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RESEARCH NOTE

Sensorimotor memory of weight asymmetry in object manipulation

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Abstract Using a precision grip-lifting task, we examined how sensorimotor memory for weight asymmetry transfers across changes in hand and object configuration. We measured object tilt when participants lifted a visually symmetric box with an offset centre of mass. Transfer was assessed after participants lifted the box 10 times, during which the large tilt observed in the first lift was reduced. Consistent with previous work of Salimi et al. (J Neurophysiol 84:2390–2397, 2000), we found that when the object was rotated 180°, participants failed to update their sensorimotor memory appropriately. Instead, participants acted as if the object did not rotate and negative transfer was observed. However, when the hand was rotated 180° around the object, participants were able to correctly update sensorimotor memory and positive transfer was observed. This finding argues against the hypothesis that sensorimotor memory is digit-specific because the rotation of the hand (like rotation of the object) changes the forces that each digit must generate to prevent tilt. Positive transfer was also observed when both the hand and object were rotated. This suggests that the rotation of the hand may facilitate rotation of an internal representation of the object. Finally, we found positive transfer of weight asymmetry across the two hands but only when the second hand was rotated such that homologous digits of each hand gripped the same contact surfaces. We suggest that good transfer is observed under these conditions because, when we pass objects from hand to hand, we typically place homologous digits of the two hands in similar locations on the object.

Introduction

We often lift objects using a precision grip with the tips of the index finger and thumb contacting opposing vertical surfaces. To lift the object, vertical load forces, tangential to the grip surfaces, must be generated. At the same time, grip forces, normal to the grip surfaces, are produced to increase friction between the fingertips and grip surfaces and prevent the object from slipping. When lifting, people generally scale their load forces to the predicted weight of the object such that they increase load force more rapidly when the expected weight is greater (Johansson and Westling 1988; Gordon et al. 1991a, b, 1993). This scaling occurs prior to lift off and is therefore anticipatory. People also typically adjust their fingertip forces and torques, predictively, to prevent objects from tilting when lifting (Goodwin et al. 1998; Jenmalm et al. 1998; Wing and Lederman 1998; Johansson et al. 1999; Salimi et al. 2000, 2003; see also Ellis et al. 1999; Lukos et al. 2007). Such predictive scaling of fingertip forces and torques is required for skilled manipulation because of lengthy time-delays in sensorimotor control loops (Flanagan et al. 2006).

When first lifting a viewed object, people rely on visual cues about object size (Gordon et al. 1991a, b; Flanagan and Beltzner 2000), shape (Jenmalm and Johansson 1997; Jenmalm et al. 1998; Wing and Lederman 1998; Johansson et al. 1999) and identity (Gordon et al. 1993) to predictively scale their fingertip forces and torques. These visual cues provide only indirect information about object mechanical properties, such as weight and weight distribution, and can

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sometimes be inaccurate. However, once an object has been lifted, direct information about object mechanical properties is provided by tactile sensors. The knowledge about object properties gained from previous lifts has been referred to as sensorimotor memory (e.g. Johansson and Westling 1984, 1988). In the absence of useful visual cues, sensorimotor memory dominates fingertip force control after a single lift. For example, when repeatedly lifting a test object, the weight of which is occasionally and unexpectedly altered, people update their force output within a single trial following a weight change (Johansson and Westling 1988). In the presence of misleading visual cues, several trials may be required before sensorimotor memory dominates (Gordon et al. 1991c; Flanagan and Beltzner 2000; Grandy and Westwood 2006).

In order to investigate sensorimotor memory for weight and weight distribution, researchers have used objects without meaningful visual cues about these mechanical properties. Studies examining sensorimotor memory for weight have used objects where size and weight are dissociated. These studies showed that sensorimotor memory for object weight is long lasting (Flanagan et al. 2001), transfers from one hand to the other (Gordon et al. 1994) and that people can remember the weights of multiple objects (Davidson and Wolpert 2004; Grandy and Westwood 2006). Sensorimotor memory for weight asymmetry was first investigated by Salimi and colleagues (2000), who used a visually symmetric box with a hidden weight that could be shifted along the grip axis of a handle (similar to the one shown in Fig. 1a) centred on top of the box. When participants first lifted the object, they applied similar load forces to the two grasp surfaces (with the tips of the thumb and index finger) and, consequently, the object tilted as it was lifted. If the object was lifted again under the same conditions, participants quickly learned to apply a larger load force at the digit closer to the centre of mass so as to greatly reduce tilt. However, if the object was rotated 180° and lifted by the same hand, participants generated similar load forces at the two digits and a large tilt was observed. A similar failure to appropriately update fingertip forces for object rotation occurs when the opposing contact surfaces have different slipperiness (Edin et al. 1992). Salimi and coworkers (2000) also showed that participants failed to appropriately scale their fingertip forces when switching hands (with the orientation of the object held constant). These results, suggesting that sensorimotor memory for weight asymmetry is not updated across changes in object orientation or hand, led the authors to suggest that the representation of weight asymmetry is digit-specific.

In the current paper, we further examined sensorimotor representations of weight asymmetry in several ways. First, we tested whether good transfer of weight asymmetry information would be observed if the object was rotated and the hand was switched such that the homologous digits of the two hands contacted the same contact surfaces. If sensorimotor memory is digit-specific but also available to corresponding digits on the other hand, good transfer should be observed. Second, we examined whether good transfer would be observed if the hand, rather than the object, was rotated. Using an object with frictional asymmetry at the contact surfaces, Quaney and Cole (2004) recently showed that whereas people do not update fingertip forces appropriately when the object rotates 180° (thus replicating Edin et al. 1992), they do correctly update their fingertip forces after rotating their hand 180° even though

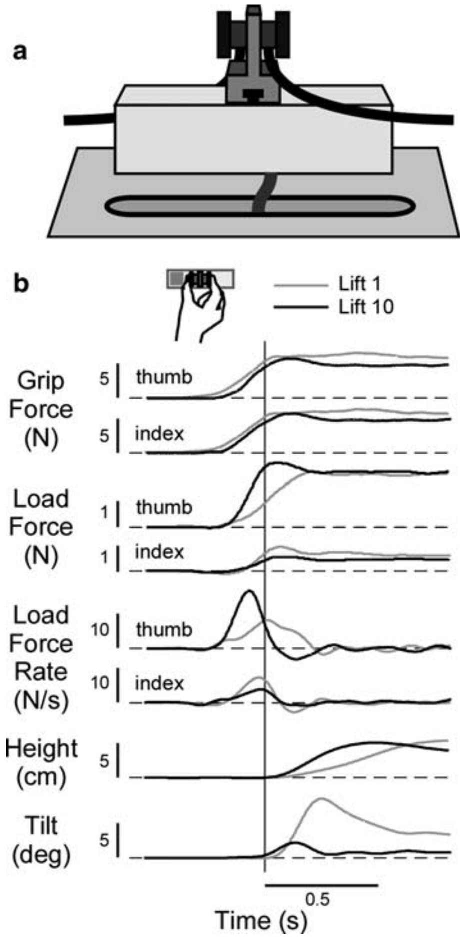

Fig. 1 Apparatus and sample records. **a** Using the tips of the index finger and thumb, participants lifted a lightweight wooden box (15 × 4 × 4 cm) from a central handle with two vertical contact surfaces mounted on force-torque sensors. A hidden weight of 150 g was inserted in one end of the box. A position-angle sensor was inserted into the bottom of the object midway along its long axis. The cable from this sensor passed through a slot in the tabletop. **b** Kinetic and kinematic data from the first and tenth lifts performed by a single participant in the *rotate object: slide* condition when lifting with the right-hand with the weight on the thumb side (see *gray square* in inset). The two trials are aligned at the time the object lifted off the surface, indicated by the *vertical line*. The large tilt seen in trial 1 (*gray traces*) was reduced in trial 10 (*black traces*)

the mapping between digits and contact surfaces reverses. If we obtain a similar result, it will challenge the notion that sensorimotor memory for weight asymmetry is digit-specific. In two additional experiments, we also tested whether good transfer would be observed if the participants switched hands but rotated the new hand and if both the object and hand rotated. In both cases, homologous digits of the two hands contacted the same contact surfaces. In addition to these four novel experiments, we also included two experiments aimed at replicating the previous results of Salimi and colleagues (2000). Thus, we included an experiment in which the object was rotated and an experiment in which the hand was switched. Finally, we also included a control experiment in which the configuration of the hand and object was held constant.

Methods

Participants

A total of 56 participants took part in this study and were paid for their participation. All participants were right-handed, had normal or corrected-to-normal vision, and did not report sensorimotor deficits. Participants gave informed consent before completing the study and the experimental procedure was approved by a local university ethics board and complied with the Declaration of Helsinki. Participants were randomly assigned to one of seven conditions with eight participants per group.

Apparatus

In all experiments, participants lifted a rectangular box made from balsa wood (see Fig. 1a). The box was 15-cm long, 4-cm wide, and 4-cm high with a hidden 150-g lead weight, the centre of which was located 2.5 cm from one end. The centre of mass of the test object was located along the long axis and the weight was inserted from the bottom of the object (with a plug holding it in place) such that no visual cues indicated its presence or location. The mass of the box alone was 191.8 g and the mass of the box with handle attached was 260.5 g. The handle was mounted centrally on top of the box with two parallel grip surfaces (3 cm diameter, 4 cm apart) oriented such that the axis normal to the two grip surfaces was parallel to the long axis of the box. The grip surfaces were mounted on miniature force/torque sensors (Nano 17 F/T sensor, ATI Industrial Automation, Garner, NC) that measured the forces and torques applied by the thumb and index finger in three dimensions. An electromagnetic position/angle sensor (FASTRAK, Polhemus, Colchester, VT) was fitted into the bottom of the box midway along the long axis. The cable to this sensor, which was very flexible and light so as not to generate torques on the box, passed through a slot cut out of the tabletop so that the box rested evenly on the table (see Fig. 1a).

Procedures

While standing, participants lifted the box from a tabletop at waist height. The box was positioned with the long axis parallel to the coronal plane of the participant, who was instructed to grasp the handle by placing the thumb and index finger in the centre of the grip surfaces and to lift the box no more than 2 cm above the surface of the tabletop. A high-pitched beep signaled them to lift the box and a second low-pitched beep signaled them to replace the box. Although no specific instructions about tilt were given, the low height of the lift forced participants to keep the box parallel to the table. The experimenter monitored each lift and suggested corrections to height, speed and finger placement as appropriate. Each participant completed 3 blocks of 10 lifts followed by a fourth block consisting of a single lift. Participants were not permitted to lift the box prior to the beginning of the experiment. In all experimental conditions, with the exception of the *control* condition, one or more task variables were alternated between blocks such that blocks 1 and 3 were the same and blocks 2 and 4 were the same. These variables included the hand used to lift, the orientation of the box, and the orientation of the hand. When the box orientation was changed, participants used their right-hand to rotate the box by sliding it over the tabletop. Drawings illustrating the seven conditions are shown in Fig. 2. For each condition (or group), half the participants began with the weighted end of the box on their right while the other half began with it on their left.

In the *control* condition, all lifts were performed with the right-hand with a short pause between blocks approximately equal to the pause in other conditions (about 30 s). In the *rotate object* condition, participants rotated the object between blocks by sliding it across the tabletop. All lifts were performed with the right-hand and the right-hand was used to rotate the objects. In the *switch hand* condition, blocks 1 and 3 were performed with the right-hand and blocks 2 and 4 were performed with the left. In the *rotate object and switch hand* condition, the box was rotated by sliding it across the tabletop between blocks. Blocks 1 and 3 were performed with the right-hand and blocks 2 and 4 performed with the left-hand. In the *rotate hand* condition, blocks 1 and 3 were performed with the hand in the normal grip position. For blocks 2 and 4, the participant rotated his or her hand such that the thumb and index finger grasped the opposite grip surfaces as in blocks 1 and 3. In the *rotate and switch hand* condition, blocks 1 and 3 were performed with the right-hand and blocks 2 and 4 were performed with

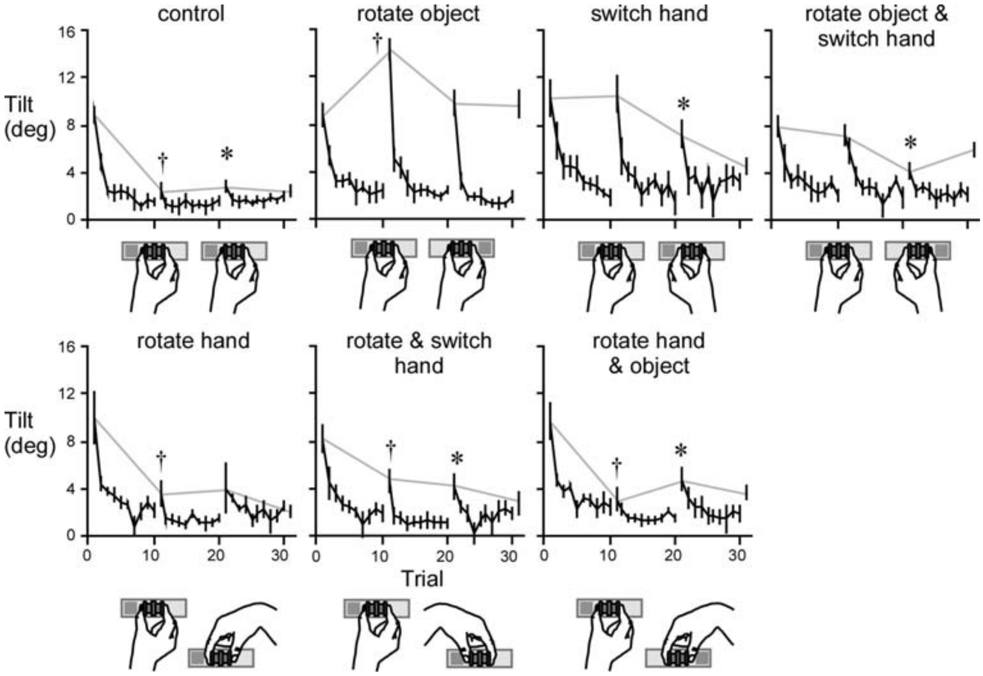

Fig. 2 Object tilt as a function of trial, block and condition. Each panel shows mean peak tilt, averaged across participants, as a function of trial for one of the eight experimental conditions. The *vertical bars* represent ±1 standard error, trials within each block are joined by a *black line*, and a *grey line* joins the first trials of the four blocks. The *left* and *right* drawing below each panel illustrate the hand and hand and object orientations used in blocks 1 and 3 and blocks 2 and 4, respectively. Two statistical comparisons were performed for each condition. The † indicates a significant difference between trial 11 and trial 1 and the * indicates and a significant difference between trial 21 and trial 1

the left-hand rotated such that the left index finger gripped the same contact surface as the right index finger and the left thumb gripped the same contact surface as the right thumb. The *rotate object and hand* condition was similar to the *rotate hand* condition except that box was rotated by the participant between blocks by sliding the block with the right-hand.

Data analysis

Force and torque signals were sampled at 1,000 Hz and the position and orientation signals, updated at 60 Hz, were over-sampled at 1,000 Hz. We defined the tilt of the box as the angle between the long axis of the box and the horizontal. The tilt was positive when the heavy end of the box (i.e. the end with the inserted weight) was lower than the light end. For each trial, the first peak tilt after lift off and the load forces for each finger at the moment of lift off were determined. Lift off was deemed to have occurred when the height of the centre of the box reached 0.2 mm and remained above 0.2 mm for at least 100 ms.

Results

Figure 1b shows, for a single participant in the *rotate object* condition, force and position traces from the first and tenth trials of block 1. On the first lift, the vertical load forces initially applied by the thumb and index finger to the grip surfaces on the heavy and light sides of the box, respectively, were similar and this led to a large initial tilt of the box towards the weighted side (positive tilt). In subsequent lifts, the two load forces were adjusted so as to reduce object tilt. On the tenth lift, the load force applied by the thumb to the heavy side was greater than the load force applied by the index finger to the light side at lift off. Consequently, the initial peak tilt was reduced. As expected, based on mechanics and previous reports (Salimi et al. 2000), we observed a tight link between load forces at the moment of lift off and initial peak tilt. For simplicity, we will only report initial peak tilt in describing the results for the different experimental conditions.

Figure 2 shows mean initial peak tilt, averaged across participants, as a function of trial for all seven conditions. As expected, participants significantly tilted the box on their initial lift in all conditions. On average, the initial peak tilt in the first trial was 9.10° (SE = 0.49°) and did not vary across groups ($F_{6,42} = 0.41$; $p = 0.87$) or depend on the orientation of the box ($F_{1,42} = 0.23$; $p = 0.64$). To characterize performance in each group, we focused on two dependent variables. To estimate transfer across the task variable(s) that changed from block to block, we examined the change in peak tilt from trial 1 to trial 11. (The crosses in Fig. 2 indicate significant effects.) To quantify retention of learning across blocks with the same task variable(s), we examined the difference in peak tilt between trial 1 and trial 21. (The stars in Fig. 2 indicate significant effects.) Because these two comparisons are not completely independent (i.e. both involve trial 1), we halved the alpha level from 0.05 to 0.025 when testing for significance.

In the *control* condition, where the right-hand was used throughout and the orientations of the box and hand were unchanged across blocks, the peak tilts on trials 11, 21, and 31 were small ($M = 2.6°$, $2.9°$ and $2.5°$, respectively). As expected, the peak tilt in trial 11 was significantly less ($F_{1,7} = 32.8$; $p = 0.001$) than in trial 1 ($M = 8.8°$).

In the *rotate object* condition, where participants rotated the box between blocks by sliding it, the peak tilt in trial 11 was greater than in trial 1 ($F_{1,7} = 14.3$; $p = 0.007$). Thus, participants failed to account for the rotation of the box and acted as if the weight was still on the same side. No reliable difference in peak tilt was observed between trials 1 and 21 ($F_{1,7} = 0.43$; $p = 0.53$). This indicates that lifting the rotated box in block 2 interfered with performance on block 3 where the box was rotated back to its original orientation.

In the *switch hand* condition, where the right and left hands were used in alternate blocks but the box orientation was held constant, the peak tilts in trials 1 ($M = 10.3°$) and 11 ($M = 10.6°$) were not reliably different ($F_{1,7} = 0.17$; $p = 0.69$). Thus, the adaptation of the right-hand to the mass asymmetry that occurred during the first block did not transfer to the left-hand; a result consistent with the findings of Salimi and colleagues (2000). The peak tilt in trial 21 ($M = 7.2°$) was smaller than in trial 1 ($F_{1,7} = 11.0$; $p = 0.013$). This suggests that some retention of sensorimotor memory occurred within the right-hand despite the intervening block with the left-hand.

In the *rotate object and switch hand* condition, where participants rotated the box (by sliding it) and switched hands between blocks, the peak tilt in trial 11 ($M = 7.2°$) was not reliably different ($F_{1,7} = 0.41$; $p = 0.55$) than in trial 1 ($M = 7.9°$). Thus, as in the *switch hand* condition, the adaptation of the right-hand in block 1 did not transfer to the left-hand. The peak tilt in trial 21 ($M = 4.2°$) was smaller than in trial 1 ($F_{1,7} = 10.8$; $p = 0.013$). Thus, despite the intervening block with the left-hand, retention of sensorimotor memory occurred within the right-hand.

In the *rotate hand* condition, where the orientation of the box was constant and the right (lifting) hand was rotated between blocks, the peak tilt in trial 11 ($M = 3.6°$) was smaller ($F_{1,7} = 14.2$; $p = 0.007$) than in trial 1 ($M = 10.0°$). Thus, the adaptation of the right-hand to the mass asymmetry transferred when the hand was rotated. A similar result has been reported for lifting objects with asymmetric frictional conditions at the two grasp surfaces (Quaney and Cole 2004). The peak tilt in trial 21 ($M = 4.1°$) was not significantly different ($F_{1,7} = 3.53$; $p = 0.10$) than in trial 1.

In the *rotate and switch hand* condition, where the left-hand was rotated so that the left thumb and index finger contacted the same grip surfaces as the right thumb and index finger, respectively, the peak tilt in trial 11 ($M = 4.7°$) was less ($F_{1,7} = 9.05$; $p = 0.02$) than in trial 1 ($M = 8.2°$). Thus, learning transferred from the right-hand to the rotated left-hand. The peak tilt in trial 21 ($M = 4.2°$) was also significantly smaller than in trial 1 ($F_{1,7} = 11.9$; $p = 0.011$). Thus, retention of sensorimotor memory occurred across successive blocks with the right-hand despite the intervening block with the rotated left-hand.

In the *rotate hand and object* condition, where the box and the right-hand changed orientation between blocks, the peak tilt in trial 11 ($M = 3.1°$) was smaller ($F_{1,7} = 22.4$; $p = 0.002$) than in trial 1 ($M = 9.7°$). Thus, the adaptation of the right-hand to the mass asymmetry transferred when both the right-hand and box, were rotated. The peak tilt in trial 21 ($M = 4.8°$) was smaller than in trial 1 ($F_{1,7} = 29.7$; $p = 0.001$) indicating retention of learning from block 1 to block 3.

Discussion

As expected, in all conditions, significant object tilt was seen on the first lift and this tilt was greatly reduced in subsequent lifts in the first block. Specifically, participants learned to compensate for the torque due to the offset centre of mass by exerting greater load force at the digit closest to the centre of mass. As previously shown (Salimi et al. 2000), this adjustment of load forces is predictive and occurs prior to lift-off.

In agreement with the results of Salimi and colleagues (2000), we found that information about weight distribution does not transfer between hands even when the object is rotated such that the homologous digits of the two hands touched the same contact surfaces. The latter result rules out the possibility that sensorimotor memory transfer across homologous digits of the two hands. Taken together, the results of these two switch hand conditions suggest that sensorimotor memory for weight asymmetry is reset after the hand is switched and that participants behave as if they expect the weight to be centered (i.e. they behave like naïve participants). Interestingly, in both of these switch hand conditions, the initial tilt in block 3 was smaller than in block 1 suggesting some transfer of learning across blocks with the same hand. Thus, although sensorimotor memory established for the right-hand in block 1 was not transferred to the left-hand, it appears that this memory was partially preserved and recalled when lifting again with the right-hand. These results suggest that separate sensorimotor memories may be established for the two hands.

In line with Salami and colleagues (2000), we found that participants could not appropriately update their sensorimotor memory for weight asymmetry when the object was rotated (*rotate object* condition). However, whereas these authors reported that there was no transfer following object rotation, we observed significant negative transfer. This suggests that participants did not reset their sensorimotor memory but instead persisted with their current (and inappropriate) sensorimotor memory when the object rotated.

The fact that no improvement occurred from block 1 to block 3, when the object was rotated back again, is consistent with the idea that participants persisted with the same sensorimotor memory across all blocks, ignoring the rotation of the object, and did not establish separate sensorimotor memories for the two object orientations.

One of our primary aims was to test whether good transfer would be observed when the hand, rather than the object, was rotated. In the *rotate hand* condition, we observed excellent transfer. Quaney and Cole (2004) showed that, following hand rotation, participants could appropriately update their fingertip forces when lifting objects with different frictional conditions at the two contact surfaces. Our results suggest that sensorimotor memory for weight asymmetry can also be appropriately updated following rotation of the hand. This finding argues against the general hypothesis that sensorimotor memory for weight asymmetry is specific to the digit forces or motor commands (or wrist torques) applied when lifting (Salimi et al. 2000). Why can participants readily update their sensorimotor memory when the configuration of the hand changes but not when the configuration of the object changes? Quaney and Cole (2004), suggested that internally driven motor plans for rotating the hand could access appropriate sensorimotor memories, whereas visual signals related to object rotation do not. Note that whereas the experimenter rotated the object in Quaney and Cole's (2004) study, participants in our study rotated the object by sliding it themselves. This suggests that only actions directly involved in lifting can update or remap sensorimotor memory for weight asymmetry.

We also observed excellent transfer when both the hand and object were rotated (*rotate object and hand* condition). Thus, participants were able to update their sensorimotor memory for object rotation but only if object rotation was accompanied by rotation of the hand. This suggests that the rotation of the hand may facilitate mental rotation of a representation of the object in memory. This capacity may develop through our extensive experience in manipulating objects where rotations of the hand and object are coupled. A link between mental rotation of an external object and effector rotation has been demonstrated by Wexler and colleagues (1998). These authors used a standard mental rotation task (see Shepard and Cooper 1982; Kosslyn 1980 for reviews) where participants were presented with two visual images that differed by rotation and, in some trials, reflection. Participants had to judge, as quickly as possible, whether one version of the image was a reflection of the other. In this task, the reaction time depends on the shortest angular displacement between the images (Shepard and Cooper 1982). Wexler and coworkers (1998[e1]) asked participants to perform this mental rotation task while simultaneously rotating the hand and found that the reaction times were shorter when the shortest rotation between the images was compatible with the direction of hand rotation.

We observed positive transfer in the *rotate and switch hand* condition. These results may seem surprising because no transfer between hands was observed in either the *switch hand* or in the *switch hand and rotate object* conditions. However, good transfer in the *rotate and switch hand* condition may make sense from a statistical perspective. When we pass an object from one hand to the other, we typically grasp the object such that the thumb (of both hands) contacts the near side of the object and the index finger contacts the far side. Similarly, if we pick up an object first with one hand and then the other, the thumb of both hands will typically contact the near side of the object. If the object does not rotate, then the homologous digits of the two hands will contact the same sides of the object. This is the situation in the *rotate and switch hand* condition. Thus, participants' ability to update sensorimotor memory in this condition may be rooted in our extensive experience with similar conditions. Indeed, such practice effects may also underlie the good transfer seen in the *rotate hand* and *rotate hand and object* conditions. Thus, our ability to remap sensorimotor representations when rotating the hand may be related to the frequency with which we re-grasp objects in everyday manipulation tasks. As noted above, our ability to accommodate object rotation when the hand rotates may be linked to the fact that these rotations are often coupled in daily manipulation tasks.

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