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The left hand disrupts subsequent right hand grasping when their actions overlap

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ABSTRACT

Adaptive motor control is premised on the principle of movement minimization, which in turn is premised on a form of sensorimotor memory. But what is the nature of this memory and under what conditions does it operate? Here, we test the limits of sensorimotor memory in an intermanual context by testing the effect that the action performed by the left hand has on subsequent right hand grasps. Target feature-overlap predicts that sensorimotor memory is engaged when task-relevant sensory features of the target are similar across actions; partial effector-overlap predicts that sensorimotor memory is engaged when there is similarity in the task-relevant effectors used to perform an action; and the action-goal conjunction hypotheses predicts that sensorimotor memories are engaged when the action goal and the action type overlap. In three experiments, participants used their left hand to reach out and pick up an object, manually estimate its size, pinch it, look at it, or merely rest the left hand before reaching out to pick up a second object with their right hand. The in-flight anticipatory grip aperture of right-hand grasps was only influenced when it was preceded by grasps performed by the left-hand. Overlap in the sizes of the objects, partial overlap in the effectors used, and in the availability of haptic feedback bore no influence on this metric. These results support the hypothesis that intermanual transfer of sensorimotor memory on grasp execution is dependent on a conjunction of action type and goal.

1. Introduction

Human manual control is remarkably fluid and flexible. Sometimes an identical action is performed with both hands, as when we push a heavy appliance across a floor. Other times both hands act with similar movements, as when we tie our shoes. And, on still other occasions, our two hands act in entirely different ways, as when we hold grocery bags with one hand and open the door with the other. We perform this range of familiar tasks almost flawlessly in our daily lives. The smoothness of our action execution under these diverse conditions is believed to result from the minimization of movement variability, which is a fundamental operating principle in motor control (Bays & Wolpert, 2007; Wolpert, Diedrichsen, & Flanagan, 2011).

A key premise of the movement minimization principle is the existence of sensorimotor memory (Keele, 1968; Schmidt, 1975; Shadmehr & Holcomb, 1997; Walker, Brakefield, Hobson, & Stickgold, 2003). Movement variability can only be minimized by a system that tracks variability. The system must record movements over some temporal window in order to measure the variability. Although the coordination of bimanual hand actions is still not fully understood (Diedrichsen, Shadmehr, & Ivry, 2009; Oliveira & Ivry, 2008) sensorimotor memory may play an important role in coordinated actions, particularly when both hands must rely on similar motor programming. Here we build on previous findings that trial-to-trial transfer occurs between hands (e.g., Tang, Whitwell, & Goodale, 2014) to explore the nature of sensorimotor memory for precision grasps of the right hand. We did this by testing pairs of trials in which right hand grasps were preceded by different actions performed by the left hand. The critical experimental factors included congruency in the size of the target objects presented to each hand; the action performed by each hand; and the goal for these actions.

The in-flight grip aperture of reach-to-grasp movements is strongly influenced by the presence (closed loop) or absence (open loop) of visual feedback such that the hand's in-flight grip aperture is larger in open loop conditions than in closed loop ones (e.g., Jakobson & Goodale, 1991; Whitwell, Lambert, & Goodale, 2008; Wing, Turton, & Fraser, 1986). Moreover, the effect of visual feedback on grip aperture is modulated by the order in which closed and open loop conditions are administered (Whitwell & Goodale, 2009). In short, the more varied the feedback schedule is, the smaller the difference in grip aperture

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between open and closed loop conditions. This trial history (or transfer) effect was attributed to the operation of sensorimotor memory, because explicit knowledge about the pending trial does not mitigate the effect (Whitwell et al., 2008; Whitwell & Goodale, 2009).

Subsequent investigations have explored the limits of this transfer effect. For example, the trial transfer effect does not depend on identical muscle groups being recruited, because it operates between one grasping hand and the other (Tang et al., 2014). In contrast, the transfer effect from one hand to the other fails if the actions and goals differ, when, for example, one hand reaches out to touch to the centre of an object and then the other hand reaches out to grasp the object (Tang, Whitwell, & Goodale, 2015). Interestingly, an overlap in task goal, from one trial to the next, is not enough to gate transfer. Tang, Whitwell, and Goodale (2016) asked participants to pick up objects and put them back down using only their own hand or a pair of tongs. Note that the action types differ – the way in which the hand is used when it controls a pair of tongs is quite different than the way it is used when merely picking up the same object. Importantly, despite an identical action goal, trial transfer did not occur. Taken together, these findings imply that sensorimotor memory is a function of a complete overlap in either 'action type' (i.e. the reactivation of a sequence of muscle ensembles or the activation of an analogous set in the other limb) or the conjunction of action type and the goal of the action.

The hypothesis that sensorimotor memory is gated by a binding of specific action types and/or task goals offers insight on how we learn to perform complex coordinated actions. Coordinated action involves the assembly of component action types (Gentilucci, Negrotti, & Gangitano, 1997). Shielding the sensorimotor repertoire of an action type (i.e. motor schema or internal model) from the memories of different action types minimizes aliasing between action type and memory (i.e., memory for updating the internal model and/or memory for planning and executing less error prone action). Put another way, encapsulated repertoires of sensorimotor models is one way to provide existing scaffolding on which to 'build' more complex actions performed with both hands and to minimize interference when updating those models. When coordinated action is required that involves a number of different action types, the action can be assembled using a repertoire of models associated with the goal and action type. In addition to encapsulation, if sensorimotor memory ignores the detailed analysis of object geometry or the spatial relationships between the target and the effectors, then the model can parameterize details of the action such as wrist orientation and in-flight hand aperture during reach-to-grasp movements. This reduces the dimensionality of the information stored in models that help guide action, reducing required capacity size for long-term storage of motor plans or programs. The parameterization can be performed de-novo and in real-time using visual information (Milner & Goodale, 2006).

Here, we test and rule out two additional possibilities that might gate sensorimotor memory. First, trial transfer for grasps may be gated by a visual cue such as an overlap in a task-relevant target feature such as size (Linscheid, An, & Gross, 1991). This 'target-feature overlap' hypothesis predicts that grip aperture for the right hand grasps would be influenced by what the left hand does provided the sizes of the target for the left-hand and right-hand tasks are identical. Second, trial transfer for grasps may be gated by a partial overlap in task-critical effectors, particularly if they are used in similar ways. This 'partial effector overlap' hypothesis predicts that grip aperture for the right hand grasps would be influenced by the left hand as long as the two actions share task-relevant effectors that are used similarly enough. Note that the size of the target and the response variable grip aperture are tightly coupled variables and critical task-features in both the grasping and manual estimation tasks.

In Experiment 1, participants first used their left hand to either manually estimate the size of an object presented at a distance, or to reach and pick up the object and put it back down, before reaching out and picking up a similar object using their right hand. In a baseline condition, participants simply rested their left hand while performing the same right-hand grasping task. The purpose of the manual estimation task was to recruit a level of visual attention and set of effectors and movements that are similar to those involved in the right hand grasping task. If sensorimotor memory is gated by a complete overlap in action type or conjunction of action-type and goal, then 1) trial transfer will not occur from left hand manual estimations to right hand grasps, because the action type differs or both the goal and action types differ; and 2) trial transfer will occur when the left hand actually grasps the target object. In contrast, if sensorimotor memory is gated by an overlap in target-feature, then transfer will occur when the object sizes are identical between the left and right hands but not when the object sizes are different. Finally, if sensorimotor memory is gated by a partial overlap in task-relevant effectors, then the right hand grasps should be influenced by both the left-hand grasps and the left-hand manual estimations, because both actions types rely on displacing the thumb and index finger in accordance with the size of the target object. To ensure that trial transfer effects were specific to sensorimotor memory, and not a more general perceptual effect, the sizes of the object presented to the left and right were unpredictably either identical or different.

2. Experiment 1

2.1. Methods

2.1.1. Participants

Thirty right-handed individuals (aged 18–36, 18 female) participated in Experiment 1. All participants were right-handed, had normal or corrected-to-normal vision, and received monetary compensation or course credit for their participation. Participants provided informed consent in accordance with the local institutional guidelines for ethical research practices. In addition, handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971).

2.1.2. Apparatus and stimuli

Kinematic data were recorded at 100 Hz using an OPTOTRAK (Northern Digital, Waterloo, ON, Canada) optoelectronic tracking system. Infrared emitting diodes (IREDs—2 in total) were attached to the inner edge of the nail on the index finger and the inner edge of the nail on the thumb. The workspace was a tabletop which had two start positions – one for the left hand and one for the right – each marked 5 cm from the edge of the table facing the participant and 30 cm from one another along a frontal plane. The participant was seated at the table such that their mid-sagittal axis divided the 30 cm distance equally in half. Thus, the start positions were 15 cm either side of the participant's midsagittal axis. The stimuli consisted of two sets of three different-sized white wooden cubes ($l \times w \times h$: 3 × 3 × 3, 4 × 4 × 4, 5 × 5 × 5 cm).

2.1.3. Procedure

The participants were seated comfortably on a chair in front of a table. They began each trial with the thumb and index finger of their left hand pressed together and their thumb and index finger of their right hand pressed together at each hand's starting position. The participants were asked to close their eyes between trials. The experimenter first positioned an object 30 cm out in front of the left hand's starting position along the participant's sagittal plane.

The participants were asked to open their eyes and perform one of two tasks with their left hand: In the Grasp condition they reached out towards the object to pick it up and place it back down on the table before returning their hand to the start position; In the Manual Estimation condition, participants indicated the size of the object by displacing their thumb and index finger while refraining from reaching towards the object. After the participants completed the left hand task, the experimenter positioned a white foam board to block the participant's view of the object on the left and the left hand, preventing online