the far transport condition (N=17). Lines represent the least-squares fit to the data obtained in each vision condition. Note that for all conditions the increase in endpoint variability was significantly correlated with the respective increase in MGA.

Figure 4: Experiment 2A: **A:** MGA as a function of object size and vision condition. Each panel depicts a different vision condition with memory demands increasing from left to right. **B:** Slopes of the functions relating MGA to object size in all five vision conditions. All error bars depict ± 1 SEM between subjects.

Figure 5: Experiment 2B: **A:** Endpoint variability in the reaching task as a function of target distance and vision condition. **B:** Distance error in the reaching task as a function of target distance

and vision condition. Each panel depicts a different vision condition with memory demands increasing from left to right. All error bars depict ± 1 SEM between subjects.

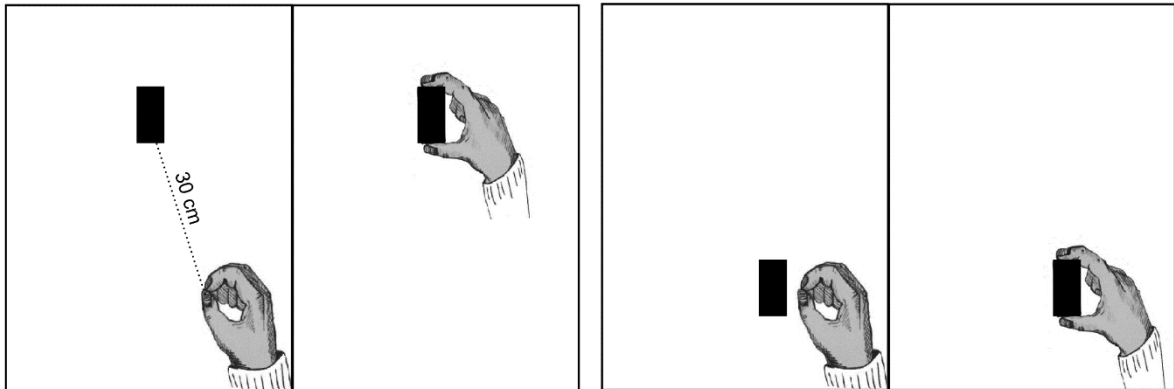
Figure 6: Experiment 3: A: Peak grip force rate and peak load force rate as a function of object size and vision condition (see methods section for more information). Each panel depicts a different vision condition with memory demands increasing from left to right. B: Slopes of the functions relating peak force rate changes (N/s) to object size in all five vision conditions. All error bars depict ± 1 SEM between subjects.

A:

Experiment 1

Far transport condition

No transport condition



Experiment 2A and 2B

B:

Grasping

Pointing

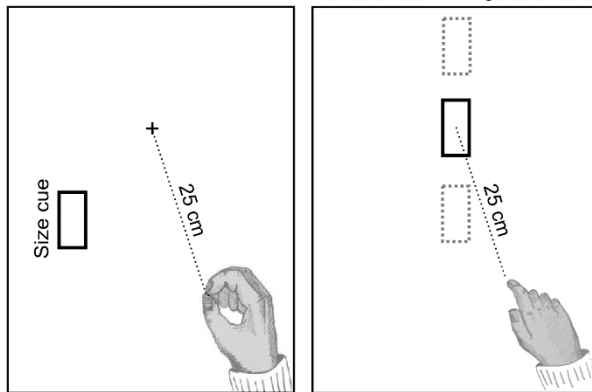


Figure 1

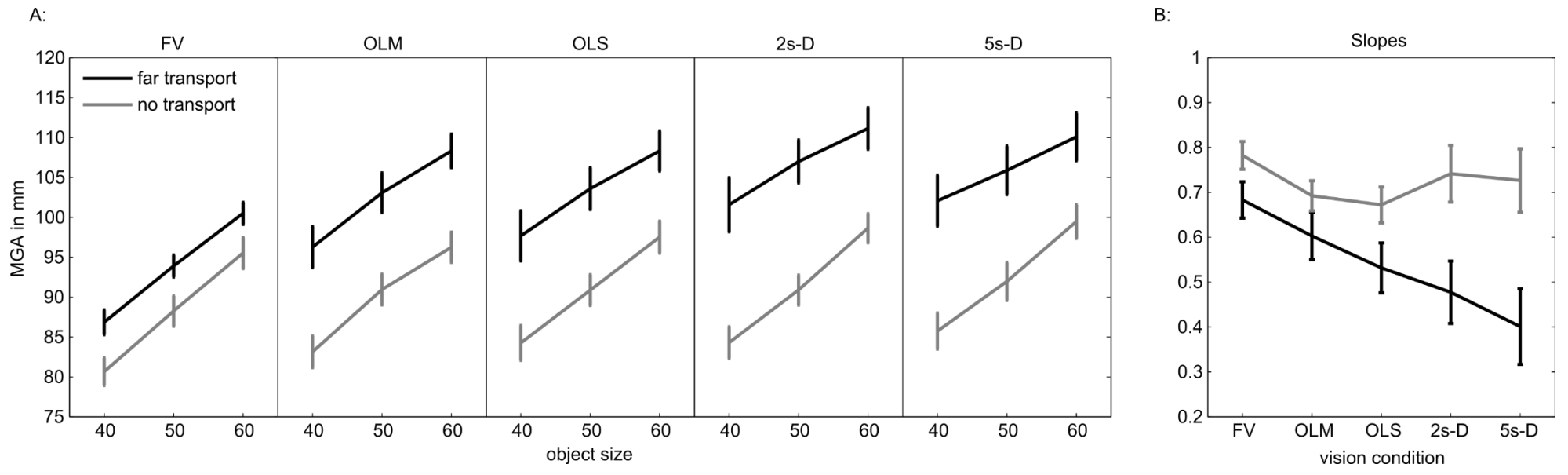


Figure 2

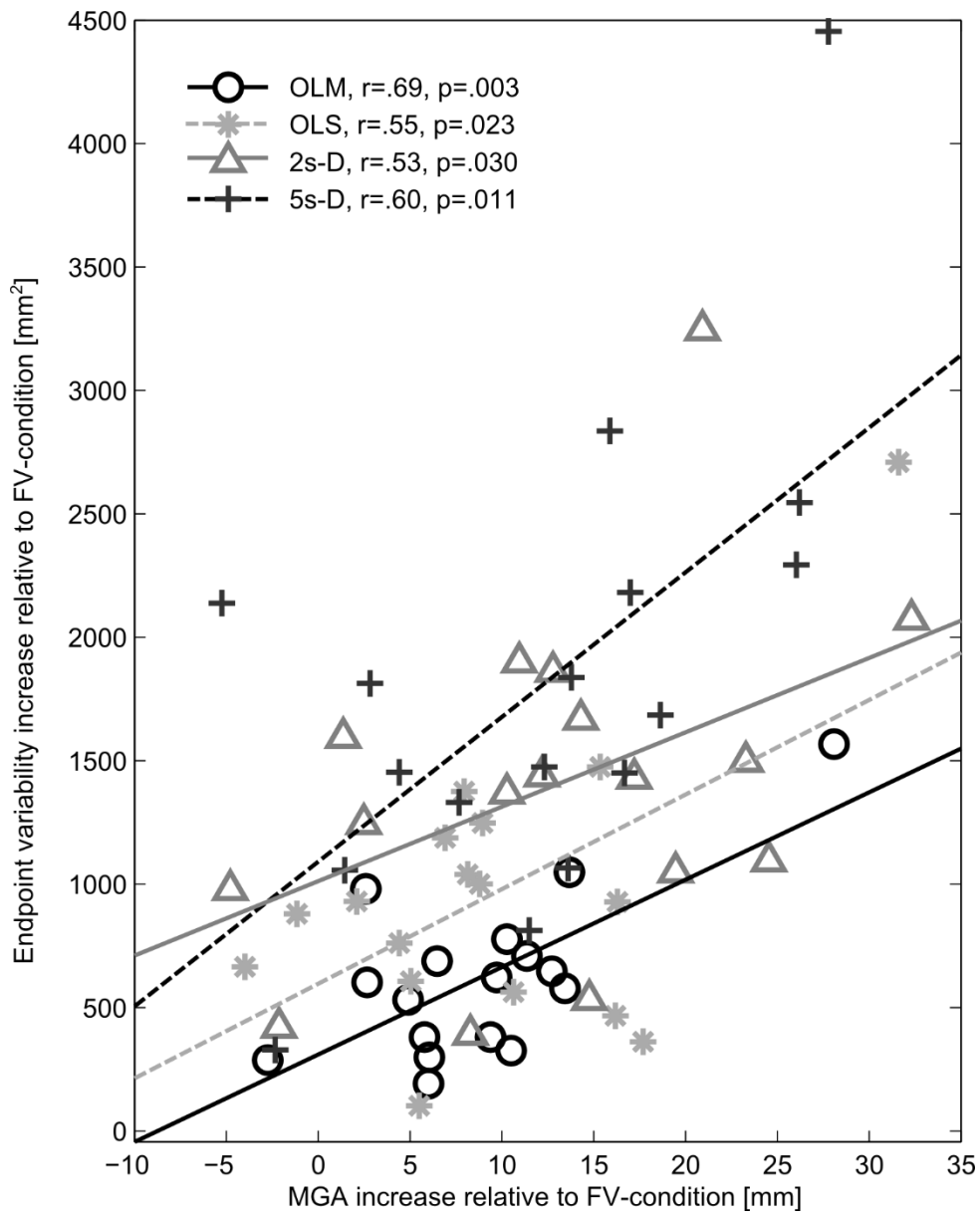


Figure 3

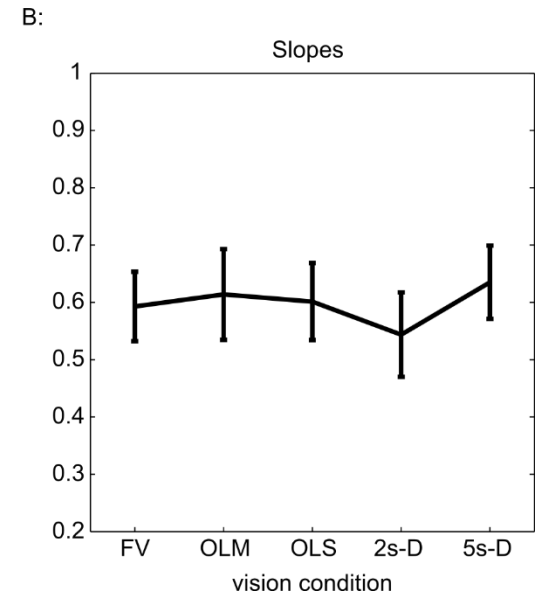
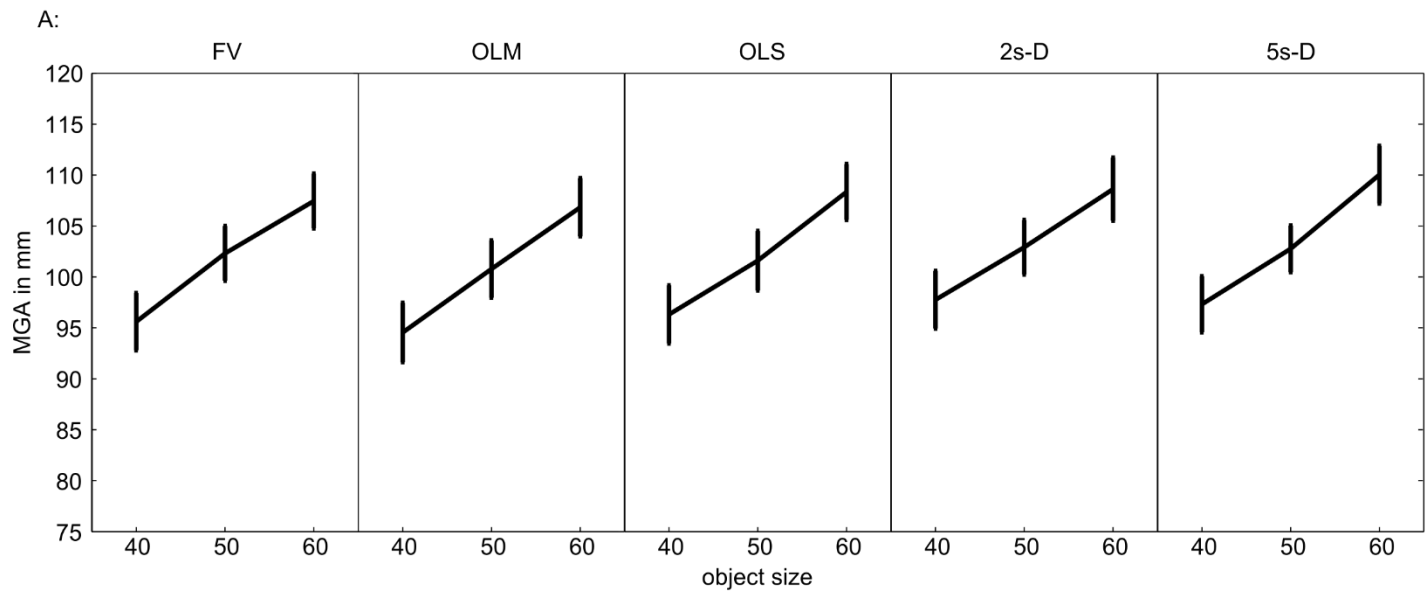


Figure 4

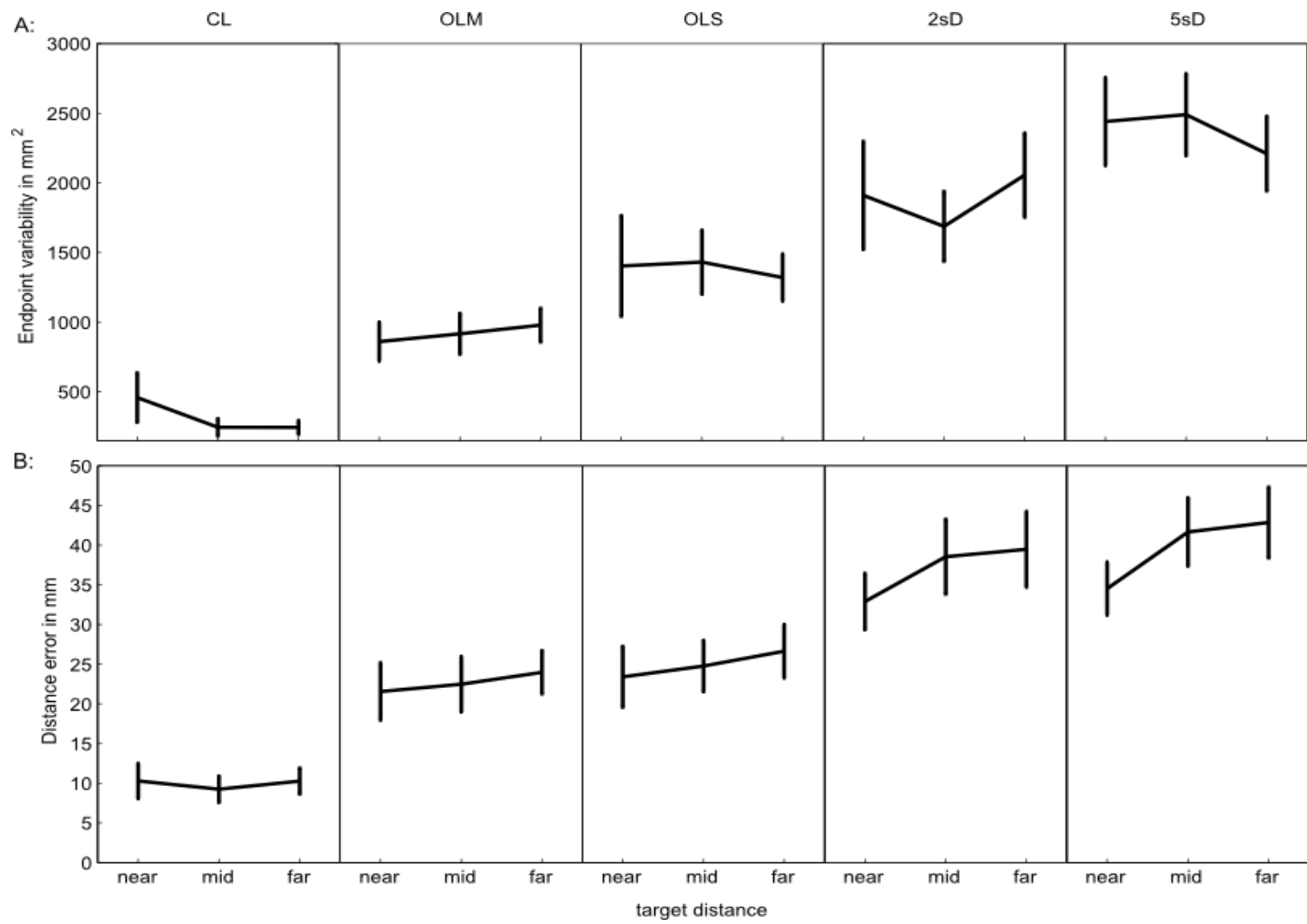


Figure 5

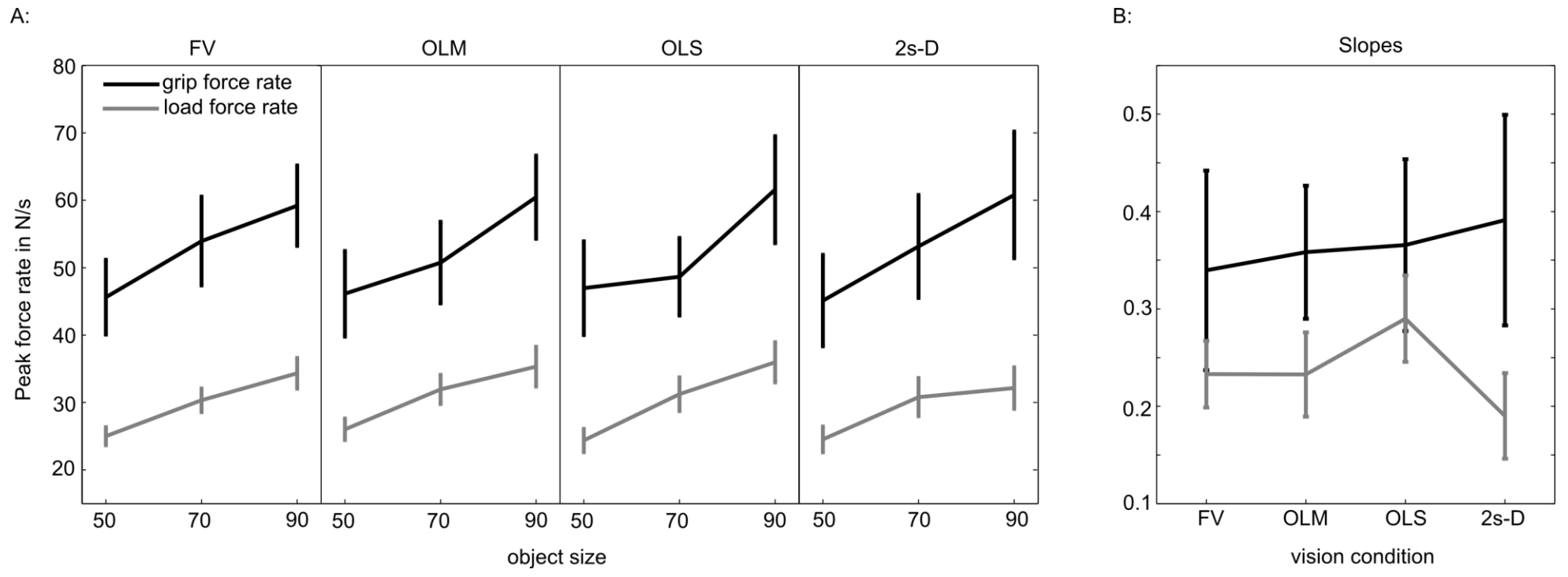


Figure 6

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