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Unusual hand postures but not familiar tools show motor equivalence with precision grasping

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ABSTRACT

A central question in sensorimotor control is whether or not actions performed with the hands and corresponding actions performed with tools share a common underlying motor plan, even though different muscles and effectors are engaged. There is certainly evidence that tools used to extend the reach of the limb can be incorporated into the body schema after training. But even so, it is not clear whether or not actions such as grasping with tools and grasping with the fingers share the same programming network, i.e. show 'motor equivalence'. Here we first show that feedback-appropriate motor programming for grasps with atypical hand postures readily transfers to stereotypical precision grasps. In stark contrast, however, we find no evidence for an analogous transfer of the programming for grasps using tools to the same stereotypical precision grasps. These findings have important implications for our understanding of body schema. Although the extension of the limb that is afforded by tool use may be incorporated into the body schema, the programming of a grasping movement made with tools appears to resist such incorporation. It could be the case that the proprioceptive signals from the limb can be easily updated to reflect the end of a tool held in the hand, but the motor programs and sensory signals associated with grasping with the thumb and finger cannot be easily adapted to control the opening and closing of a tool. Instead, new but well-practiced motor programs are put in place for tool use that do not exhibit motor equivalence with manual grasping.

1. Introduction

Reaching out and grasping an object with our fingers is a simple movement that we perform countless times every day. In addition, we routinely use tools to grasp objects. Even though using tools in this way also involves opening and closing the fingers, it is not clear whether or not grasping with tools and grasping with the hands share the same underlying motor plan, i.e. show 'motor equivalence' (Lashley, 1930). The classic example of motor equivalence can be seen when we write our signature using different effectors. Whether we sign our name by holding the pen with our fingers or with our toes, the signature is remarkably similar (Wing, 2000). In other words, there is some sort of limb-independent neural coding of skilled movements. Neuroimaging evidence suggests that the motor programs for these highly-practiced movements are stored in secondary motor areas and can be accessed by different effectors when required (Rijntjes et al., 1999).

Of course, there are important differences between grasping and writing. Hand-writing is internally generated and depends on a stored long-term procedure. In contrast, grasping is essentially goal-driven and is largely determined by the features of the object one wants to pick up. Nevertheless, there is evidence that grasping movements made with effectors as different as the hand and the mouth share many characteristics in common, are closely coordinated, and may share a common neural substrate for programming actions, particularly during feeding (Castiello, 1997; Gentilucci, Benuzzi, Gangitano, & Grimaldi, 2001; but see Quinlan & Culham, 2015). Thus, it is possible that there is some sort of general procedure for grasping that is routinely accessed no matter whether people grasp objects with their index finger and thumb, with two hands, with their mouth, or even with a tool.

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A recent neuroimaging study, for example, found that grasp-related areas in the anterior intraparietal and caudal ventral premotor cortices are also active when participants use a tool to grasp the same objects (Jacobs, Danielmeier, & Frey, 2010). But even though the same brain areas were activated, the patterns of activation associated with manual grasping appeared to be independent from those associated with tool use. Although this would appear to suggest that the programming of grasping and the programming of tools may at some level be effector-specific, other evidence from single-unit studies in monkeys trained to use tools suggests that some of the same neural circuitry involved in manual grasping may be invoked when tools are used to accomplish the same goal (Umiltà et al., 2008). Nevertheless, evidence of overlap in the brain does not necessarily imply that the two kinds of grasping make use of the same underlying motor programming. At present, it is not clear whether the shared representations underlying grasping with tools and grasping with the fingers reflect motor equivalence or instead a much more abstract or conceptual communality between the two ways of picking up a goal object.

In the current study, we took advantage of the fact that the specification of motor parameters on trial n in a sequence of trials is transferred to trial $n+1$ – but only if those actions share the same motor programming network (Tang, Whitwell, & Goodale, 2014, 2015). This transfer is particularly evident in the programming of grip aperture when the availability of visual feedback is varied over trials (Whitwell & Goodale, 2009; Whitwell, Lambert, & Goodale, 2008). Grip aperture is typically smaller when visual information about the goal object and the moving hand is available during the execution of the grasp (closed loop) than it is when visual information is denied during the execution of the movement (open loop) (Wing, Turton, & Fraser, 1986). This difference is particularly striking when these different feedback conditions are blocked. But if open- and closed-loop trials are randomized, or even alternated, then grip aperture is more homogeneous across trials; i.e., the difference in grip aperture between open and loop trials is significantly smaller (Whitwell & Goodale, 2009; Whitwell et al., 2008). The fact that homogenization occurs when the two kinds of trials are interleaved means that performance on the current trial is affected by what happened on the previous trial. In blocked conditions, the effect of the previous trial on the current trial accumulates over trials because the feedback condition remains the same from trial to trial.

These trial-to-trial effects appear to be action-specific. In other words, transfer occurs between successive grasping trials, even between grasping with the left hand and grasping with the right, but such trial-to-trial transfer does not occur between successive pointing and grasping trials, in which the underlying motor programming networks for the two actions are quite different (Tang et al., 2015). The presence or absence of trial-to-trial transfer provides a new way to investigate whether or not grasping with the fingers and grasping with tools show motor equivalence. If the same underlying motor network is accessed in these two situations, then there should be transfer from grasping with a tool on trial n to precision grasping with the thumb and finger on trial $n+1$. The results were clear: there was absolutely no evidence for trial-to-trial transfer from tools to the precision grip. As we discuss later, the results have important implications for our understanding of body schema.

2. Method

2.1. Participants

In all the experiments, participants were right-handed and had normal or corrected-to-normal vision. Handedness was assessed using the Edinburgh Handedness Inventory (Oldfield, 1971). In experiment 1, twelve participants (6 males, 6 females, 18–38 years, mean age = 24.5) were recruited; in experiment 2, eighteen participants (8 males, 10 females, 18–36 years, mean age = 22.6); in experiment 3, eighteen (9 males, 9 females, 19–38 years, mean age = 22.8); and finally, in experiment 4, eighteen participants (8 males, 10 females, 18–41 years, mean age = 23.5). All participants provided informed consent before participating in the experiment. They were compensated for their time and were naive with respect to the purpose of the experiment. The experiments were approved by the local ethics committee at the University of Western Ontario.

2.2. Materials

Three different sized white wooden rectangles were used as target objects for all the experiments (small: 10 cm × 1.5 cm × 2 cm; medium: 10 cm × 1.5 cm × 3.5 cm; large: 10 cm × 1.5 cm × 5 cm). On each trial, one of these objects was placed at one of three distances (near: 10 cm; middle: 20 cm; far: 30 cm) from the start button, which was located 5 cm from the edge of the tabletop closest to the participant. Squeeze-action tongs and scissor-action tongs, both of which were approximately 30 cm long, were used to grasp the objects (see Fig. 1). The tongs were purchased from a local supermarket. Visual feedback was controlled with liquid crystal goggles (PLATO goggles; Translucent Technologies, Toronto, ON, Canada). The default state of the PLATO goggles in the experiment was translucent. The real-time kinematic data were collected at 200 Hz with an OPTOTRAK Certus optoelectronic recording system (Northern Digital, Waterloo, ON, Canada). To measure the movements of the fingers, one IRED was attached to the cuticle of the thumb and another IRED attached to the cuticle of the index-finger. Care was taken to permit freedom of hand movement and proper tactile feedback from the object during grasping. To measure the movements of the tongs, one IRED was attached to the outside edge of one pincer and another IRED was attached to the outside edge of the other pincer. Data were analyzed offline with in-house software written in C, which was designed to calculate the distance between the IRED on thumb/tool and the IRED on index finger/tool during the grasping movement.

2.3. Experimental design

In the present study, we used this trial-to-trial transfer to test whether or not there is a common underlying motor program for different kinds of grasping, including precision grasping with the index finger and thumb, grasping with an unusual hand posture, bimanual grasping, and grasping with tongs. We reasoned that if different forms of grasping shared a common program, then there would be transfer from different kinds of grasping to precision grasping when feedback conditions (open- vs. closed-loop) were alternated. For example, if grasping objects with tongs shares a common motor program with grasping the same objects with the finger and thumb, then picking up an object with tongs under a particular feedback condition should influence picking up an object with the index finger and thumb on a subsequent trial. In all cases, except bimanual grasping, participants used their right hand. Altogether five different kinds of precision grasps were used: (1) grasping with the index finger and thumb, (2) grasping with the ring finger and thumb, (3) bimanual grasping with the middle fingers of the two hands, (4) grasping with squeeze-action tongs, and (5) grasping with scissor-action tongs.

In Experiment 1, we established that all of the different hand postures and tools that used in this study show (1) grip scaling to object size and (2) sensitivity to feedback conditions (larger grip apertures in open loop than closed loop). In Experiments 2, 3, and 4, we tested participants to see whether or not the homogenizing