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Transfer of adaptation reveals shared mechanism in grasping and manual estimation

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ABSTRACT

An influential idea in cognitive neuroscience is that perception and action are highly separable brain functions, implemented in distinct neural systems. In particular, this theory predicts that the functional distinction between grasping, a skilled action, and manual estimation, a type of perceptual report, should be mirrored by a split between their respective control systems. This idea has received support from a variety of dissociations, yet many of these findings have been criticized for failing to pinpoint the source of the dissociation. In this study, we devised a novel approach to this question, first targeting specific grasp control mechanisms through visuomotor adaptation, then testing whether adapted mechanisms were also involved in manual estimation – a response widely characterized as perceptual in function. Participants grasped objects in virtual reality that could appear larger or smaller than the actual physical sizes felt at the end of each grasp. After brief exposure to a size perturbation, manual estimates were biased in the same direction as the maximum grip apertures of grasping movements, indicating that the adapted mechanism is active in both tasks, regardless of the perception-action distinction. Additional experiments showed that the transfer effect generalizes broadly over space (Exp. 1B) and does not appear to arise from a change in visual perception (Exp. 2). We discuss two adaptable mechanisms that could have mediated the observed effect: (a) an afferent proprioceptive mechanism for sensing grip shape; and (b) an efferent visuomotor transformation of size information into a grip-shaping motor command.

1. Introduction

1.1. Visuomotor versus perceptual behavior: grasping and manual estimation

To execute a skilled grasping movement, the hand must be positioned around the target in a way that supports appropriate timing and balance of applied grip forces (Jeannerod, 1981; Iberall et al., 1986; Santello and Soechting, 1998). This careful behavior is guided by an anticipatory control system that transforms a visual estimate of the target's 3D shape into an appropriate set of motor parameters. Researchers have modeled this process as a feedforward transformation from visual to motor coordinates, presumably instantiated by parietal grasping circuits, which are known to exhibit complex, multi-modal responses before and during grasping movements (Jeannerod et al., 1995; Sakata et al., 1997; Pouget and Snyder, 2000; Buneo et al., 2002).

Despite continued progress in understanding the neural computations supporting grasp planning and execution, the degree of interaction between these visuomotor processes and the perceptual mechanisms that support explicit 3D shape judgments remains a topic of significant debate (Schenk and McIntosh, 2010, and associated Commentaries). A central point of contention is whether motor behaviors rely on the same visual processes that produce spatial perception, or if they rely on specialized visual processing in an independent "vision-for-action" system, as proposed by Goodale and Milner (1992). According to the latter view, the perceptual mechanisms that support explicit 3D shape judgments do not provide information to the visuomotor processes supporting skilled actions like grasping. The standard experimental approach to testing this idea has been to directly compare the results of a perceptual task and a visuomotor task to determine whether they respond differentially to some manipulation of the visual input. If the selected tasks are mediated by the same spatial attribute of the target object, then a differential response could indicate the existence of two separate visual processes for estimating the relevant attribute, one for perception and one for action guidance.

Object size is one spatial attribute for which the possibility of dissociated visual processing has been extensively investigated. Many studies have compared the maximum in-flight grip apertures produced during grasping movements with a type of explicit perceptual report known as *manual estimation*. Manual estimation involves separating the

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index finger and thumb in an attempt to match the spatial extent of a visual target object, while keeping the hand near the body. Although this clearly involves some degree of motor control to move the fingers, the standard assumption with respect to the two visual streams debate is that manual estimation should be considered a purely perceptual task, lacking the requirement of real-time physical interaction that is said to engage the putative vision-for-action system. Instead, the observer is explicitly communicating their current visual size percept to the experimenter, providing a direct "readout" by matching the visual estimate with the felt shape of the grip. Indeed, natural grasping rarely seems to require this level of explicit attention to visual size percept.

Based on these qualitative arguments, manual estimation has been widely adopted as a perceptual task. Manual estimates have been compared to maximum grip apertures of grasping movements under a variety of experimental manipulations, including visual illusions (Haffenden and Goodale, 1998; Vishton and Fabre, 2003; Bruno and Franz, 2009; Kopiske et al., 2016; Cesanek et al., 2018), Weber's law (Ganel et al., 2008; Bruno et al., 2016), Garner interference (Ganel and Goodale, 2003), and visual cortical lesions (Milner et al., 1991; Goodale et al., 1991). Surprisingly, however, there is no empirical evidence to support the assumption that it engages a different output system than grasping, which is the fundamental basis of a functional distinction.

1.2. Testing for a functional distinction with adaptation-transfer

In this study, we address this issue by using an adaptation-transfer paradigm to measure the degree of overlap between the grasp control system and the control system for manual estimation. Our approach is based on the fact that visuomotor mechanisms are highly adaptable. Even the simplest and most extensively practiced movements, like grasping, rely on sensory feedback signals to maintain appropriate tuning of the underlying visuomotor processes. When haptic feedback is not provided, reaches tend to fall short of the target and the hand does not open wide enough to ensure stable grasping (Bingham et al., 2007). The short-term plasticity of the grasp control system has been investigated directly in studies of grasp adaptation: when a visual size perturbation is induced using a magnifying lens or virtual reality, the visuomotor mapping rapidly adapts based on sensory feedback (Gentilucci et al., 1995; Säfström and Edin, 2004; Weigelt and Bock, 2007; Coats et al., 2008; Cesanek and Domini, 2017; Kopiske et al., 2017). For example, when a visual target is made to appear smaller than its true physical size, the very first grasp will inevitably be too small, with the fingers inadvertently bumping the edges of the object. However, with repeated grasps, the system learns to compensate for the distortion by mapping the same visual size estimate onto a larger planned grip aperture. In the present experiment, we investigated the novel question of whether grasp adaptation causes neural changes that are specific to grasp control, or if these changes also affect the processing of manual estimates.

One hypothesis is that grasping and manual estimation rely on completely separate control systems as a result of their differing functions. As discussed above, separate control systems are frequently assumed in studies that use manual estimation as a perceptual measure to pit against grasping movements – *e.g.,* Haffenden and Goodale (1998; pp. 125) assert that "although hand and finger movements were required in this manual estimation task, the programming and execution of those movements does not involve the same control systems used in grasping." Given the specific functional requirements of grasping, which include temporal synchronization with a reaching movement and stable physical contact with the target, it is plausible that grasp adaptation might selectively affect grasping movements. On the other hand, manual estimation must rely on some motor as well as proprioceptive processing to change and sense the grip shape. Therefore, an alternative hypothesis is that these processes are among the adapted components of the visuomotor mapping for grasp control; under this hypothesis, we should expect transfer of grasp adaptation to manual estimation. Critically, this result would demonstrate that the neural effects of visuomotor adaptation are not constrained in a way that respects a functional distinction between perception and action, thus weakening the claim that this distinction is a strong organizational principle in the human brain.

1.3. Experiment overview

Participants were asked to grasp 3D wireframe objects of varying lengths viewed in a virtual reality environment. We presented real physical objects in the same location as the rendered virtual objects, so participants received haptic feedback from a real physical object at the end of each grasp. To elicit visuomotor adaptation of grasping, we systematically changed the visual sizes of the objects, making them appear smaller or larger than the corresponding physical targets. With small perturbations, participants do not notice anything strange about this altered arrangement, but the misleading visual information causes the grip aperture to be scaled incorrectly during grasping. As a result, unexpected sensory feedback signals are generated that can be used to determine how the current visuomotor mapping must be modified to achieve the desired task goals (Säfström and Edin, 2008). We have reported clear evidence of trial-by-trial error corrections and traditional aftereffects under nearly identical task conditions in an earlier study (Cesanek and Domini, 2017; see also Kopiske et al., 2017).

To test for transfer of grasp adaptation to manual estimation, participants performed a manual estimation pre-test after grasping objects under normal conditions, then performed a post-test after exposure to a visual size perturbation. This four-phase procedure was completed once with a positive (+7.5 mm) perturbation, and once with a negative (−7.5 mm) perturbation, with order counterbalanced across participants. In each condition, we measured the change in size of manual estimates from pre-test to post-test; reported transfer effects are within-subjects differences between the two conditions. Based on previous work demonstrating directional selectivity in grasp adaptation, we also sought to determine whether transfer effects would generalize broadly or narrowly across the workspace. To evaluate the spread of the generalization function, we tested participants in two variations of the manual estimation task. In Experiment 1A, participants reached toward the target location (30 cm in front of the eyes) and then produced the manual estimate, while in Experiment 1B, participants produced the manual estimate at the starting hand location (near the right shoulder). Lastly, to investigate whether transfer effects could be caused by changes in visual perception, we conducted a control experiment involving a visual size judgment task instead of manual estimation (Exp. 2).

2. Method

2.1. Participants

Twenty-four participants were recruited for Experiment 1A; twelve were called back to the laboratory for Experiment 1B. A new sample of twenty-one participants were recruited for Experiment 2. Participants were required to be right-handed with normal or corrected-to-normal vision and they were granted course credit or paid $8/hour as compensation. Informed consent was obtained from all participants prior to any participation, in accordance with protocol approved by the Brown University Institutional Review Board and performed in accordance with the ethical standards set forth in the Declaration of Helsinki.

2.2. Apparatus

Participants viewed and grasped 3D stimuli within a tabletop virtual reality apparatus (Fig. 1A). The apparatus consisted of a chinrest, a 19" CRT monitor, a pair of NVIDIA 3D Vision® 2 Wireless Glasses (NVIDIA Corporation, Santa Clara, CA), a half-silvered mirror arranged at a 45°