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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 et al., 1981; Milner and Goodale, 1995; Winges, Weber, and 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

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http://dx.doi.org/10.1016/j.neuropsychologia.2016.09.016 0028-3932/© 2016 Elsevier Ltd. All rights reserved. counterparts (for review see Heath et al., 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 and Lee, 1995; Hesse and Franz, 2010; Wing, Turton, and Fraser, 1986). There is, however, far less consensus about (a) how long accurate visual representations persist (e.g., Elliott et al., 1991; Elliott and Madalena, 1987; Goodale et al., 2005; Hesse and Franz, 2009; Westwood et al., 2003) and (b) if dissociable neural substrates underpin visually-guided and memory-guided hand movements (e.g., Connolly et al., 2003; Fiehler et al., 2011; Himmelbach et al., 2009; Lacquaniti et al., 1997; Singhal et al., 2013).

Regarding a possible functional dissociation between visuallyguided 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 and Goodale, 2003; Westwood et al., 2003). To date, the question of whether





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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 et al., 2009; Heath et al., 2010; Hesse and Franz, 2009; Himmelbach and Karnath, 2005; Milner and 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 et al., 2006; Elliott and Madalena, 1987; Hesse and Franz, 2009; Rolheiser et al., 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) 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 (see also Jennerod et al., 1995). 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 et al., 2010b; 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 and Valvear, 2006; Monaco et al., 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 and Goodale, 1991; Schlicht and Schrater, 2007; Smeets and 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 and 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 and Watt, 2002; Elliott et al., 1991; Heath and 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 and Franz, 2009; Hu et al., 1999; Hu and 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 et al. (2010a) 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 premovement 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 and Smeets, 1996; Flanagan et al., 2009), and that changes in the estimated size are reflected in the grip and lift forces applied to objects when picking them up (Buckingham and Goodale, 2010; Gordon et al., 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

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