CHAPTER 12

Culture in the mind's mirror: how anthropology and neuroscience can inform a model of the neural substrate for cultural imitative learning

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Abstract: Cultural neuroscience, the study of how cultural experience shapes the brain, is an emerging subdiscipline in the neurosciences. Yet, a foundational question to the study of culture and the brain remains neglected by neuroscientific inquiry: "How does cultural information get into the brain in the first place?" Fortunately, the tools needed to explore the neural architecture of cultural learning — anthropological theories and cognitive neuroscience methodologies — already exist; they are merely separated by disciplinary boundaries. Here we review anthropological theories of cultural learning derived from fieldwork and modeling; since cultural learning theory suggests that sophisticated imitation abilities are at the core of human cultural learning, we focus our review on cultural imitative learning. Accordingly we proceed to discuss the neural underpinnings of imitation and other mechanisms important for cultural learning: learning biases, mental state attribution, and reinforcement learning. Using cultural neuroscience theory and cognitive neuroscience research as our guides, we then propose a preliminary model of the neural architecture of cultural learning. Finally, we discuss future studies needed to test this model and fully explore and explain the neural underpinnings of cultural imitative learning.

Keywords: cultural learning; imitative learning; imitation; neuroimaging; mirror neuron system; cultural neuroscience

Introduction

The emerging subfield of cultural neuroscience is based on the concept that cultural experience shapes the human brain, an idea that is increasingly accepted and studied in neuroscience. Yet a more basic question remains unaddressed in the realm of neuroscience: "How did the cultural information get into the brain in the first place?" In this paper we review literature from both anthropology and cognitive neuroscience that may help to elucidate the neural architecture of enculturation.

Before we can design effective studies to investigate how differential cultural experience shapes the human brain, we must have a better

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understanding of the neurocognitive mechanisms of cultural learning. Fortunately, the conceptual and methodological tools needed to conduct effective neuroscientific investigations of cultural learning already exist; anthropology provides a number of complementary theories of cultural learning, while cognitive neuroscience provides the methods and technologies needed to discover the neural architecture that likely underlies cultural learning. Boundaries between these disciplines, however, have until recently prevented their union.

Anthropological theories of cultural learning are based on fieldwork, computational modeling, and laboratory experiments. These theories converge on several cognitive mechanisms suggested to be fundamental to human cultural learning. The prevailing view is that the core of human cultural learning is sophisticated imitative learning (Higgs, 2000; Hurley and Chater, 2005; Kannetzky, 2007; Meltzoff and Prinz, 2002; Sommerville and Decety, 2006; Tomasello et al., 1993b) which is augmented by forms of learning biases (Henrich and McElreath, 2003), mental state attribution (Tomasello et al., 1993a), and reinforcement learning (Castro and Toro, 2004).

Fortunately, cognitive neuroscience studies have already provided us a great deal of knowledge about the neural architecture of imitation, learning biases, mental state attribution, and reinforcement learning in vivo through the use of neuroimaging techniques such as functional magnetic resonance imaging (fMRI) and electroencephalography (EEG). Thus, by using anthropological cultural learning theory to guide future neuroimaging investigations of imitation, we can better understand the neurocognitive architecture of cultural learning. This can, in turn, inform our study of how differing cultural experience shapes other neurocognitive systems and of the neurocognitive machinery of cultural learning itself.

This review is organized into three sections. The first section treats theoretical and behavioral accounts of cultural learning, with a focus on imitative learning. The second section describes neural systems that may underlie the cognitive components of cultural imitative learning. In the third section, we propose a preliminary model of the neural architecture of cultural imitative learning and suggest future studies needed to test this model.

Section I: cultural learning and imitation — theory and behavior

Cultural learning

In the following discussion of cultural learning theory we will briefly define cultural learning and highlight aspects of human cultural learning that differ from the cultural capacities of other animals. We utilize this comparative perspective to focus our discussion of cultural learning on aspects of human cognition that may be most informative for elucidating the neural underpinnings of the sophistication of human cultural capacities.

The first step in discussing cultural learning is defining culture itself. Bates and Plog (1990, p. 7) define culture as "the system of shared beliefs, values, customs, behaviours, and artifacts that the members of society use to cope with their world and with one another, and that are transmitted from generation to generation through learning". This definition highlights a critical point: culture is not merely the sum of cultural products: beliefs, behaviors, and artifacts; instead culture is created through the transmission and modification of these products within and between generations: cultural learning. Thus, by studying cultural learning and its neural basis, we will not only be studying the way in which culture is transmitted, we will also be studying a critical component of culture itself.

Tomasello et al. (1993a) describe cultural learning as a form of social learning in which perspective-taking plays a critical role in both the transmission of information and the resulting cognitive product. In other words, during cultural learning, information in addition to modeled behaviors, such as the inferred intentions and emotional states of the model, are encoded and retained along with the behavior in order to give that behavior contextual meaning. Tomasello et al. (1993a) propose that cultural learning includes imitative learning, instructed learning,

and collaborative learning — these types of learning emerge in successive stages of development. Cultural learning is distinguished from other forms of learning by its social nature and the niche it occupies within the learning environment. Modeling work by McElreath (2004) demonstrates that cultural learning is favored when individual learning is costly and inaccurate. Boyd and Richerson (1985) suggest that human social learning abilities were evolutionarily favored as a strategy for learning information relevant to rapidly changing environmental conditions.

Culture and cultural transmission are most fully developed in humans; however, great apes, especially chimpanzees, also have basic cultural capacities. A number of studies in both captive and wild chimpanzees have documented rich behavioral traditions specific to particular groups (Boesch, 2003; McGrew, 1992; Wrangham et al., 1994). Additionally, several recent experimental studies in groups of captive chimpanzees have demonstrated faithful transmission of food retrieval techniques (Whiten et al., 2007), as well as arbitrary actions (Bonnie et al., 2007) taught to a few group members throughout the group and, in the case of Whiten et al. (2007), between groups that had only visual contact. These experiments demonstrate with a new level of empirical certainty that chimpanzee groups can not only maintain unique cultural repertoires, but also that — as in humans — a prominent means of chimpanzee cultural transmission is imitative learning.

The notion of chimpanzee culture and chimpanzee imitative cultural learning raises the question, "What explains the formidable differences between human and chimpanzee culture?" The answers may lie in the accuracy and complexity of human imitation abilities, compared to those of chimpanzees, and in the other cognitive mechanisms that augment human imitation, such as learning biases, mental state attribution, and reinforcement learning. The unique combination, and degree of sophistication, of these cognitive abilities enable humans to encode inferred intentions, emotions, and reward values along with learned behaviors. This contextual information allows individuals to modify culturally learned behaviors. In turn, the continual modification of culturally learned behavior leads to the summing of cognitive resources within and between generations and the creation of distinct and rich cultures that are constantly evolving (Henrich and McElreath, 2003; Tomasello, 1999; Tomasello et al., 1993a). We will structure our discussion of cultural learning around the suite of cognitive mechanisms that distinguish human from nonhuman cultural capacities as the neural underpinnings of these abilities may be most informative in revealing the neural architecture of human cultural learning.

Imitation and imitative learning

Imitation learning is at the core of cultural learning; therefore, cultural imitative learning will be the focus of our review. In the following section we will provide a broad overview of imitative learning including its definition, theoretical accounts of the mechanisms of imitation, and behavioral accounts of imitation learning at different stages of development.

Although the meaning of the word "imitation" seems intuitive, the precise definition of imitation and imitative learning has been the subject of much debate (Chalmeau and Gallo, 1993). The imitation controversy is due in part to the question of whether there are any uniquely human abilities (Miklósi, 1999). Additionally, there are a number of mimetic but nonimitative processes, such as contagion and observational conditioning, that can result in the appearance or behavior of one individual resembling that of another (Zentall, 2006). Two mimetic processes closely related to but distinct from imitation are stimulus enhancement, in which an individual's attention is drawn toward a particular *object*, and goal emulation, where an individual learns the *goal* of an action but may accomplish that goal by other means (Whiten, 2000). True imitation is distinguished by the faithful copying of the *means* by which a goal is achieved (Whiten, 2000; Zentall, 2006). Tomasello et al. (1993a) argues that true imitation requires recognizing the intentional structure of the modeled behavior. Intention recognition is especially important during a

special type of imitation termed opaque imitation (Piaget, 1962) [also called blind or cross-modal imitation (Moore, 2004)], which involves imitation with a body part to which the imitator does not have direct visual access, such as the face.

There is also some debate over the neurocognitive mechanism of imitation. Iacoboni (2009) states that the two psychological theories of imitation mechanisms that best fit neurophysiological data are the ideomotor framework and the associated sequence-learning model. The ideomotor framework postulates that imitation is achieved through a shared neural representation system for observation and execution (Prinz, 2005). In the associative sequence-learning model, rather than a single neural substrate linking observation and execution, experience-based Hebbian learning (the strengthening of neural connections due to repeated coincident neural firing) links separate neural systems for observation and execution (Heyes, 2005).

In addition to theoretical accounts of the mechanisms of imitative behavior, extensive behavioral studies of imitation have been conducted from the neonatal period through adulthood. There is considerable evidence that the basic neurocognitive machinery of imitation is hardwired. For example, Meltzoff and Moore (1977, 1983, 1989) found imitation of facial and manual gestures such as protruding the tongue in infants only hours old; this finding has since been replicated in 13 independent laboratories (Meltzoff and Decety, 2003). In addition to innate imitation mechanisms, which results in the basic forms of imitation seen in infants, elements of the human socio-cultural environment, such as joint attention and turn-taking, promote the rapid development of more sophisticated imitative abilities (Kumashiro et al., 2003). The imitation-promoting effects of the human socio-cultural environment are strikingly illustrated by Tomasello et al.'s (1993b) finding that children and enculturated chimpanzees perform similarly on an imitation task and outperform non-enculturated chimpanzees.

Human imitative abilities reach a high level very early in life. Infants as young as 12 months are sensitive to the rationality of modeled actions (Schwier et al., 2006), and at 18 months, they have been found to imitate object-directed real and pretend actions (Rakoczy et al., 2005), as well as imitate the goal of incomplete actions (Meltzoff, 1995). Because of the early emergence of imitative abilities, imitation makes up a large portion of social interaction during early development (Masur, 2006) and is the likely means by which many important types of cultural information, such as language and behavioral norms, are learned (Arbib, 2005).

An ongoing debate is whether the motor system is engaged during action observation, as suggested by the ideomotor framework, or whether connections between observation and action only happen during reenactment of the behavior (Iacoboni, 2009; Vogt and Thomaschke, 2007). A number of studies suggest that, in the domains of imitative learning of sequences, timing, and task dynamics, pure observation has an equivalent effect to motor practice on later behavioral performance. However, for configural postures and inter-limb coordination the data are less clear and motor practice may result in superior behavioral performance (for a review see Vogt and Thomaschke, 2007). It is important to note that even in cases when observational and motor practice appear equivalent, nether strategy results in a carbon copy of the imitated action. Rather, observational practice results in elements of the imitator's own behavioral repertoire being activated and built upon (Greer et al., 2006; Iacoboni, 2009; Vogt and Thomaschke, 2007).

Reinforcement is another critical element of imitation learning as it guides both the likelihood and direction of learning. Both internal and external reinforcement of the imitator influence the likelihood and direction of imitative learning (Greer et al., 2006). Reward and punishment of the model (vicarious reinforcement) has also been found to influence imitation (Bandura, 1971). Finally, motivation at the time of observation (e.g., whether the imitator is hungry or sated while observing a food retrieval task) can also affect the probability of later imitation (Dorrance and Zentall, 2001).

Greer et al. (2006) distinguished between performance of modeled behaviors already in the imitator's repertoire and imitative learning

of novel behaviors. In particular, they suggest that learning of novel behaviors and performance of previously learned behaviors can be differentially affected by reinforcement. An imitation learning study by Bandura (1965) illustrates these differential effects of reward on learning and performance. Bandura showed subjects modeled behavior that was either vicariously rewarded or punished. Following behavioral modeling, subjects were directly provided incentives for imitation. These incentives resulted in the production of learned but previously unimitated behaviors, suggesting that vicarious reinforcement influenced the imitation but not the learning of modeled behaviors (Bandura, 1965).

In summary, imitative learning consists of many components including imitation of timing, configural postures, sequences, and reinforcement sensitivity. Action observation likely activates the motor system, which facilitates imitative learning. Sophisticated imitation abilities are clearly key to human cultural learning especially early in life, but they are likely not the whole story. Comparative studies of primate cognition, modeling studies, and human ethnographic work have identified several other cognitive mechanisms that augment our imitative abilities during cultural learning and have likely been instrumental in the dramatic explosion of cultural capacities in *Homo sapiens*. In the following section we will discuss three of these hallmarks of human cultural learning: learning biases, mental state attribution, and flexible reinforcement learning.

Learning biases

Cultural learning is not indiscriminate; rather it is biased toward certain contexts and content, which likely results in the more efficient acquisition of knowledge, beliefs, and practices (Henrich and McElreath, 2003). Context biases result in the information held by certain individuals (model-based bias) or the highest frequency information (frequency-based bias) being favored (Henrich and McElreath, 2003). Henrich and Boyd (1998) argue that the cognitive mechanisms supporting these learning biases were likely shaped by natural selection.

A number of empirical laboratory studies conducted by Bandura and his colleagues (Bandura et al., 1961, 1963) suggest that high model-observer similarity favorably biases social learning. Based on these studies, Bandura proposed his Social Learning Theory (SLT) which describes the conditions governing the occurrence of social learning. SLT emphasizes the importance of model-observer similarity in biasing social learning because, Bandura suggested, model-observer similarity increases the observer's identification with the model making it easier for the observer to relate modeled actions to his or her own (Bandura, 1977). More recent studies in fields ranging from sports psychology (Vescio et al., 2005) to health behaviors (Larsen et al., 2009; Perry et al., 1979) have continued to emphasize the importance of the similarity bias in cultural learning.

Both empirical and theoretical studies have suggested that another important model-based bias exists for high prestige individuals (Henrich and Gil-White, 2001). More broadly, Coussi-Korbel and Fragaszy (1995) stress the general importance of social dynamics such as egalitarianism and social dominance hierarchies in shaping model-biased cultural transmission. Laboratory experiments using the closed group method, in which information is circulated through a fixed group of individuals, have also found similarity and prestige biases and revealed an additional model-based biases for learning from successful individuals (Mesoudi and Whiten, 2008).

Content biases result in certain types of information being learned preferentially. Laboratory experiments using the transmission chain method, in which information transfer fidelity is measured among a group of people, have substantiated theoretical accounts of content biases. These studies have shown that counterintuitive information, gender stereotypes, social situations, and situations involving hierarchical relationships transmit with high fidelity (Mesoudi and Whiten, 2008).

Mental state attribution (a.k.a. Theory of mind)

Many cultural learning theorists argue that a unique human adaptation for culture is our sophisticated mental state attribution abilities

(Boyd, 2008; Tomasello, 1999; Tomasello et al., 1993a). During mental state attribution individuals develop ideas about the mental states of others and distinguish these mental states from their own. The ability to infer and subsequently encode the mental states of behavioral models during learning allows humans to modify cultural objects with their original purpose in mind. Iterative modification of cultural objects in turn creates a "ratchet effect" which allows for the summing of cognitive resources within and between generations (Tomasello, 1999).

Basic mental state attribution abilities emerge early in life and rapidly develop as the abilities for coordinated perspective-taking (intersubjectivity) and integrated perspective-taking (reflective intersubjectivity) come online (Tomasello et al., 1993a). Around the first birthday, human infants already recognize that other individuals have intentions as evidenced by their gaze-following and attention-sharing abilities (Tomasello et al., 1993a). Gergely et al. (2002) convincingly illustrate the intention understanding of 14-month olds by showing that they will only imitate a novel behavioral strategy when that strategy appears to be the most rational means to achieve a goal. By around 4 years of age, children recognize others as mental agents with thoughts different from their own (Perner et al., 1987). The ability of children to distinguish between their own thoughts and the thoughts of others is often explored using false belief tasks in which children have to predict the behavior of another individual based on that individual's false belief (Frith and Frith, 2003). The final developmental milestone of mental state attribution abilities occurs by 5 or 6 years of age when children are able to think about others reflecting on the beliefs of third parties (Sullivan, 1994). Mental state attribution abilities continue to improve into adulthood, with increasing social experience, and continue to constitute key elements of cultural learning.

Reward

Reward is another critical component of many types of learning including imitative learning, as described above, and cultural learning in general.

Schultz (2006) defines the purpose of reward to be threefold: (1) induction of learning, (2) approach behavior for the reward itself, and (3) positive feelings associated with the reward and rewarded behavior. Rewards can be primary reinforcers (unlearned and culturally invariant), such as food and pleasant smells or secondary reinforcers (classically or instrumentally conditioned and culturally specific), such as money and attractive cars (Walter et al., 2005). Social stimuli such as smiling faces and cooperative behaviors are also powerful primary reinforcers (Walter et al., 2005).

Tomasello et al. (2005) suggest that the social situations inherent in cultural learning are powerful primary reinforcers and that the intrinsic reward value of cultural learning is a keystone of human cultural evolution. This means that the first time an individual engages in cultural learning, the experience is rewarding and thus the likelihood of learning and future learning is increased. While cultural learning in general may be rewarding, Castro and Toro (2004) suggest that the preferential learning of particular cultural information is dependent on the development of parental ability to approve or disapprove of offspring behavior. The child's sensitivity to both reward and punishment allows for preferential learning of correct, rewarded, behaviors over incorrect, punished ones. Castro and Toro (2004) suggest that this reward- and punishment-guided learning is a necessary addition to mental state attribution abilities in order for the ratchet effect to occur.

These three characteristics of human culture: learning biases, mental state attribution, and flexible reinforcement learning, when combined with humans' sophisticated imitative learning abilities, provide promising starting places for investigations into the neural architecture of human cultural transmission. The neural systems that subserve these functions are likely to play important roles in human cultural transmission.

Section II: candidate neural mechanisms of imitative cultural learning

A number of cognitive neuroscience studies have already identified neural systems underlying some

of the key components of cultural imitative learning described above. In this section we review primate and specifically human cognitive neuroscience studies that investigate neural mechanisms associated with imitation and imitative learning, and model-based learning biases. We also briefly discuss how these neural mechanisms may implement mental state attribution and how they can potentially interact with neural systems processing reward.

The human mirror system, imitation, and imitative learning

Imitation learning is at the core of cultural learning and imitation learning processes have been well characterized behaviorally. Major cognitive neuroscience discoveries over the last decade have also given us a great deal of information about the neural mechanisms of imitation behavior. Recall that the ideomotor framework of imitation suggests that there is a common neural substrate for perception and action (Prinz, 2005). The mirror neuron system (MNS), first discovered in macaque monkeys using depth electrode recordings, has these perception-action coupling properties (Gallese et al., 1996). Neurons in the monkey's premotor cortex (area F5) (Gallese et al., 1996) and inferior parietal lobe (area PF) (Fogassi et al., 2005) fire both when the monkey performs a goal-directed action and when it sees a human or conspecific perform the same or a related action (Gallese et al., 1996).

Convergent evidence from a variety of imaging modalities, including fMRI, EEG, positron emission tomography (PET), transcranial magnetic stimulation (TMS), and most recently, single unit recordings (Mukamel et al., 2007) has suggested the presence of an MNS in humans (for a review see Iacoboni and Mazziotta, 2007). Putative human mirror neuron areas are present in the frontal lobe [posterior inferior frontal gyrus (piFG) and ventral premotor cortex (the human homologue of monkey F5)], and in the parietal lobe [rostral inferior parietal lobule (riPL)] (Rizzolatti and Craighero, 2004). Human studies have demonstrated brain responses compatible with mirror neuron activity while viewing and

imitating object-oriented hand and foot actions (Buccino et al., 2001, 2004b), and hearing the sounds associated with these actions (Gazzola et al., 2006; Kaplan and Iacoboni, 2007). Additionally, the human MNS is also activated by viewing and imitating intransitive actions such as gestures (Iacoboni et al., 1999; Koski et al., 2003), mouth actions (Buccino et al., 2001), and facial expressions (Carr et al., 2003; Pfeifer et al., 2008).

Because mirror neurons provide a neural mechanism for pairing action observation and action execution, it has been hypothesized that the MNS is a key component of the neural substrate underlying imitation and imitative learning (Iacoboni, 2005; Iacoboni et al., 1999; Rizzolatti and Craighero, 2004). Iacoboni (2005) suggests, based on human neuroimaging and TMS data, that the core neural circuitry involved in human imitation consists of frontal and parietal MNS components as well as the superior temporal sulcus (STS). In this model, the STS gives rise to a higher-order visual description of the observed action, which is then fed into the MNS where the action's goal (piFG) and the motor plan to achieve the action (riPL) are coded. Finally, the predicted motor plan is fed back into the STS, where a comparison is made between the visual description of the action and the predicted sensory consequences of the imitative motor plan. It is at this point in the action-observation neural circuitry — when the observed and simulated motor plans are compared — that imitation accuracy and model-based cultural learning biases might be especially important. Presumably, the motor plans of self and other will be more similar in those cases where imitation accuracy and model-observer physical similarity is higher, though future studies will be needed to empirically test this hypothesis.

Iacoboni (2005) also proposes a model of the circuitry involved in imitative learning in which the aforementioned core circuitry communicates with the dorsolateral prefrontal cortex and motor preparation areas including the mesial frontal, dorsal premotor, and superior parietal regions. Though few neuroimaging studies of imitative learning have been conducted, the extant studies support the involvement of the MNS in imitation learning in general and support the imitative

learning model proposed by Iacoboni (2005) in particular. In an fMRI study of observational learning of guitar chords by non-guitarists, Buccino et al. (2004b) found that the MNS and the above motor preparation areas were active. In a subsequent fMRI study, Frey and Gerry (2006) found more MNS activity when subjects observed complex hand action sequences with the intention to learn them and reproduce them later than when the same actions were viewed passively. Thus, the MNS is likely a key player in imitative learning of novel actions, a critical component of cultural learning.

The MNS and experience — could culture shape the MNS?

In addition to connecting executed and observed action, several studies discussed below indicate that activity of the MNS and interconnected regions is influenced by motor practice both in the short term (hours) and in the long term (years). Thus, the MNS may not only play a role in the acquisition of culturally mediated behaviors, but the MNS itself may be shaped by the presence of culturally mediated behaviors in one's motor repertoire.

Behavioral studies have demonstrated that action execution can be affected by previous experience observing related actions. For instance, Gillmeister et al. (2008) found that action imitation was facilitated by previous observation of task-irrelevant actions with the same effector; this priming effect was decreased by incongruent practice (observe foot and imitate with hand). Research using TMS has demonstrated that the behavioral effects of observational practice described above are directly mediated by the motor system. Stefan et al. (2008) had subjects practice thumb movements in the opposite direction of their baseline TMS-evoked thumb movements. The authors found that simultaneous movement execution and observation altered the direction of TMS-evoked thumb movements more than physical practice alone. Most intriguingly, Catmur et al. (2007) used an incongruent training strategy similar to Gillmeister et al. (2008) to create a "counter mirror" effect. After incongruent

practice, observing the movements of one finger increased motor evoked potentials (MEPs) resulting from TMS in the finger paired during practice, rather than the same finger.

fMRI studies demonstrate that the behavioral and TMS-evoked practice effects described above are likely related to changes in MNS activity. Vogt et al. (2007) found increased activity in a number of brain regions (including putative mirror neuron areas) during observation of practiced versus nonpracticed guitar chords. On a longer timescale, Cross et al. (2006) demonstrate practice-related increases in MNS activity over the course of five fMRI scans at weekly intervals while subjects learned a novel dance sequence. Finally, Calvo-Merino et al. (2005) demonstrate that practice-related changes in MNS activity extend to real-world expertise built over many years. The authors find greater MNS activity when experienced dancers observe their own style of dance rather than a comparable but unfamiliar style. Collectively, these data suggest that daily experiences and those that extend over a lifetime, such as the practices of one's culture, have the potential to influence MNS function.

The MNS and model-based biases

In addition to playing a key role in human imitation, the MNS may represent the neural substrate of the similarity cultural learning bias, at least for the visuomotor aspects of similarity. Several studies have demonstrated that the MNS responds more intensely to the observation of conspecifics. For example, Buccino et al. (2004a) found that activity in the putative human MNS is modulated by model-observer similarity for the observation of biting actions of humans (greatest activity), monkeys (intermediate activity), and dogs (least activity). These species-dependent differences in MNS responses were even more pronounced for communicative actions (no measurable response for the dog barking action). This finding suggests that differences in physical appearance alone cannot explain these differential responses.

The MNS is also preferentially responsive to human biological motion. For example, Press et al.

(2006) compared subjects simultaneously observing and imitating human hands, human hands disguised to look like robotic hands, and actual robotic hands. The authors found that human hand observation, regardless of the hand's appearance, had a greater facilitatory effect on action performance than did robotic hand observation, even when the robotic and human hand were matched on size, color, and brightness (Press et al., 2006). Thus, human-like motion preferentially activates the MNS even when the effector is robotic. Gazzola et al. (2007) found MNS activity while subjects observed a robotic hand performing in a human-like fashion (by performing a variety of actions); however, neither Gazzola et al. (2007) nor Tai et al. (2004) found MNS activity when subjects viewed a robotic hand that was performing the same action repeatedly, which is less typical of human behavior. Intriguingly, Press et al. (2007) found that practice simultaneously observing and imitating a robotic hand abolished the human-biased action facilitation found pre-training, suggesting that human-biased activity in the MNS is, at least in part, the result of experience. Biological-motion related activity in the MNS extends to motion of the entire body. Ulloa and Pineda (2007) and Saygin et al. (2004) both found that the MNS responds to human actions represented by point-light walkers (moving groups of white dots representing the joints of a human) but not to the same stimuli when other dots were added to obscure motion the human form.

Current data suggest that the human MNS is also sensitive to more subtle aspects of model-observer physical similarity, such as ethnicity and gender, which may be more relevant cultural learning. For example, Molnar-Szakacs et al. (2007) found greater corticospinal excitability (a proxy for MNS activity, measured with TMS) in European American observers while they observed an ethnic in-group member versus an ethnic out-group member performing hand gestures, suggesting a positive relationship between MNS activity and model-observer similarity. In contrast, two other studies found more activity in the MNS when individuals viewed ethnic (Désy and Théoret, 2007) or gender (Cheng et al., 2006) out-group members, suggesting a

negative relationship between MNS activity and model-observer similarity. Taken together, these data suggest that the MNS is sensitive to the visual similarity between model and observer at the level of species-typical appearance and biological motion, and in more culturally relevant domains such as gender and ethnicity. However, because of the variety of conclusions reached by these studies, and the potential role of experience in shaping MNS activity, the relationship between the degree of model-observer similarity and MNS activity remains unclear.

Neural mechanisms for mental state attribution

The cultural learning theories previously discussed (Tomasello et al., 1993a, 1999; Henrich and McElreath, 2003) propose that the ability to think about the intentions and mental states of others is critical for understanding the goal of observed actions. Intention understanding is thus vital for efficient and flexible imitative learning. After the discovery of mirror neurons, Gallese and Goldman (1998) proposed that the properties of these cells supported a simulation model of mental state attribution (simulation theory). Simulation theory assumes that we understand the intentions of others via a process of simulation, as if we were the other person. During simulation, the observation of another individual activates a similar suite of neural areas to when the observer performed the behavior himself "creat[ing] in the observer a state that resembles the target" (Gallese and Goldman, 1998). Indeed, subsequent studies in both monkeys (Fogassi et al., 2005) and humans (Iacoboni et al., 2005) suggested that mirror neurons are able to code the intention of an action, not simply the action itself. In Iacoboni et al. (2005) subjects were shown a hand picking up a cup, in one of two different contexts, a table set for tea, or the same table at the end of the meal. Despite the hand action being identical in both conditions, putative MNS regions demonstrated different levels of activity when the actions were viewed in the two different contexts. Thus, mirror neurons may implement not only imitation but also the function of mental state attribution in cultural learning.

Another model of mental state attribution assumes that we understand others' mental states by using an inferential process (Gopnik and Schulz, 2004). We observe the behavior of other people and then relate it to a set of folk psychology laws. By doing so, we can make theories about the mental states of other people as scientists make theories about the natural phenomena they study. From a functional standpoint, this inferential route to intention understanding does not map well onto the properties of mirror neurons. Indeed, a set of tasks typically used to study mental state attribution (the false belief task, the comparison of social interaction story listening to physical interaction story listening, and the comparison of viewing moving geometric shapes that depict social interactions to viewing randomly moving geometric shapes), consistently activate a set of neural regions that are not typically considered part of MNS: the dorsomedial prefrontal cortex (dmPFC), the posterior STS (pSTS), and the temporal pole (see Gallagher and Frith, 2003; Frith and Frith, 2003 for reviews). Activity in the pSTS area, however, is largely indistinguishable from the STS activations observed in imitation tasks (Iacoboni, 2005).

A number of individuals have proposed that the MNS and the above suite of brain areas (dmPFC, pSTS, and temporal poles) represent complementary neural systems underlying mental state attribution (Keysers and Gazzola, 2006, 2007; Pineda and Hecht, 2008; Uddin et al., 2007). For example, Keysers and Gazzola (2007) suggest the MNS provides a "pre-reflective" description of intention based on the visual description of a model's actions while cortical midline structures such as the dmFPC provide a "reflective" description of intentions based social introspection. Keysers and Gazzola (2007) suggest the inferential route to intention understanding may be especially important under circumstances when model-observer similarity is low or modeled behaviors were not previously present in the observer's repertoire, as is commonly the case during cultural learning. However, the interpretation of the activity in dmPFC in mentalizing tasks is rather difficult, due to the peculiar activation profile of this brain region (i.e., cognitive tasks result in signal decreases, rather than the typical signal increases, as compared to baseline activity; Iacoboni et al., 2004). Thus, it is at present unclear whether there is a distinct network for mental state attribution that relies on inferential mechanisms and that is anatomically located outside the MNS.

The reward system, sharing intentions, and imitation accuracy

The neural mechanisms of reward learning have been well mapped in animals ranging in complexity from *Aplysia* slugs (Hawkins et al., 1983) to rats (for a review see Schultz, 2006). Neural systems related to reward have been investigated in humans through the use of neuroimaging (for a review see O'Doherty, 2004). As is the case for the MNS, the current belief is that there is a putative reward system in the human brain encompassing brain systems homologues to the neural systems processing reward in animals. Three neural structures that are believed important in human reward processing are the ventral striatum, the nucleus accumbens, and the orbitofrontal cortex (OfC) (Hollerman et al., 2000; McClure et al., 2004; O'Doherty, 2004; Walter et al., 2005).

Reinforcement learning theory suggests reward is used to bias action selection and accordingly reward circuitry is often active during motor task performance (McClure et al., 2004). Significantly for the study of cultural learning, components of the reward network are also active during imitation. Activity in the lateral OfC was one of the main effects observed in the Chaminade et al. (2002) study of deferred imitation of Lego® assembly and a study by Williams et al. (2007) involving finger movement imitation. The lateral OfC activity in both of these studies was interpreted to reflect the uncertainty involved in producing the appropriate action as well as error monitoring between executed and observed actions, both functions suggested by Elliott, Dolan, and Frith (2000) to be reward-related. Lee et al. (2006) also found OfC activity during facial mimicry, perhaps related to the intrinsic reward value of viewing human faces (Walter et al., 2005).

In addition to the previous studies of generalized imitation, OfC activity has also been reported in studies comparing imitation or observation of actions with differing levels of familiarity to the subject. Jackson et al. (2006) report more OfC activity when subjects imitate models from a first person perspective than from a third person perspective. The authors attribute this activity to the increased similarity between imitation and observation in the first person perspective. Similarly, Calvo-Merino et al. (2005) find more OfC activity when dancers watch their own compared to an unfamiliar style. Elliott et al. (2000) suggest that the selection of stimuli on the basis of familiarity is related to the reward-related value of these stimuli. A more parsimonious explanation of these findings may simply invoke the role of OfC in inhibitory control (Elliott et al., 2000; Roberts and Wallis, 2000). For instance, dancers may have a stronger tendency to imitate, and therefore stronger need for motor inhibition, while watching the style of dance they typically practice. Future studies will have to disentangle the alternative hypotheses of reward processing and inhibitory control regarding the involvement of OfC in imitation.

Reward is also a central component of robotic models of human imitation, further highlighting the importance of reward in imitative learning. Mataric (1994) incorporate both vicarious reward and direct reward for conformity into their imitative learning algorithms used to drive social learning robots. Similarly, Atkeson and Schaal (1997) develop a robotic control strategy for single trial learning in which a reward function is learned from a demonstration and the behavior itself is acquired through trial and error learning.

Taken together, the neuroimaging studies discussed in this section highlight neural systems that play important roles in the cognitive mechanisms suggested by both theoretical and empirical work to be hallmarks of human cultural learning.

Section III: a model of the neural architecture of cultural imitative learning and future directions

We propose a tentative neural architecture of cultural imitative learning that has the MNS and associated imitative learning areas as its core. In our model, the reward network may support the motivation to imitate and reinforcement sensitivity important for cultural learning. MNS regions likely support mental state attribution through motor simulation (Koski et al., 2003). Under certain circumstances, medial prefrontal areas, typically considered ''mentalizing'' areas in the imaging literature (Frith and Frith, 2003; Gallagher and Frith, 2003), may also contribute to mental state attribution through an inferential route. Though tentative, the proposed cultural imitative learning circuitry generates testable hypotheses that future studies of cultural imitative learning can explore.

Future neuroscientific studies of imitative learning embedded in ecologically valid cultural contexts are needed to truly elucidate how the previously described neural systems (including those sub serving mental state attribution and reward processes) may function during real-world cultural imitative learning. In the remaining sections, we will discuss some future studies that will be required to further characterize the neural architecture of cultural imitative learning.

Future directions: the human mirror system and imitation

Though many neuroimaging studies of action execution, observation, and imitation have been conducted, relatively few studies of imitative learning of novel actions or action combinations exist to date (Buccino et al., 2004b; Frey and Gerry, 2006). Additionally, stimuli in existing imitation studies typically consist of photographs or videos of an isolated effector of a single individual performing simple movements against a blank backdrop. Though this type of reduction makes interpretation more straightforward, future studies investigating the role of imitation in cultural learning will need to employ more ecologically valid stimuli. By including the face, in addition to the acting effector, in action stimuli, important social information portrayed by the face can be utilized in action understanding. Facial information may change the way in which the action itself is processed and/or interpreted.

Action stimuli with increased complexity, such as action sequences rather than single actions, and increased social relevance, such as communicative actions directed toward others will more closely approximate the natural conditions in which cultural learning occurs. Finally, embedding imitation paradigms in a social context, such as imitative learning of the communicative gestures will also be useful in engaging neurocognitive mechanisms involved in cultural imitative learning.

Future directions: the MNS and model-based biases

The sensitivity of the MNS to aspects of model-observer similarity, such as ethnicity and gender, suggested by several studies (Cheng et al., 2006; Désy and Théoret, 2007; Molnar-Szakacs et al., 2007), may underlie the well-documented cultural learning biases for self-similar individuals (Bandura, 1977; Henrich and McElreath, 2003; Mesoudi and Whiten, 2008). These studies have examined model-observer similarity only in the context of action observation. No studies to date have addressed model-observer similarity during imitation or imitative learning. Furthermore, whether there is a positive or negative correlation between model-observer similarity and MNS activity in terms of ethnicity and gender remains unclear from present studies.

Other socially salient physical characteristics such as age, socioeconomic status (as reflected in physical appearance), as well as action quality and model-observer familiarity should also be considered in the context of neurobehavioral investigations of cultural learning. A final point concerns the relationship between the physical and nonphysical elements of social characteristics such as gender, ethnicity, and age. In order to determine which aspects of similarity — physical/bottom-up or social/top-down — influence brain activity during imitation, it will be necessary to design studies in which the physical appearance of observed models and social information can be disassociated.

Future directions: the MNS, mental state attributions, and the reward system

It is clear that mental state attribution abilities are of central importance for cultural imitative learning. However, the question of whether mental state attribution is achieved via simulation mechanisms supported by the MNS, "mentalizing" mechanisms supported by neural regions including the dmPFC, or some integration of these two remains unanswered. The use of tasks that differentiate between simulative and inferential mechanisms during imitation will be useful in identifying the neural substrates of mental state attribution during cultural imitative learning.

The human reward system is critical for learning and is some times active during action observation and imitation. Cultural learning theory suggests that reward is important for the motivation to learn imitatively, for sharing intentions, as well as for learning behaviors accurately. A next step in elucidating the role of reward circuitry in human imitative learning will be to investigate the neural basis of imitation and imitative learning of directly and vicariously rewarded actions. Comparison of tasks when motivation to imitate differs, such as virtual food retrieval tasks in hungry and sated subjects as in Dorrance and Zentall (2001), will be useful for determining the role of motivation in the neural basis of cultural imitative learning.

Conclusion

Cultural learning theory suggests that imitation, mental state attribution, and reinforcement learning are key cognitive mechanisms underlying human cultural learning. Cognitive neuroscience studies provide insight into the neural systems associated with these functions. Thus, anthropology and cognitive neuroscience provide the neuroscientific study of cultural learning a head start. However, many studies of imitation learning in cultural contexts that will engage mental state attribution and reinforcement learning will be

needed to fully explore and explain the neural architecture of cultural imitative learning.

Acknowledgments

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