

What imitation tells us about social cognition: a rapprochement between developmental psychology and cognitive neuroscience

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Both developmental and neurophysiological research suggest a common coding between perceived and generated actions. This shared representational network is innately wired in humans. We review psychological evidence concerning the imitative behaviour of newborn human infants. We suggest that the mechanisms involved in infant imitation provide the foundation for understanding that others are 'like me' and underlie the development of theory of mind and empathy for others. We also analyse functional neuroimaging studies that explore the neurophysiological substrate of imitation in adults. We marshal evidence that imitation recruits not only shared neural representations between the self and the other but also cortical regions in the parietal cortex that are crucial for distinguishing between the perspective of self and other. Imitation is doubly revealing: it is used by infants to learn about adults, and by scientists to understand the organization and functioning of the brain.

Keywords: imitation; theory of mind; empathy; parietal cortex; mirror neurons; shared neural representations

1. INTRODUCTION

Our ability to imitate others' actions holds the key to our understanding what it is for others to be like us and for us to be like them. The past two decades of research have significantly expanded our knowledge about imitation at the cognitive and neurological levels. One goal of this article is to discuss striking convergences between the cognitive and neuroscientific findings. A second goal is to make a theoretical proposal. We wish to make a three-step argument:

- (i) imitation is innate in humans;
- (ii) imitation precedes mentalizing and theory of mind (in development and evolution); and
- (iii) behavioural imitation and its neural substrate provide the mechanism by which theory of mind and empathy develop in humans.

Metaphorically, we can say that nature endows humans with the tools to solve the 'other minds' problem by providing newborns with an imitative brain. In ontogeny, infant imitation is the seed and the adult theory of mind is the fruit.¹

We are thus proposing a 'linking argument'. We think there is a large gap between mirror neurons and theory of mind. Monkeys have mirror neurons, but they lack a theory of mind, and they do not imitate. The missing link, we shall argue, is motor imitation. Through imitating

others, the human young come to understand that others not only share behavioural states, but are 'like me' in deeper ways as well. This propels the human young on the developmental trajectory of developing an understanding of other minds.

This linking argument is missing from the literature. One can find excellent reviews about mirror neurons and common perception-action coding from both neuroscientific (Rizzolatti *et al.* 2002; Gallese 2003) and cognitive (Prinz & Hommel 2002) perspectives. One can find theory of mind reviewed from both neuroscientific (Frith & Frith 1999) and cognitive (Astington & Gopnik 1991; Taylor 1996; Wellman & Gelman 1998; Flavell 1999) perspectives. What is missing is a proposal for how a neural mirror system begets theory of mind. In this paper we focus on a missing link—imitation.

2. SIMPLE IMITATION AND ITS NEURAL SUBSTRATE

(a) Evidence from developmental science: innate imitation

At what age can infants imitate facial acts, and how can they do so? Infants can see the adult's face but can not see their own faces. They can feel their own faces move, but have no access to the feelings of movement in the other. If they are young enough they will have never seen their own face. There are no mirrors in the womb. The holy grail for cognitive- and neuro-science theories of imitation is to elucidate the mechanism by which infants connect the felt but unseen movements of the self with the seen but unfelt movements of the other.

Classical theories such as that of Piaget (1962) considered facial imitation a cognitive milestone first passed at

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Figure 1. Photographs of 12–21-day-old infants imitating facial expressions demonstrated by an adult. Imitation is innate in human beings, which allows them to share behavioural states with other 'like me' agents. (From Meltzoff & Moore (1977).)

ca. 1 year. Piaget argued that infants learned to associate self and other through mirror play and tactile exploration of their own and others' faces. Mirrors made the unseen visible, rendering one's own body and that of the other in visual terms. Tactile exploration of faces rendered both self and other in tangible terms.

Over the past 25 years, empirical work from developmental science has forced a revision of the conventional view of imitation, and with it, the theory that perceptual and motor systems are initially independent and uncoordinated in the human newborn (see figure 1).

To eliminate associative learning experiences, Meltzoff & Moore (1983, 1989) tested facial imitation using newborns in a hospital nursery. A large sample of newborns was tested ($n=80$). The oldest infant in these studies was 72 hours old. The youngest was 42 minutes old. The results demonstrated successful facial imitation. This finding of early imitation came as a surprise to developmental psychology, which had long held the idea of independent visual and action spaces. It has now been replicated and extended in more than two dozen studies from 13 independent laboratories (see Meltzoff & Moore (1997) for a review). Evidently, the capacity for facial imitation is part of the innate endowment of human beings.

Several studies further illuminate the imitative capacity. One study showed that 12–21-day-old infants could imitate four different adult gestures: lip protrusion, mouth opening, tongue protrusion and finger movement (Meltzoff & Moore 1977). These results revealed that infants confused neither actions nor body parts. They accurately responded to tongue protrusion with tongue protrusion not lip protrusion (and vice versa) demonstrating that the specific *body part* could be identified. They also accurately responded to lip protrusion versus lip opening, showing that two different *action patterns* could be duplicated using the same body part.

Interestingly, the newborns' first response to seeing a facial gesture is activation of the corresponding body part (Meltzoff & Moore 1997). For example, when they see tongue protrusion, there is often a quieting of other body parts and an activation of the tongue. They do not necessarily protrude the tongue at first, but may elevate it or move it slightly in the oral cavity. The important point is that the tongue, rather than the lips or fingers, is energized before the movement is isolated. It is as if young infants isolate *what* part of their body to move before *how* to move it. Meltzoff & Moore (1997) call this 'organ identification'. Neurophysiological data show that visual displays of parts of the face and hands in monkeys activate specific brain sites (Perrett *et al.* 1987, 1992; Desimone 1991; Gross 1992; Gross & Sergent 1992; Rolls 1992). Thus, specific body parts could be neurally represented at birth and serve as a foundation for infant imitation.

Meltzoff & Moore (1997) describe a model of infant facial imitation. According to the model, there is a very primitive and foundational 'body scheme' that allows the infant to unify the seen acts of others and their own felt acts into one common framework. The infant's own facial movements are invisible to them, but they are not unperceived by them. Infants monitor their unseen facial acts through proprioception. Infants can link self and other through what Meltzoff & Moore (1977, 1983, 1997) termed a 'supramodal' representation of the observed body act. This representation allows them to imitate from memory: infants store a representation of the adult's act and subsequently compare their own acts to this internal model (Meltzoff & Moore 1992, 1994). This representation also allows them to correct their imitative movements to more faithfully match the target they see, which infants do when the adult model demonstrates novel actions such as tongue-protrusion-to-the-side (Meltzoff & Moore 1994). A fuller exposition of the crossmodal equivalence metric used to

establish self–other correspondences is provided elsewhere (Meltzoff & Moore 1997). The important point for the purposes of this paper is that infant imitation provides clear behavioural evidence for an *innate* link between the perception and production of human acts, which suggests shared neural representations.

(b) Evidence from neuroscience: mirror neurons and the neural bases for common coding

Compatible with the findings of newborn imitation, there is a large body of data from adult experimental psychology suggesting a common coding between perception and action (Prinz 1997, 2002; Viviani 2002). However, it is only in the past 15 years that neurophysiological evidence started to accumulate (Decety & Grèzes 1999). The most dramatic discovery was that ‘mirror neurons’ in the monkey ventral premotor cortex discharge during the execution of goal-directed hand movements and also when the monkey observes similar hand actions (Rizzolatti *et al.* 1996a). Another region in the monkey brain containing neurons specifically responsive to the sight of actions performed by others is in the STS (Perrett *et al.* 1989; Jellema *et al.* 2002). These discoveries and others have boosted the search for a comparable mechanism in humans.

In humans, Fadiga *et al.* (1995) recorded motor evoked potentials elicited by TMS in subjects asked to observe grasping movements performed by an experimenter. At the end of the observation period, TMS was applied to the subject’s motor cortex and motor evoked potentials were recorded from their hand muscles. The pattern of muscular response to this stimulus was found to be selectively increased in comparison to control conditions, demonstrating increased activity in the motor system during the observation of actions. This finding was confirmed by neuromagnetic measures made with MEG over the premotor cortex while subjects observed another person manipulating an object (Hari *et al.* 1998). Using electroencephalography, similarities in signal desynchronization were found over the motor cortex during execution and observation of finger movements (Cochin *et al.* 1999). There are also PET studies in humans showing recruitment of premotor, parietal and temporal activation during action observation. In an experiment by Rizzolatti *et al.* (1996b), subjects observed the grasping of objects by an experimenter. In another condition, the subjects reached and grasped the same object themselves. Significant activation was detected in the left middle temporal gyrus and in the left inferior frontal gyrus in both conditions. Recently, a functional magnetic resonance imaging study also reported that observing actions activates the premotor cortex in a somatotopic manner, similarly to that of the classical motor cortex homunculus (Buccino *et al.* 2001). In summary, these studies all demonstrate activation of the motor cortex during observation of actions. In humans, there is a kind of direct resonance between the observation and execution of actions, and the possible relation to monkey mirror neurons has been discussed (e.g. Iacoboni *et al.* 1999; Rizzolatti *et al.* 2002; Gallese 2003).

Humans do not simply directly resonate, however. Our goals affect how we process stimuli in the world. A series of studies performed by Decety’s group show a top–down effect on the brain regions involved during the observation

of the actions. More specifically, subjects were instructed to remember an action either for later imitation or for later recognition (Decety *et al.* 1997; Grèzes *et al.* 1998, 1999). In the condition of encoding-with-the-intention-to-imitate, specific haemodynamic increase was detected in the SMA, the middle frontal gyrus, the premotor cortex and the superior and inferior parietal cortices in both hemispheres. A different pattern of brain activation was found when subjects were simply observing the actions for later recognition. Here the parahippocampal gyrus in the temporal lobe was activated. There is thus a top–down effect of intention upon the processing of observed action. Intending to imitate already tunes regions beyond simple motor resonance. Altogether, these studies strongly support the view that action observation involves neural regions similar to those engaged during actual action production. However, it is equally important that the pattern of cortical activation during encoding-with-the-intention-to-imitate is more similar to that of action production than the mere observation of actions. It is also noteworthy, as will be seen in §§ 4 and 5, that the right inferior parietal cortex is consistently activated in conditions involving imitation.

Interestingly Perani *et al.* (2001) presented subjects with object-grasping actions performed by either a real hand or by means of 3D virtual reality or 2D TV screen. Results showed common activation foci in the left posterior parietal cortex and in the premotor cortex for observing both real-hand and artificial ones, with greater signal increase for the real-hand condition. A striking finding was the selective involvement of the right inferior parietal cortex and the right STG only in the real condition. We suggest that this region plays a part in the recognition of another’s action and may be specific to registering human actions rather than the motions of mechanical devices.

Humans often imagine actions in the absence of motor execution. What are the neural correlates for imagined actions (Decety 2002)? Does it matter whether you imagine an action performed by the self or that same action performed by another person? Ruby & Decety (2001) asked subjects to imagine an action being performed by themselves (first-person perspective) or by another individual (third-person perspective). Both perspectives were associated with common activated clusters in the SMA, the precentral gyrus and the precuneus. However, there were differences depending on whether subjects were imagining their own versus another person’s actions. First-person perspective taking was specifically associated with increased activity in the left inferior parietal lobule and the left somatosensory cortex, whereas the third-person perspective recruited the right inferior parietal lobule, the posterior cingulate and the frontopolar cortex. A similar pattern of activation was confirmed in a follow-up functional neuroimaging study involving more conceptual perspective-taking tasks (Ruby & Decety 2002). These results support the notion of shared representations of self and other, even in the case of imagined actions of self and other. The results also suggest a crucial role of the inferior parietal cortex in distinguishing the perspective of self and other.

(i) Going beyond mirror neurons

Human newborn imitation demonstrates an innate connection between the observation and execution of human

acts. One assumption often made is that the mirror neurons discussed by Rizzolatti *et al.* (2002) are also innate. This assumption deserves scrutiny, however. Based on the evidence to date, it is possible that the mirror neurons found in adult monkeys are the result of learned associations. Consider the case of a mirror neuron that discharges to 'grasping-with-the-hand'. This same cell fires regardless of whether that act is performed by the monkey or is observed in another actor. A cell that discharges in both cases could mean that 'grasping' is an innate act; perhaps a cell is pre-tuned to this evolutionarily significant act whether performed by the self or the other. Alternatively, it could be based on the fact that the monkey has repeatedly observed itself perform this action. Observation and execution occur in perfect temporal synchrony whenever the monkey watches itself grasp an object. After such experience, the visual perception of grasping by another animal could activate neurons based on a visual equivalence class between the sight of one's own and another's hand. Monkeys are known to be capable of such visual generalizations and categorization. Thus, mirror neurons could result from learning by association and visual generalization.

It is crucial to investigate the ontogeny of mirror neurons. One needs to determine whether monkeys are born with functioning mirror neurons that activate the first time the animal sees an act, which would be equivalent to the newborn work done by Meltzoff & Moore (1983, 1989) with 42-minute-old human infants. To the best of our knowledge this work has not been done with newborn monkeys. Thus, we are left with unfinished empirical work. There is behavioural evidence of an innate observation-execution system in humans (imitation) but work is lacking on the neural basis in this newborn population; and there is research addressing the neural bases for an observation-execution system in monkeys (mirror neurons), but work is lacking on the innateness question.

A further interesting question for the future is whether innate human imitation relies chiefly on neural machinery in the premotor cortex (akin to monkey mirror neurons), or, alternatively, on neural systems involving the inferior parietal lobule (which have been shown to be crucial in human studies involving the processing of similarities and differences between the actions of self and other). The infancy work shows that young babies *correct* their imitative behaviour, which suggests an active comparison and lack of confusion between self and other (Meltzoff & Moore 1997). It also shows that infants can store a model and imitate *from memory* after delays as long as 24 hours (Meltzoff & Moore 1994; Meltzoff 1999), which requires more than simple visual-motor resonance. These features of human imitation may go beyond the workings of the mirror neurons *per se*. Furthermore, monkeys do not imitate (Tomasello & Call 1997; Byrne 2002; Whiten 2002), although they certainly have the basic mirror neuron machinery. Something more is needed to prompt and support behavioural imitation, especially the imitation of novel actions and imitation from memory without the stimulus perceptually present. This may involve the inferior parietal lobe, which is implicated in registering both the similarity and the distinction between actions of the self and other.

3. KNOWING YOU ARE BEING IMITATED BY THE OTHER: SELF-OTHER RELATIONS

Human beings do not only imitate. They also recognize when they are being imitated by others. Such reciprocal imitation is an essential part of communicative exchanges. A listener often shows interpersonal connectedness with a speaker by adopting the postural configuration of the speaker. If the speaker furrows his or her brow, the listener does the same; if the speaker rubs his chin, the listener follows. Parents use this same technique, however unconsciously, in establishing intersubjectivity with their preverbal infants. Imitation seems to be intrinsically coupled with empathy for others, broadly construed.

(a) *Evidence from developmental science: emotional reactions to being imitated*

Adults across cultures play reciprocal imitative games with their children. Some developmentalists have focused exclusively on the temporal turn-taking embodied in these games (Trevarthen 1979; Brazelton & Tronick 1980). Timing is important, but we think these games are uniquely valuable owing to the structural congruence between self and other. Physical objects may come under temporal control. Only people who are paying attention to you and acting intentionally can match the form of your acts in a generative fashion. Only people can act 'like me'.

Meltzoff (1990) tested whether infants recognize when another acts 'like me' and the emotional value of this experience. One experiment involved 14-month-old infants and two adults. One of the adults imitated everything the baby did; the other adult imitated what the previous baby had done. Each adult copied one of the infants, so each acted like a perfect baby. Could the infants distinguish which adult was acting just like the self?

The results showed that they could. They looked longer at the adult who was imitating them; smiled more at this adult; and most significantly, directed testing behaviour at that adult (for similar results, see also Asendorph (2002) and Nadel (2002)). By testing we mean that infants often modulated their acts by performing sudden and unexpected movements to check if the adult was following what they did. The Marx brothers are famous for substituting a person who imitates in place of a true reflection in a mirror. The actor in such a situation systematically varies his acts to see if the other is still in congruence. Infants acted in this same way, testing in a concerted fashion whether the other person would follow everything they did.

Further research revealed that even very young infants are attentive to being imitated. However, we found an important difference between the younger and the older infants. Although younger infants increase the particular gesture being imitated, they do not switch to mismatching gestures to see if they will be copied. For example, if an adult systematically matches a young infant's tongue protrusion, her attention is attracted and she generates more of this behaviour, but does not switch to gestures to test this relationship. The older infants go beyond this interpretation and treat the interaction as a matching game that is being shared.

By saying that the older infant appreciates the shared matching game, we mean that the relationship is being **abstractly considered** and the particular behaviours are

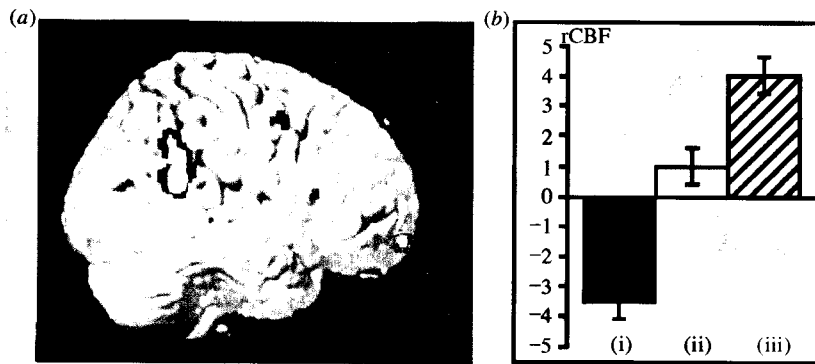


Figure 2. (a) Right inferior parietal lobule activation superimposed on an average MRI. (b) The relative haemodynamic variation during self action, when subjects acted at will (i), when they imitated the actions demonstrated by the experimenter (ii), and when they saw their actions being imitated by the experimenter (iii). Note the dramatic increase in right inferior parietal lobe activation in this last condition. (Adapted from Decety *et al.* (2002).) rCBF indicates regional cerebral blood flow.

substitutable. It is not the notion that tongue protrusion leads to tongue protrusion (a mapping at the level of a particular behaviour), but the abstract notion that the other is doing 'the same as' me. By 14 months, infants undoubtedly know that adults are not under their total control, and part of the joy of this exchange is the realization that although the infant does not actually control the other, nonetheless the other is choosing to do just what I do. Together these two factors may help to explain why older infants will joyfully engage in mutual imitation games for 20 minutes or more—much longer and with greater glee than watching themselves in a mirror. The infants recognize the difference between self and other and seem to be exploring the sense of agency involved—exploring who is controlling whom in this situation.

(b) Evidence from neuroscience: imitation and the neural basis of differentiating actions of self and other

The developmental work shows that infants not only imitate but also know when they are being imitated by others. This is interesting because the situation in the physical world is the same—there are two bodies in correspondence with one another—whether one is the imitator or the imitatee. An external observer might not know who imitated whom. How does the brain keep track of this? What is the neural basis for distinguishing the self's imitation of the other from the other's imitation of the self?

Decety *et al.* (2002) designed a PET study focusing on this question. In the two imitation conditions, the subjects either imitated the experimenter's actions on objects or saw their own actions imitated by him. Three control conditions were used: (i) action-generation control: subjects allowed to freely manipulate the objects any way they wanted to; (ii) observing action control: subjects simply watching the demonstrator's actions; or (iii) visual-motor mismatch control: subjects performed actions while watching the other person simultaneously performing mismatched movements.

Several regions were involved in the two imitation conditions compared to the control conditions, namely the STG, the inferior parietal lobule, and the medial prefrontal cortex. Interestingly for our view linking imitation and mentalizing, the medial prefrontal cortex is known to

be activated in tasks involving mentalizing (Frith & Frith 1999; Blakemore & Decety 2001). The inferior parietal lobule also proved to be a key region (see figure 2). When the two imitation conditions were contrasted to the control condition in which subjects acted differently from the experimenter, a lateralization of the activity was found in this region. The left inferior parietal lobule was activated when subjects imitated the other, while the right homologous region was associated with being imitated by the other. In comparing the imitation and control conditions, activation was also detected in the posterior part of the STG, known to be involved in the visual perception of socially meaningful hand gestures (Allison *et al.* 2000). This cluster was found in both hemispheres when contrasting the imitation conditions to the action-generation control condition. However, it was only present in the left hemisphere when the condition of being imitated was subtracted from the condition of imitating the other. This lateralization in the STG is an intriguing finding. We suggest that the right STG is involved in visual analysis of the other's actions, while its homologous region in the left region is concerned with analysis of the other's actions in relation to actions performed by the self.

This involvement of the inferior parietal cortex in the sense of agency is supported by converging evidence from neuropsychology (Kinsbourne 2002), and other neuroimaging studies (e.g. Ruby & Decety 2001; Chaminade & Decety 2002; Farrer & Frith 2002; Farrer *et al.* 2003), as well as from abnormalities in self-other distinctions found in schizophrenic patients (e.g. Spence *et al.* 1997). All these studies have pointed out the specific involvement of this region in tasks that require subjects to distinguish actions produced by the self from those produced by another agent. This, of course, is the essential ingredient in knowing 'who is imitating whom'—a common situation in parent-child games and empathic resonance.

4. READING OTHERS' GOALS AND INTENTIONS

Persons are more than dynamic bags of skin that I can imitate and which imitate me. In the mature adult notion, persons have internal mental states—such as beliefs, goals and intentions—that predict and explain human actions.

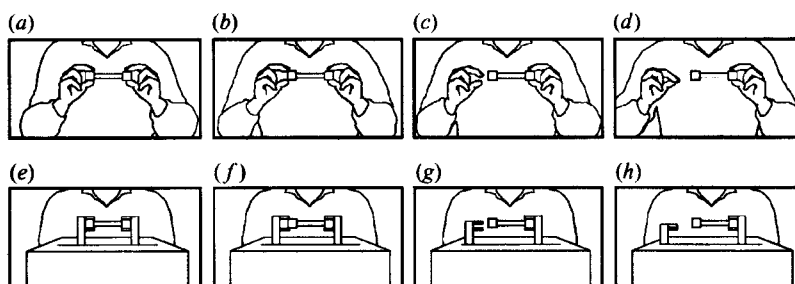


Figure 3. Human demonstrator (a–d) and inanimate device performing the same movements (e–h). Infants attribute goals and intentions to the person but not the inanimate device. (From Meltzoff (1995).)

Recently, attention has turned to the earliest developmental roots and neural substrate of decoding the goals and intentions of others.

(a) Evidence from developmental science: infants' understanding of others' goals and intentions

Developmental psychologists have attempted to use preferential-looking procedures to explore infants' understanding goals (see Gergely *et al.* 1995; Woodward *et al.* 2001; Csibra 2003). These visual tests assess infants' ability to recognize discrepancies from visible goal states, such as grasping one object versus another, or moving towards/away from a visible location in space. These studies do not involve adopting the goals of others and using them as the basis for self action. Nor do they involve inferring unseen goals and intentions, such as drawing a distinction between what a person means to do versus what they actually do (a crucial distinction in the law and morality).

Meltzoff (1995) introduced a more active procedure to address these issues. The procedure capitalizes on imitation, but it uses this proclivity in a new, more abstract way. It investigates infants' ability to read below the visible surface behaviour to the underlying goals and intentions of the actor. It also assesses infants' capacity to act on the goals that they inferred.

One study involved showing 18-month-old infants an unsuccessful act, a failed effort (Meltzoff 1995). For example, the adult 'accidentally' under- or overshot his target, or he tried to perform a behaviour but his hand slipped several times; thus the goal state was not achieved. To an adult, it was easy to read the actor's intentions although he did not fulfil them. The experimental question was whether infants also read through the literal body movements to the underlying goal of the act. The measure of how they interpreted the event was what they chose to re-enact. In this case the correct answer was not to copy the literal movement that was actually seen, but to copy the actor's goal, which remained unfulfilled.

The study compared infants' tendency to perform the target act in several situations: (i) after they saw the full target act demonstrated, (ii) after they saw the unsuccessful attempt to perform the act, and (iii) after it was neither shown nor attempted. The results showed that 18-month-old infants can infer the unseen goals implied by unsuccessful attempts. Infants who saw the unsuccessful attempt and infants who saw the full target act both produced target acts at a significantly higher rate than controls. Evidently, young toddlers can understand our goals

even if we fail to fulfil them. They choose to imitate what we meant to do, rather than what we mistakenly did do.

In further work, 18-month-old infants were shown an adult trying and failing to pull apart a dumbbell-shaped object, but they were handed a trick toy. The toy had been surreptitiously glued shut before the study began. When infants picked it up and attempted to pull it apart, their hands slipped off the ends of the cubes. This, of course, matched the surface behaviour of the adult. However, this imitative match at the behavioural level did not satisfy them. They sought to fulfil the adult's intention. The infants repeatedly grabbed the toy, yanked on it in different ways, and appealed to their mothers and the adult. Fully 90% of the infants immediately ($M < 2$ s) looked up at an adult after failing to pull apart the trick toy, and they vocalized while staring directly at the adult.

If infants are picking up the underlying goal or intention of the human act, they should be able to achieve the act using a variety of means. Meltzoff (unpublished data) tested this with a dumbbell-shaped object that was too big for the infants' hands. The infants did not attempt to imitate the surface behaviour of the adult. Instead they used novel ways to struggle to get the gigantic toy apart. They put one end of the dumbbell between their knees and used both hands to pull upwards, or put their hands on the inside faces of the cubes and pushed outwards, and so on. They used different means than the experimenter, but their actions were directed towards the same end. This fits with the hypothesis that infants had inferred the goal of the act, differentiating it from the literal surface behaviour that was observed.²

In the adult psychological framework, people and other animate beings have goals and intentions, but inanimate devices do not. Do infants carve the world in this way? To assess this, Meltzoff designed an inanimate device made of plastic and wood (Meltzoff (1995), experiment 2). The device had poles for arms and mechanical pincers for hands. It did not look human, but it traced the same spatiotemporal path that the human actor traced and manipulated the object much as the human actor did (see figure 3). The results showed that infants did not attribute a goal or intention to the movements of the inanimate device when its pincers slipped off the ends of the dumbbell. Infants were no more (or less) likely to pull the toy apart after seeing the failed attempt of the inanimate device than they were in baseline levels when they saw nothing. This was the case despite the fact that infants pulled the dumbbell apart if the inanimate device successfully completed this act. Evidently, infants can pick up cer-

tain information from the inanimate device, but not other information: they can understand successes, but not failures. (This makes sense because successes lead to a change in the object, whereas failures leave the object intact and therefore must be interpreted at a deeper level.)

This developmental research shows that infants distinguished between what the adult meant to do and what he actually did. They ascribed goals to human acts; indeed, they inferred the goal even when it was not attained. This differentiation between behaviour versus goals and intentions lies at the core of our mentalizing, and it underlies our moral judgements. The infants in these experiments were already exhibiting a fundamental aspect of our adult framework: the acts of persons (but not the motions of inanimates) are construed in terms of goals and intentions.³

(b) Evidence from neuroscience: means and goals

This research shows that even infants draw a distinction between observed behaviour and the goals towards which it is heading. We designed a functional neuroimaging experiment to differentiate the neural correlates of two key components of human actions, the goals and the means to achieve it (Chaminade *et al.* 2002). The 'goal' in this experiment was operationalized as the end state of the object manipulation and the means as the motor programme used to achieve this end. Actions consisted of sequentially moving Lego blocks from a start position to a specific place in a Lego construction. Depending on the experimental conditions, subjects were asked to imitate a human model who presented either: (i) the goal only, (ii) the means only, or (iii) the whole action. The control condition involved free action, during which the subject could manipulate the Lego blocks at will, and thus did not involve imitation.

The results revealed partially overlapping clusters of increased regional cerebral blood flow in the right dorso-lateral prefrontal area and in the cerebellum when subjects imitated either the goal or the means. Moreover, specific activity was detected in the medial prefrontal cortex during the imitation of the *means*, whereas imitating the *goal* was associated with increased activity in the left premotor cortex. The finding of the involvement of the right dorso-lateral prefrontal cortex in our imitation tasks confirms its role in the preparation of forthcoming action based on stored information (Pochon *et al.* 2001). Interestingly, the medial prefrontal region was primarily activated in the experimental condition involving the imitation of the means. The medial frontal region is known to play a critical role in inferring others' intentions and is consistently involved in mentalizing tasks (Blakemore & Decety 2001). Its activation during imitation of the means indicates that observing the means used by an actor prompts the observer to construct/infer the goals towards which this human agent is aiming. The fact that the same neural regions are activated in imitation and mentalizing tasks fits with the ideas we advanced earlier in this paper (see § 1).

5. THEORETICAL SPECULATIONS

The conundrum of social cognition stems from the simple truth that persons are more than physical objects. Giving a person's height and the shape of his fingerprint does

not exhaust our description of that person. We have skipped their psychological makeup. A longstanding question is how we come to know others as persons like ourselves.

We suggest that infant imitation provides an innate foundation for social cognition. Imitation indicates that newborns, at some level of processing no matter how primitive, can map actions of other people onto actions of their own body. Human acts are especially relevant to infants because they look like the infant feels himself to be and because they are events infants can intend. When a human act is shown to a newborn, it may provide the first recognition experience, 'something familiar! That seen event is like this felt event'.

(a) Developmental science: innate imitation as the root of mentalizing

We are now in a position to see how the imitative mind and brain may contribute to the development of mentalizing. We offer a three-step developmental sequence as follows.

- (i) **Innate equipment.** Newborns can recognize equivalences between perceived and executed acts. This is that starting state, as documented by newborn imitation (Meltzoff & Moore 1997).
- (ii) **Constructing first-person experience.** Through everyday experience infants map the relation between their own bodily acts and their mental experiences. For example, there is an intimate relation between 'striving to achieve a goal' and the concomitant facial expression and effortful bodily acts. Infants experience their own unfulfilled desires and their own concomitant facial/postural/vocal reactions. They experience their own inner feelings and outward facial expressions and construct a detailed bidirectional map linking mental experiences and behaviour.
- (iii) **Inferences about the experiences of others.** When infants see others acting 'like me', they project that others have the same mental experience that is mapped to those behavioural states in the self.

In sum, given the innate state (step no. (i)) and the knowledge that behaviour *X* maps to mental state *X'* in their own experience (step no. (ii)), infants have relevant data to make inferences about relations between the visible behaviour of others and the underlying mental state (step no. (iii)).

Infants would not need the adult theory of mind innately specified. Infants could infer the internal states of others through an analogy to the self. Infants imbue the acts of others with 'felt meaning', because others are intrinsically recognized as 'like me'.

(b) Neuroscience: the importance of the human inferior parietal cortex in representing self-other relations

Imitation indicates a common coding between the observation and execution of acts. However, that is not the end of the story. Infants also correct their imitative behaviour, which indicates that their representation of the target is kept distinct from the representation of their own movements. Similarly, infants recognize being imitated by

others, and they 'test' whether the other will follow what they do. Here, again, there is a recognition of self-other equivalence, but not a total confusion between the two. Thus, one highly relevant issue concerns how the self-versus-other distinction operates within these shared representations and which neural mechanisms are engaged in integrating and discriminating the representations activated from within and those activated by external agents.

Our functional neuroimaging studies on imitation were designed to explore both what is common as well as distinct between self and other. The results highlight the role of the posterior part of the temporal cortex and the inferior parietal cortex, in conjunction with medial prefrontal and premotor areas. Indeed, all of our imitation tasks across several studies activate the posterior part of the temporal cortex and the medial prefrontal cortex. It is noteworthy that the former region is activated by tasks that require detection of biological agents (Griffiths *et al.* 1998; Grossman *et al.* 2000; Grézes *et al.* 2001). The latter region is consistently activated in mentalizing tasks involving the attribution of intentions to oneself and to others (Frith & Frith 1999; Blakemore & Decety 2001), as well as in executive functioning (a cluster of high-order capacities, including selective attention, behavioural planning and response inhibition; e.g. Siegal & Varley 2002).⁴

In our studies, there was more increase in the left inferior parietal lobule when subjects imitated the other, and more increase in the right homologous region when they saw that their actions were imitated by the other. We suggest that the left inferior parietal lobule computes the sensory-motor associations necessary to imitate, which is compatible with the literature on apraxia (Halsband 1998), whereas the right inferior parietal lobule is involved in recognizing or detecting that actions performed by others are similar to those initiated by the self and determining the locus of agency for matching bodily acts.

This proposal about the importance of the right inferior parietal lobule fits with the clinical neuropsychological evidence that it is important for body knowledge and self-awareness and that its lesion produces disorders of body representation such as anosognosia, asomatognosia or somatoparaphrenia (Berlucchi & Aglioti 1997). Ramachandran & Rogers-Ramachandran (1996) reported cases of patients with right parietal lesions in whom the denial of hemiplegia applies both to their own condition and to the motor deficits of other patients. This indicates that availability of an efficient body schema is necessary not only for recognizing one's own behavioural states but also for understanding those states in others.

Finally, in light of our neuroimaging experiments, we suggest that the right inferior parietal lobule plays a key role in the uniquely human capacity to identify with others and appreciate the subjective states of conspecifics as both similar and differentiated from one's own. This may well be a qualitative difference between human and non-human primates, not just a quantitative one (Povinelli & Prince 1998; Tomasello 1999). In other words, the adult human framework is not simply one of resonance. We are able to recognize that everyone does not share our own desires, emotions, intentions and beliefs. To become a sophisticated mentalizer one needs to analyse both the similarities and differences between one's own states and those of others. That is what makes us human.

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ENDNOTES

¹We use the terms 'theory of mind' and 'mentalizing' interchangeably in this paper.

²Work with older children, in the 3–6 year age range, also underscores the importance of goals in children's imitation (Bekkering *et al.* 2000; Gleissner *et al.* 2000), and the present work shows that goal detection is connected to imitation right from infancy.

³None the less, both infants and adults sometimes make confusions. People sometimes attribute goals to their computer (because it exhibits certain functionality), and one could build a robot that fooled children and even adults; consider Star Trek androids. However, in the present case an inanimate device was used that only mimicked the spatiotemporal movements of a hand, and did not look or otherwise act human. The results of Meltzoff (1995) dovetail with the finding that there are certain neural systems activated by human actions and not similar movements produced by a mechanical device (Decety *et al.* 1994; Perani *et al.* 2001; Castiello *et al.* 2002), and the demonstration that infants process animate body parts differently from inanimate objects (e.g. Brooks & Meltzoff 2002).

⁴Prefrontal, inferior parietal and temporoparietal areas have evolved tremendously in humans compared to non-human primates (Passingham 1998). The parietal cortex is roughly 'after' vision and 'before' motor control in the cortical information-processing hierarchy (Milner 1998). The inferior parietal lobule is a heteromodal association cortex which receives input from the lateral and posterior thalamus, as well as visual, auditory, somesthetic and limbic input. It has reciprocal connections to the prefrontal and temporal lobes (Eidelberg & Galaburda 1984). It is claimed by some scholars (e.g. Milner 1997), following Brodmann (1907), that the human superior parietal lobe, taken alone, is equivalent to the whole of the monkey posterior parietal cortex. If so, the monkey and human inferior parietal lobes may not be fully equivalent. This is a highly speculative position, but it is interesting in light of the role we have found for the inferior parietal lobe in representing the relationship between self and other. Further information on the evolution and development of this brain region is needed.

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GLOSSARY

- MEG: magnetoencephalography
 PET: positron emission tomography
 SMA: supplementary motor area
 STG: superior temporal gyrus
 STS: superior temporal sulcus
 TMS: transcranial magnetic stimulation