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Research Report

Brain and cognitive processes of imitation in bimanual situations: Making inferences about mirror neuron systems

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ABSTRACT

The relationship between mirror neuron systems and imitation is being widely studied. However, most if not all, studies on imitation have investigated only the mirror mode. The present study examined whether imitation in a mirror (specular) mode is likely to reflect similar or distinct neural processes and psychological principles as imitation in a non-mirror (anatomical) mode. Experiment 1 examined whether altering sensory information may reverse the typical mirror mode advantage, resulting in superior performance in the non-mirror mode. Experiment 2 examined whether the two different modes of imitation rely differentially on target selection (goals) and effector selection (means). Experiment 3 examined whether spatial translations are likely to occur in a typical non-mirror imitation mode. Experiment 4 examined whether non-mirror imitation would be the naturally selected mode of imitation under some situations. Findings from all experiments demonstrated marked differences between mirror and non-mirror modes of imitation. The implications of these findings may raise challenges for theories and models of mirror neurons.

1. Introduction

The last decade has witnessed a rapid proliferation of research on the topic of human imitation, following landmark neurophysiological studies that demonstrated in monkeys the existence of specialized 'mirror neurons' that respond to both action observation and execution (Pellegrino et al., 1992; Rizzolatti et al., 1996). Understanding the principles of imitation seems a crucial step toward learning the precise role of mirror neuron systems in imitative processes. The present study attempts to elucidate the principles that underlie imitation in specular (mirror) and anatomical (non-mirror) response modes. As will be discussed below, virtually no studies have made direct comparisons between these two modes; thus, present theories and models reflect primarily the principles underlying mirror imitation. Following a brief review of the relevant literature, four experiments will be presented that test hypotheses aimed at elucidating critical similarities and differences in mirror and non-mirror modes of imitation. The findings are then discussed in terms of possible challenges for mirror neuron accounts.

Before the discovery of mirror neurons, experimental studies on humans focused primarily on the development of imitation in infants (Meltzoff and Moore, 1977; Schofield, 1976; Wagner and Cirillo, 1968). One of the initial studies by Meltzoff and Moore (1977) reported that very young infants are much more likely to produce a particular gesture (e.g., a tongue protrusion) if that same gesture was just produced by the experimenter, than if a completely different gesture was previously shown. The theory they proposed to account for

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these findings is that humans have an inborn ability to match visually perceived input of movement with proprioceptive (but not necessarily seen) sensations of the same movement in one's self. More recent electrophysiological and neuroimaging studies have provided indirect evidence of an analogue mirror neuron system in humans that includes a network of brain areas in occipital, temporal, and parietal visual areas in addition to rostral regions of the inferior parietal lobe and part of Broca's area (Grafton et al., 1996; Decety et al., 2002). Notably, the initial work in monkeys suggested that mirror neurons were selective for goal-directed transitive actions. Thus, although the monkeys were able to emulate the goal of actions performed on real or unseen (virtual) objects, they did not necessarily imitate by identical means (Byrne, 2002; Rizzolatti et al., 2002). Contrary to studies on monkeys, the human mirror system appears to code not only the goals of actions but also the means for achieving those actions.

Support for the coding of goals in human imitation dates back to the classic studies by Head. Head (1920) examined imitation of hand movements made to a point in space or an object such as a body part (e.g., grasping the ear) or an object external to the body (e.g., reaching to a colored dot). In these studies, young children (the precise age varying somewhat across studies) more often than older children or adults, tended to produce ipsilateral hand movements to reach an object when imitating what was presented by a model as a contralateral (crossed) movement of the other hand to that same object (Schofield, 1976; Kephart, 1971; Wagner and Cirillo, 1968; Bekkering et al., 2000). More recent studies (Bekkering et al., 2000) employed a modified version of Head's task (to include bimanual responses), and also incorporated variants of object goal manipulations that were initially introduced by Wagner and Cirillo (1968). Specifically, Bekkering et al. attempted to manipulate the saliency of different goals to address the assumption that goals guide the current action plans. In all experiments, Bekkering et al. encouraged use of the mirror (specular) mode by telling children to act as though they are looking in a mirror, given young children tend to naturally imitate in a mirror mode (in contrast to a non-mirror, anatomical mode). Their studies found that error rate was highest when contralateral imitative movements were required (e.g., the correct imitation response would be to move the hand or hands across the midline to touch the ear or ears on the opposite side of the body). On these trials, rather than producing contralateral movements, participants tended to produce ipsilateral movements of the wrong hand(s) to the correct target ear(s). In contrast, imitation of ipsilateral movements tended to be correct on the majority of trials.

In another experiment (Bekkering, et al., Experiment 3), the researchers used as target objects, either two dots or two spatial locations on a table. According to the researchers' logic, the dots would now serve as target objects and therefore would produce behavior similar to that found when the ears were used as target objects. With some exceptions, this prediction was supported, with the dot present condition revealing the highest error in contralateral trials where participants again erred by producing ipsilateral movements. However, nearly 10 percent of ipsilateral trials produced errors of contralateral movements (compared to less than half that amount in Experiment 1), and these ipsilateral errors are difficult to account for. The researchers claimed that these findings support their hypothesis that when the goal hierarchy is altered by eliminating the dominant goal of the target object (the ears in Experiment 1 and the dots in Experiment 3), the hand choice becomes the dominant goal, supporting a hierarchy of goals. Perhaps it is also worth considering that both the ears and pairs of dots constitute nearly bilaterally identical and visually symmetrical objects (with respect to a reference midline). Thus, it is possible that experiments using some form of bilateral symmetry will demonstrate important principles of imitation that cannot be discerned solely on the basis of tasks employing single objects (e.g., point to your nose) or locations in space. As we will demonstrate in the present study, the use of bilateral targets and choice of effectors making up a bilateral system (left versus right hands) reveal some important differences between the mirror mode (which has been tested extensively) and the non-mirror mode, which has received relatively little empirical investigation so far. As we will show, although goal-directed performance generally occurs under the mirror mode of imitation, this is not necessarily the case for the non-mirror mode (to be discussed below). Moreover, the use of stimulus information (such as dots on either the target locations or the hands) can significantly alter the properties of responding.

Koski et al. (2003) recently used the term anatomical to refer to a non-mirror mode of responding in which a participant imitates a model by moving the anatomically corresponding hand. Consider a task in which a model (experimenter) places her left and right hands, respectively, on left and right home locations, and then moves one hand from its home location to a target located either on a left or right position some distance in front of her body. The participant's task is to imitate the model. Note that there are two modes of imitation that can be used. One is a mirror mode (specular) in which the performer (participant) mimics the model as though looking in a mirror, producing a right hand movement when the model moves her left hand, and a left hand movement when the model moves her right hand. Using the mirror mode, the target choice also is based on a left hand (model) versus right hand (performer) match, and vice versa for the other hand. In contrast, in the non-mirror (anatomical) mode, the performer mimics the model by using the same (anatomically-matched) hand. Interestingly, aside from preliminary comparisons of response mode from one neuroimaging study (Koski et al., 2003) and a very recent laboratory study (Bertenthal et al., 2006, which was brought to our attention during the final review stages of the present paper), the non-mirror mode of imitation and its underlying principles have rarely been investigated. Note too that the two studies that used the non-mirror mode employed finger imitation of one hand. None to our knowledge has employed the use of bilateral choices (left versus right hand choice of movement), to directly compare mirror and non-mirror modes. In our view, without such studies, it is not possible to assess the generality of existing theories and models of imitation. Nor is it possible to evaluate whether the mirror system in humans operates in a similar manner across different imitative tasks. Some current theories of imitation can be considered.

Ideomotor theory, which is based on the notion of ideomotor compatibility as defined by Greenwald (1970), was