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The influence of visual feedback from the recent past on the programming of grip aperture is grasp-specific, shared between hands, and mediated by sensorimotor memory not task set

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ABSTRACT

Goal-directed movements, such as reaching out to grasp an object, are necessarily constrained by the spatial properties of the target such as its size, shape, and position. For example, during a reach-to-grasp movement, the peak width of the aperture formed by the thumb and fingers in flight (peak grip aperture, PGA) is linearly related to the target's size. Suppressing vision throughout the movement (visual open loop) has a small though significant effect on this relationship. Visual open loop conditions also produce a large increase in the PGA compared to when vision is available throughout the movement (visual closed loop). Curiously, this differential effect of the availability of visual feedback is influenced by the presentation order: the difference in PGA between closed- and open-loop trials is smaller when these trials are intermixed (an effect we have called 'homogenization'). Thus, grasping movements are affected not only by the availability of visual feedback (closed loop or open loop) but also by what happened on the previous trial. It is not clear, however, whether this carry-over effect is mediated through motor (or sensorimotor) memory or through the interference of different task sets for closed-loop and open-loop feedback that determine when the movements are fully specified. We reasoned that sensorimotor memory, but not a task set for closed and open loop feedback, would be specific to the type of response. We tested this prediction in a condition in which pointing to targets was alternated with grasping those same targets. Critically, in this condition, when pointing was performed in open loop, grasping was always performed in closed loop (and vice versa). Despite the fact that closed- and open-loop trials were alternating in this condition, we found no evidence for homogenization of the PGA. Homogenization did occur, however, in a follow-up experiment in which grasping movements and visual feedback were alternated between the left and the right hand, indicating that sensorimotor (or motor) memory can operate both within and between hands when the response type is kept the same. In a final experiment, we ruled out the possibility that simply alternating the hand used to perform the grasp interferes with motor or sensorimotor memory. We did this by showing that when the hand was alternated within a block of exclusively closed- or open-loop trials, homogenization of the PGA did not occur. Taken together, the results suggest that (1) interference from simply switching between task sets for closed or open-loop feedback or from

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switching between the hands cannot account homogenization in the PGA and that (2) the programming and execution of grasps can borrow not only from grasping movements executed in the past by the same hand, but also from grasping movements executed with the other hand.

1. Introduction

When we reach out to pick up an object, the movements of our limb, wrist, hand, and fingers are tuned to the spatial features of that object, such as its position and geometry, well before our fingers make contact with it. The control of these movements has been argued to reflect an analysis of the extrinsic (e.g., position, orientation) and intrinsic (e.g., shape, size) spatial features of the object (Jeannerod, 1981, 1988, 1999; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995), an analysis of the grasp opposition space in the context of learned motor schemas for different grasp types (Arbib, 1981; Iberall & Arbib, 1990; Iberall, Bingham, & Arbib, 1986), or an analysis of the spatial positions on opposing edges of the goal object (Smeets & Brenner, 1999, 2001; Smeets, Brenner, & Martin, 2009). Regardless of the nature of the movement programming, under most normal circumstances in which a static object is grasped, the visuomotor system relies more on visual input provided before and up to the moment the movement is initiated than it does on visual input that is available as the movement unfolds. The evidence for this comes from the fact that suppressing vision throughout the movement does not abolish or seriously affect many of the relationships between a goal object's spatial features (e.g. distance, position, orientation, and geometry) and the resultant movement parameters of the limb, hand, and fingers (e.g. speed, reach vector, orientation, and grip aperture) (Gentilucci, Daprati, Gangitano, Saetti, & Toni, 1996; Hesse & Franz, 2009, 2010; Hu, Eagleson, & Goodale, 1999; Jakobson & Goodale, 1991; Jeannerod, 1986; Rand, Lemay, Squire, Shimansky, & Stelmach, 2007; Whitwell, Lambert, & Goodale, 2008; Tang, Whitwell, & Goodale, 2014).

Nevertheless, some motor output parameters do show reliable changes when online visual feedback is unavailable. One of these parameters is grip aperture (the distance between the tips of the thumb and fingers of the grasping hand. Peak grip aperture (PGA), which is usually achieved about 70% of the way through the grasp, is correlated with the size of the goal object (e.g. Hesse & Franz, 2010; Jakobson & Goodale, 1991; Jeannerod, 1981; Jeannerod, 1984; Whitwell et al., 2008). PGA is typically larger than the goal object, reflecting the need to ensure that the approach angles of the thumb and fingers are relatively perpendicular to the surface of the object when contact is made (Smeets & Brenner, 1999). If vision is suppressed throughout the movement (visual 'open loop'), PGA is almost always larger than when vision is available (visual 'closed loop') (Fukui & Inui, 2006; Gentilucci et al., 1996; Hesse & Franz, 2009, 2010; Hu et al., 1999; Jakobson & Goodale, 1991; Jeannerod, 1986; Rand et al., 2007; Whitwell et al., 2008; Tang et al., 2014; for review see Fukui, Takemura, & Inui, 2006; Smeets & Brenner, 1999). The wider PGA in open loop is thought to provide a greater 'margin of error', reducing the likelihood that the fingers might bump into the object or knock it away during the reach.

Interestingly, the difference in PGA between visual closed-loop and visual open-loop trials (PGA_D) is influenced by the way in which these two trial types are administered: the PGA_D is larger when the closed- and open-loop trials are administered in separate blocks and smaller when they are randomly interleaved (Fukui & Inui, 2006; Tang et al., 2014; Whitwell et al., 2008) or even abolished (Jakobson & Goodale, 1991). The simplest explanation for this modulatory influence is that the participants strategize their response based on the predictability/randomness of the trial order: participants optimize their response to closed- and open-loop trials when these two trial types are blocked separately, but when they are randomly interleaved, the participants adopt a 'worst-case scenario' strategy and open their hand wider on every trial (Jakobson & Goodale, 1991). As it turns out, however, this account is not correct. Whitwell et al. (2008) showed that alternating closed- and open-loop trials predictably, one after the other, resulted in the same reduction in PGA_D as randomizing the two trial types. This means that the effect of trial order on PGA_D cannot be due to predictive knowledge about the availability of visual feedback on an upcoming trial. The fact that explicit strategies cannot explain these findings lends credence to an alternative explanation – one that is based on either a memory of the motor program used on the previous trial (motor memory) or both the motor program and sensorimotor feedback on that trial (sensorimotor memory). According this memory-based account, a motor or sensorimotor trace from the previous grasping movement persists and is incorporated into the next grasping movement.

In line with this new interpretation, Whitwell and Goodale (2009) went on to show that PGA is reliably smaller on trials preceded by a closed-loop trial than on trials preceded by an open-loop trial (and vice versa). Furthermore, these effects accumulate over consecutive closed- or open-loop trials. According to Whitwell and Goodale, this explains why a large PGA_D results when closed- and open-loop trials are blocked separately – but when closed- and open-loops trials are interleaved the PGA_D becomes much smaller. In other words, the PGA is affected not only by the conditions of the current trial but also by what happened on the previous trial. Interleaving the closed- and open-loop trials, whether randomly or alternately, leads to 'homogenization' of the PGA: relative to blocked trial orders, the PGA on closed-loop trials increases, whereas