

The manifold nature of interpersonal relations: the quest for a common mechanism

Vittorio Gallese

Istituto di Fisiologia Umana, Università di Parma, Parma, Italy (vittorio.gallese@unipr.it)

It has been proposed that the capacity to code the 'like me' analogy between self and others constitutes a basic prerequisite and a starting point for social cognition. It is by means of this self/other equivalence that meaningful social bonds can be established, that we can recognize others as similar to us, and that imitation can take place.

In this article I discuss recent neurophysiological and brain imaging data on monkeys and humans, showing that the 'like me' analogy may rest upon a series of 'mirror-matching' mechanisms. A new conceptual tool able to capture the richness of the experiences we share with others is introduced: the *shared manifold* of intersubjectivity. I propose that all kinds of interpersonal relations (imitation, empathy and the attribution of intentions) depend, at a basic level, on the constitution of a shared manifold space. This shared space is functionally characterized by automatic, unconscious embodied simulation routines.

Keywords: empathy; imitation; mirror neurons; mind reading; simulation

1. INTRODUCTION

Intersubjectivity is one of the most controversial topics within the ongoing debate in the cognitive sciences. Various modalities of normal and pathological interpersonal relations are the focus of many different disciplines such as neuroscience, cognitive and developmental psychology, philosophy of mind, and psychiatry. *Imitation, empathy* and *mind reading* denote, among others, different levels and modes of interaction by means of which individuals establish meaningful bonds with others; therefore, they have been variously used to characterize mechanisms and modes of intersubjective relation.

Why has intersubjectivity progressively gained the centre of the stage? Because more and more scholars are experiencing a growing sense of discomfort with respect to the heuristic value of accounts of human cognition exclusively focusing on a solipsistic, monadic dimension. Intersubjective relations are interesting not only because they capture an essential trait of the human mind—its social character—but also, and even more importantly, because they provide a greater opportunity to understand how the *individual* mind develops and works.

Imitation, empathy and mind reading are different in many respects. When we engage in re-enacting the observed behaviour of someone else, we translate the *observed* actions into executed ones. When we empathize with others, we understand what others are feeling, be it a particular *emotion* or *sensory state*. Finally, when we witness the actions of others, we supposedly understand their meaning and the reasons that possibly promoted them. In these three different types of interpersonal relation we are confronted with *apparently different* objects (actions, emotions and sensations, and thoughts, respectively), and we reply with different modalities (actions, feelings and thoughts, respectively). It therefore seems legitimate to assume that imitation, empathy and mind reading depend on totally different mechanisms.

I suggest a different perspective. I demonstrate that imitation, empathy and mind reading do share, *at a basic level*, a crucial common feature: they all depend on the constitution of a shared meaningful intersubjective space. I propose that the shared manifold space—orthogonal to imitation, empathy and to the attribution of intentions relies on a specific functional mechanism, which is probably also a basic feature of how our brain/body system models its interactions with the world: embodied simulation.

Furthermore, I clarify how embodied simulation can be characterized from a neurobiological perspective, by proposing that the mirror-matching neural system, originally discovered in the premotor cortex of monkeys—but also present in the human brain—might be part of the neural correlate of simulation, and therefore provide an integrated neuroscientific account of the basic aspects of intersubjectivity.

2. SOCIAL IDENTITY: WHY IT MATTERS

From the very beginning of our life, the social dimension seems to play a very powerful role within the network of interactions shaping our view of the world. Social behaviour is not peculiar to primates; it is diffuse across species very different from humans, such as bees and ants. Within different species, social interactions certainly play different roles, and are probably subsumed by different mechanisms. Nevertheless, central to all social species and, within more evolved species of primates, central to all social cultures of whatever complexity, is the notion of *identity* of the individuals within those species and cul-

One contribution of 15 to a Theme Issue 'Decoding, imitating and influencing the actions of others: the mechanisms of social interaction'.

tures. It follows, that *all* levels of social interaction that can be employed to characterize cognition in single individuals must intersect or overlap, to enable the development of mutual recognition and intelligibility.

As humans, we implicitly 'know' that all human beings have four limbs, walk in a certain way, act and *think* in special ways. If we share the same culture, we will, for example, all tattoo our body in a special striped fashion, pierce different parts of our body, or wear the same striped scarf when attending the games of our favourite soccer team. If we share with other individuals a given perspective on how our society should be governed, together with other citizens sharing our views, we will vote for the same political party.

Social identity can therefore be articulated at many different levels of complexity: it can be analysed by means of increasingly complex tests in which different species might score differently. However, whatever their complexity might be, identity relations are necessary to allow the sense of belonging to a larger community of other organisms. Why is this so? Why in the course of evolution has this feature been preserved?

Identity is important within a group of social individuals because it provides them with the capacity to better *predict* the consequences of the ongoing and future behaviour of others. The attribution of identity status to other individuals automatically contextualizes their behaviour. This, in turn, reduces the variables to be computed, thus optimizing the employment of cognitive resources by reducing the 'meaning space' to be mapped. By contextualizing content, identity reduces the amount of information our brain has to process. In § 3 I examine the issue of identity from a developmental perspective.

3. INVESTIGATING SOCIAL COGNITION: THE DEVELOPMENTAL COGNITIVE REVOLUTION

One of the major contributions to our understanding of human social cognition has been provided during recent decades by research in developmental psychology. Developmental psychology has literally revolutionized our way of looking at newborns and infants as cognitive agents. These results have shown, among other things, that at the very beginning of our life we are capable of performances which, if and when instantiated by adult individuals, we would readily ascribe to the most abstract resources of our cognitive system.

One aspect of infants' proclivity to 'abstraction' is their astonishing capacity to operate cross-modal mapping of sensory information. Three-week-old infants are able to visually identify pacifiers that they previously felt having sucked on them when blindfolded (Meltzoff & Borton 1979). What was previously experienced as *haptically different* was later recognized as being *visually different*. Other studies have shown that infants can easily map the intensity and timing of sensory stimulation independently from the modality through which it is conveyed, be it somatosensory, visual or auditory (for a review of this literature, see Stern 1985). Cross-modal transfer seems, therefore, to be a basic capacity we are born with, or that, at the very least, we develop very early.

This capacity appears to be crucial for the development of social cognition, because it is exploited to constitute interpersonal bonds. As shown by Meltzoff and Moore, newborns as young as 18 hours old can reproduce mouth and face movements displayed by the adult they are facing (Meltzoff & Moore 1977; see also Meltzoff & Moore 1997; Meltzoff 2002). What is remarkable is that this behaviour is instantiated by body parts such as the mouth to which newborns have no visual access. Infants, nevertheless, can re-enact the observed behaviour as displayed by the adult demonstrator. The visual information about the observed behaviour is translated into motor commands for reproducing it.

Meltzoff & Moore (1997) have defined this apparently innate mechanism as AIM. According to Meltzoff (2002), intermodal mapping can be conceived of as a 'supramodal act space', unconstrained by any particular mode of interaction, visual or motor. Modes of interaction as diverse as seeing or doing something *must* share some peculiar feature making the process of equivalence carried out by AIM possible.

Early imitation appears to constitute a further example of infants' capacity to establish equivalence relations between different modalities of experience. The importance of early imitation for our understanding of social cognition is that it shows that interpersonal bonds are established at the very onset of our life, when no subjective representation can yet be entertained by the organism, because a *conscious subject* of experience is not yet constituted.

The absence of a self-conscious subject does not preclude, however, the constitution of a primitive '*self-other* space', a paradoxical form of intersubjectivity without subjects. The infant shares this 'we-centric' space with the other individuals inhabiting his world.

The discoveries of developmental psychology are also of vital importance in our discussion of social cognition for another reason: these data show that our cognitive system is capable of conceiving an 'abstract' multimodal way to map apparently unrelated sensory sources of information, well before the development and mastery of language (the cognitive tool of abstraction *par excellence*) and of more sophisticated forms of social interaction.

4. EARLY AND MATURE IMITATION

A striking feature of the early type of imitation discovered by Meltzoff and co-workers is that it cannot be elicited after the third month or so of life. Later on, however, a more mature form of imitation will develop, one implying the capacity to fully grasp the meaning and relevance of what is to be imitated (see Wohlschläger *et al.* 2003).

It is this second type of imitation which stirs the debate among psychologists and primatologists concerning whether such behaviour can also be ascribed to nonhumans, or if it has to be considered a unique endowment of our species (for a discussion of imitation from an ethological point of view, see Whiten & Custance 1996; Tomasello & Call 1997; Byrne 1995; Visalberghi & Fragaszy 1990, 2001; Byrne 2003).

I will not delve into this controversial debate here. Rather, what I would like to emphasize is the following aspect: early and mature forms of imitation in humans share a basic feature, which is independent of the presence of highly developed cognitive faculties such as language, or from the capacity to identify the individual to be imitated as a *different self*.

What is common between a neonate who replies to his mother sticking out her tongue with an equivalent behaviour, and the skilled repetition by an adolescent of the piano chords as demonstrated by the piano teacher? Both instances of imitative behaviour are made possible only by the capacity to solve the computational difficulties inherent in any type of interpersonal mapping, due to the different perspectives of demonstrator and imitator (see Schall et al. 2003). If I want to reproduce the behaviour of someone else, no matter how complex it is, or whether I understand it or not, I always need to translate my external perspective of the demonstrator into my own personal body perspective. This problem can, however, be overcome if both the actions of the demonstrator and of the imitator share a basic neural format. Later on we will see that this is exactly the case. For the time being what we can say is that the basic feature shared by early and mature forms of imitative behaviours is the presence of a shared, multimodal, we-centric, blended space. In § 5, basic feature is also shown to lie at the core of a different mode of interpersonal relation: empathy.

5. EMPATHY

When we observe other acting individuals, we are exposed to a full range of *expressive* power, which is not confined to what their actions are, but it also encompasses the emotions and feelings they display. When this occurs, an affective meaningful interpersonal link is automatically established (see Blair 2003). Empathy constitutes precisely the capacity to establish this link (for a recent discussion of the historical origin of the notion of empathy, see Prigman 1995; Gallese 2001, 2003a,b).

The empathic link is not confined to our capacity to understand when someone is angry, happy or sad. Empathy, if conceived, as I am doing, in a broader sense, also enables us to understand what is happening when someone else is experiencing sensations such as pain, touch or tickling.

Again, the results of developmental psychology research are highly relevant in showing that this particular type of interpersonal relationship is present at a very early age. Starting from the second month of age, the infant engages with the mother in what Stern (1985) has called 'affective attunement': a cross-modal matching of interpersonal affective expressions. More precisely, what is matched is not a particular aspect of the other person's behaviouras typically occurs in imitation. What is matched is '...some aspect of the behaviour that reflects the person's feeling state' (Stern 1985). These expressions can be different in form and intensity (body movements, facial expressions, vocalizations), but they all share the same affective dimension of emotional resonance. Incidentally, it is worth noting that according to Lipps (1903), empathy (Einfühlung) can be conceived of as a sort of 'inner imitation'.

Since the very beginning of our life we therefore inhabit a *shared multidimensional interpersonal space*, which, I posit, also constitutes a substantial part of our social semantic space during adulthood. When we observe other acting individuals, and face their full range of *expressive* power (the way they act, the emotions and feelings they display), a meaningful embodied interpersonal link is automatically established.

The point is how to characterize this special form of understanding. Do we apply our capacity for mental logic? Do we apply theories to figure out what kind of emotion or sensation is expressed and felt by the individual we are facing? In principle, we can certainly achieve this goal in the aforementioned ways. However, we must note that in everyday life we are able to 'decode' the quality of the sensations or emotions embedded in the witnessed behaviour of others without the need to exert any conscious cognitive effort. The meaning of the expressions of affective behaviour seems to be automatically understood by the observer without the necessity of any intervening complex cognitive mediation. How is this possible? And what is the functional mechanism at the basis of our capacity for empathy, as I have defined it? In \S 7, I propose that this mechanism can also be envisaged as a kind of simulation.

6. MIND READING

Inter-individual relations have played a fundamental role in the evolution of primate cognition. Humphrey (1976) originally suggested that the intelligence of primates primarily evolved to solve social problems. This view is supported by empirical data. Several studies have revealed the unique capacity of non-human primates to understand the *quality* of the relationships within their social group, not only in terms of kin, but also in terms of coalitions, friendship and alliances. As pointed out by Tomasello & Call (1997), primates can categorize and understand third-party social relationships. The evolution of this cognitive trait seems to be related to the necessity to deal with the social complexities that arose when individuals living in groups had to compete for scarce and patchily distributed resources.

An ever-increasing literature has raised questions about the possibility that the social behaviour of non-human primates might be driven by intentions and that their understanding of others' behaviour might be intentional. There is general agreement that monkeys and apes behave *as if* possessing objectives and goals. However, unless human their awareness of purpose is not assumed.

The capacity to understand conspecifics' behaviours as goal related provides considerable benefits to individuals, as they can predict others' actions. The advantage of such a cognitive skill would also allow individuals to influence and manipulate the behaviour of conspecifics (see the Machiavellian Intelligence hypothesis; Whiten & Byrne 1997).

The problem of intentionality in primates was almost simultaneously and independently raised by Humphrey (1978, 1980) and Premack & Woodruff (1978). The traditional view in the cognitive sciences holds that human beings are able to understand the behaviour of others in terms of their *mental states* by exploiting what is commonly designated as 'Folk Psychology'. The capacity for attributing mental states—intentions, beliefs and desires—to others has been defined as ToM (Premack & Woodruff 1978). The attributes of 'Folk Psychology' have been largely identified with the notion of ToM (see Carruthers & Smith 1996; Frith & Frith 2003). A common trend on this topic has been to emphasize that non-human primates, apes included, do not rely on mentally based accounts for others' behaviour (Hayes 1998; Povinelli *et al.* 2000).

The notion of ToM has been addressed from many different perspectives. ToM has been characterized in terms of a domain-specific ability, supported by an innate, encapsulated and specific module, whose function is segregated from the other intellectual capacities of the individual (Leslie 1987; Baron-Cohen 1995; Fodor 1992, 1994; Frith & Frith 2003).

A different view holds that ToM constitutes the final stage of a developmental process in which different scientific theories about the world and its inhabitants are tested and eventually discarded to adopt new ones (see the 'child-as-scientist' hypothesis by Gopnik & Meltzoff 1997). Both accounts of ToM are often collectively identified under the heading TT.

Finally, according to a radically different perspective, the capacity to interpret others' behaviour in a meaningful way is conceived as the result of a *simulation routine* by means of which we can *purposely pretend* to be in the other's 'mental shoes' and use our own mind as a model for the mind of others (Gordon 1986; Harris 1989; Goldman 1989, 1992, 1993*a*,*b*, 2000).

All of these different perspectives on mind reading make distinct assumptions about the brain mechanisms at the basis of this distinctive cognitive feature and, even more importantly from a neuroscientific perspective, about its phylogenetic aspects. The TT approach basically emphasizes the cognitive discontinuity between human beings and other non-human primates. ToM is considered to be a sort of 'mental Rubicon', sanctioning the uniqueness of human cognitive capacities.

The simulationist approach, however, seems to make greater allowance for a possible evolutionary continuity between behaviour reading and mind reading. This perhaps explains why Simulation Theory has progressively gained a larger consensus among neuroscientists and among those cognitive scientists—still not the majority! fully aware of the intimate relationship between brain mechanisms and cognition.

It is nevertheless an oversimplification to address the issue of how individuals understand the behaviour of others only in terms of a confrontation between behaviour readers and mind readers. To say that human beings mind read, while other animals do not, simply denies the possibility that mind reading can be considered part of a more general model of cognition.

If a process such as ToM really underpins our understanding of others' behaviour, this cognitive feature must still have evolved from a non-human ancestor who shared with the present primates, humans included, several cognitive features. The behavioural study of social cognition of non-human primates and the enquiry of the neural mechanisms supporting it are therefore necessary for a thorough understanding of how the human mind evolved and how it works.

It is reasonable to suggest that this evolutionary process proceeded along a line of continuity (see Gallese & Goldman 1998; Gallese 2000*a*,*b*, 2001; Gallese *et al.* 2002*a*). This suggests that we should pursue a different heuristic: investigating whether apparently different cognitive strategies may be underpinned by similar functional mechanisms. This is the precise aim of this paper.

Whenever we are exposed to behaviours of others requiring our response, be it reactive or simply attentive, we seldom engage in *explicit and deliberate interpretative acts*. The majority of the time our understanding of the situation is immediate, automatic and almost reflex-like.

According to the TT approach, when faced with the problem of understanding the meaning of others' behaviour, adult human beings must *necessarily* translate the sensory information about the observed behaviour into a series of *mental representations* that share, with language, the propositional format. This enables one to ascribe to others' intentions, desires and beliefs, and therefore to understand the *mental antecedents* of their overt behaviour.

According to this view if, while sitting in a public house I see someone reaching for a pint of ale, I will immediately realize that my neighbour is going to sip some ale from it. The point is, how do I do it? In order to interpret the behaviour of the person sitting beside me in the public house, I must translate his biological motions into a series of mental representations regarding his *desire* to drink beer, his *belief* about the fact that the glass sitting on the table is indeed full of beer, and his *intention* to bring it to the mouth in order to sip beer from it.

Though perhaps a bit caricatured, this account essentially captures how TT characterizes interpersonal relations. I think that the view heralded by classic cognitivism, according to which our capacity of understanding the intentions determining others' behaviour is *solely determined* by metarepresentations created by ascribing propositional attitudes to others, is biologically implausible. The traditional TT perspective on mind reading exemplifies, or perhaps better, *modularizes* within this particular aspect of cognition, a more general view on the mind: a *disembodied* one. I think that there is now enough empirical evidence to reject a disembodied theory of the mind as biologically implausible.

We observe other people behaving and, most of the time, we understand what they are doing and what they are going to do. The crucial point is to clarify what the term 'understanding ' means. The observed behaviour is obviously the starting point of any understanding. But the way we characterize *what* we are supposed to understand constrains the quality and structure of our understanding. Much depends on the nature of *what* we are supposed to understand.

The point is that the behaviour of others is not *objectively given* and expressed by *objectively given creatures*. If we accept this distinction between apparent/real aspects of reality, we must also accept that the brain, in order to *represent an external objective reality*, must operate according to the normative dictates of rationality. According to this disembodied view of the human mind, the invisible attitudes governing the ostensive behaviour of others *must be interpreted* by employing the cognitive tool-kit of the rational mind.

However, things look quite different. We now know that there is no such thing as an objective reality that our brain is supposed to represent. For example, there are no objective colours in the world, colour being the result of the wavelength reflectance of objects, the surrounding lighting conditions, the colour cones in our eyes, and the neural circuitry connected to those colour cones. *There is no colour out there independent of us.*

The same argument holds for interpersonal relations. There can be no other persons out there independent of us. When we try to understand the behaviour of others, our brain is not representing an objective external personal reality. Our brain models the behaviour of others, much the same as it models our own behaviour. The results of this modelling process enable us to understand and predict what the behaviour of others is. This point will become clearer later, when introducing neuroscientific data.

If Folk Psychology were the only game in town, a further difficulty we would have to overcome would be the problem of explaining the remarkable capacities of infants and children to 'tune in' in meaningful ways to their social environment, at an age at which the supposed capacity to ascribe propositional attitudes is not yet in place.

I am not, of course, maintaining that we *never* ascribe intentions, desires or beliefs in an *explicit* way. What I am saying is that these explicit forms of mind reading, whatever they might be, are at best only one part of our 'mental social space'. This space is multidimensional, with different dimensions individuating different types of *relational specification* defining the various kinds of interactions of the individual (a biological system) with 'the world outside'.

Relational specifications constitute the almost infinite number of ways that we can *act upon* the world, or *simulate* doing so. The same different types of interaction, when ascribed to others, pertain to different beings, which, nevertheless, we feel, recognize and 'represent' as *persons similar to us*. The point is that we do not *necessarily* need to apply theories of any kind to do this.

My proposal is that all these different levels of organism-organism interactions, whatever the complexity of the relational specifications defining them might be, rely first on the same basic functional mechanism: *embodied simulation*. Embodied simulation enables the constitution of a shared and common background of *implicit certitudes* about ourselves and, simultaneously, about others. In § 7 I demonstrate that embodied simulation is a pervasive brain mechanism, intimately related to apparently 'abstract' aspects of human cognition.

7. THE MANY SIDES OF SIMULATION

The Oxford English Dictionary provides three different definitions of 'simulation':

- (i) The action or practice of simulating, with intent to deceive; false pretence, deceitful profession.
- (ii) A false assumption or display, a surface resemblance or imitation, of something.
- (iii) The technique of imitating the behaviour of some situation or process (whether economic, military, mechanical, etc.) by means of a suitably analogous situation or apparatus, esp. for the purpose of study or personnel training.

The first two definitions convey the idea of simulation as of something fake, something supposedly aimed to deceive, by *pretending to be similar* to what really differs

Phil. Trans. R. Soc. Lond. B (2003)

in many respects. The third definition conveys a totally different meaning: namely, it characterizes simulation as a process meant to produce a better understanding of a given situation or state of affairs, by means of modelling it.

The third definition of simulation appears to be much closer than the previous ones to the etymology of the word. Indeed 'to simulate' comes from the Latin '*simulare*', which in turn derives from '*similis*', which means 'like', 'similar to'. The third definition of simulation, incidentally, also defines the prevalent epistemic approach of the classic Greek–Roman western world: knowledge is conceived as a process in which the knower *assimilates* what he is supposed to know (see the Latin expression *similia similibus*, *or* the Greek verb *homologhêin*). (For a discussion of the philosophical history of simulation, see Romano 2002.)

I will use the term *simulation* in a way that is close to the third definition given above: an *implicit mechanism meant to model the objects and events that the mechanism itself is supposed to control while interacting with them.* The term interaction is considered here in its broadest sense. Simulation is a *control functional mechanism*, its function being the modelling of the objects to be controlled. Indeed, a current authoritative view on motor control envisages simulation as the mechanism employed by forward models to predict the sensory consequences of impending actions (see Wolpert *et al.* 2003). According to this view, the predicted consequences are the simulated ones.

It should be clear that the way I characterize simulation is different from the notion of simulation discussed by the proponents of Simulation Theory. According to Simulation Theory, the pretend state used by the interpreter in order to understand the behaviour of the agent is the result of a deliberate and voluntary act on the side of the interpreter. The simulation process I am discussing is instead *automatic, unconscious* and *pre-reflexive*.

Furthermore, I argue that simulation is not a prerogative of the motor system. In other words, simulation is not just confined to the executive control strategies presiding over our functioning in the world, but is a basic functional mechanism, used by vast parts of the brain. I propose that simulation, that is, how we model reality, is the only epistemic strategy available to organisms such as ourselves deriving their knowledge of the world by means of interactions with the world. What we call the *representation of reality* is not a copy of what is objectively given, but an interactive model of what cannot be known in itself. Of course, this also holds for the social interpersonal reality in which we spend all our lives.

Perception requires the capacity to predict forthcoming sensory events. Similarly, action requires the capacity to predict the consequences of action. Both predictions are the result of unconscious and automatic simulation processes. The advantage of this theory is that it is extremely parsimonious: if my theory is correct, a single mechanism embodied simulation—can provide a common functional framework for all the apparently different aspects of interpersonal relations.

In the next section I review the neuroscientific evidence showing that simulation is a pervasive functional characteristic of the monkey and human brain.

(a) Mental imagery

As human beings we have the capacity to imagine worlds that we have or have not seen before, to imagine doing things that we did or did not do before. The power of our imagination is seemingly infinite. Indeed, mental imagery has long been considered as one of the most characteristic aspects of the human mind, in that it was thought to best epitomize its disembodied nature.

However, in the light of neuroscientific research, things look quite different. We have learned from neuroscience that visual imagery shares, with visual perception, several features (for comprehensive reviews see Farah 2000; Kosslyn & Thompson 2000). For example, the time employed to scan a visual scene is matched by the time employed to mentally imagine the same scene (Kosslyn *et al.* 1978). Furthermore, and more importantly, brain imaging studies show that when we engage in imagining a visual scene, we activate regions in the brain that are normally active when we actually perceive the same visual scene (Farah 1989; Kosslyn *et al.* 1993; Kosslyn 1994), including areas supposedly involved in mapping low-level visual features, such as the primary visual cortex (Le Bihan *et al.* 1993).

As with visual imagery, motor imagery also shares many features with its actual counterpart (Jeannerod 1994). Mentally rehearsing a physical exercise induces an increase of muscle strength comparable to that attained by a real exercise (Decety et al. 1989; Yue & Cole 1992). When we engage in imagining performing a given action, several bodily parameters behave similarly to when we actually carry out the same action. Decety et al. (1991) have shown that heartbeat and breathing frequency increase during motor imagery of physical exercise. Furthermore, as with real physical exercise, they increase linearly with the increase of the imagined effort. Finally, brain imaging experiments have shown that motor imagery and real action both activate a common network of brain motor centres such as the primary motor cortex, premotor cortex, the SMA, the basal ganglia and the cerebellum (Roland et al. 1980; Fox et al. 1987; Decety et al. 1990; Parsons et al. 1995; Porro et al. 1996; Roth et al. 1996; Schnitzler et al. 1997).

All these data show that typical human cognitive activities, such as visual and motor imagery, far from being of exclusive symbolic and propositional nature, rely on and depend upon the activation of sensorimotor brain regions. Visual imagery is equivalent to simulating an actual visual experience and motor imagery is equivalent to simulating an actual motor experience. There is, however, an important point to bear in mind: in mental imagery the simulation process is not automatic and implicit. The subject deliberately engages in it.

(b) Action understanding

Action observation constitutes another instance of simulation. Why does this happen? About 10 years ago a class of premotor neurons was discovered in the macaque monkey brain that discharged not only when the monkey executed goal-related hand actions but also when observing other individuals (monkeys or humans) executing similar actions. We called these neurons 'mirror neurons' (Gallese *et al.* 1996, 2002*a*; Rizzolatti *et al.* 1996*a*, 2000, 2001; Gallese 2000*a*, 2001).

Phil. Trans. R. Soc. Lond. B (2003)

In order to be activated by visual stimuli, mirror neurons require an interaction between the agent (be it a human being or a monkey) and its target object. The visual presentation of objects does not evoke any response. Similarly, actions that, although achieving the same goal and looking similar to those performed by the experimenter's hand, are made with tools such as pliers or pincers have little effect on the response of mirror neurons (Gallese *et al.* 1996). Neurons with similar properties were later discovered in a sector of the posterior parietal cortex reciprocally connected with area F5, area PF or 7b (PF mirror neurons; see Gallese *et al.* 2002*b*).

The discovery of mirror neurons has changed our views on the neural mechanisms at the basis of action understanding. The observation of an action leads to the activation of the same neural network active during its actual execution: action observation causes in the observer the automatic simulated re-enactment of the same action. It was proposed that this mechanism could be at the basis of an implicit form of action understanding (Gallese *et al.* 1996, 2002*a*,*b*; Rizzolatti *et al.* 1996*a*; Gallese 2000*a*, 2003*b*).

The relationship between action understanding and action simulation is even more evident in the light of the results of two more recent studies. In the first series of experiments, F5 mirror neurons were tested in two conditions: in the first condition the monkey could see the entire action (e.g. a hand grasping action); in the second condition the same action was presented, but its final critical part, that is the hand–object interaction, was hidden. Therefore, in the hidden condition the monkey only 'knew' that the target object was present behind the occluder. The results showed that more than half of the recorded neurons responded also in the hidden condition (Umiltà *et al.* 2001).

Behavioural data have shown that, like humans, monkeys can also infer the goal of an action even when the visual information about it is incomplete (Filion *et al.* 1996). Data from myself and colleagues reveal the probable neural mechanism at the basis of this cognitive capacity. The inference concerning the goals of the behaviour of others appears to be mediated by the activity of motor neurons coding the goal of the same action in the observer's brain. Out of sight is not 'out of mind' just because, by simulating the action, the gap can be filled.

Some transitive actions are characteristically accompanied by a sound. Imagine hearing the sound produced by your doorbell. This sound will induce you to think that someone is standing in front of the door, waiting to be let into your apartment. That particular sound enables you to understand what is going on even if you have no visual information about what is currently happening outside your closed door. The doorbell sound has the capacity to make an invisible action inferred, and therefore present and understood.

A recent series of experiments were aimed specifically at investigating the neural mechanism possibly underpinning this capacity. F5 mirror neurons were recorded from two monkeys under four different experimental conditions: when the monkey executed noisy actions (e.g. breaking peanuts, tearing sheets of paper apart, and similar actions); when the monkey saw and heard, or just saw or just heard the same actions performed by another individual. The results showed that a consistent percentage of the tested mirror neurons fired when the monkey *executed* the action, just *observed* or just *heard* the same action performed by another agent (see Kohler *et al.* 2001, 2002).

These 'audio-visual mirror neurons' not only responded to the sound of actions, but also discriminated between the sounds of different actions. The actions whose sounds were preferred were also the actions producing the strongest responses when observed or executed. It did not matter at all for the activity of this neural network if the actions were specified at the motor, visual or auditory level. The activation of the premotor neural network controlling the execution of action A in the presence of sensory information related to the same action A, can be characterized as simulating action A.

The multimodal-driven simulation of action goals instantiated by neurons situated in the ventral premotor cortex of the monkey instantiates properties that are strikingly similar to the symbolic properties so characteristic of human thought. The similarity to conceptual content is quite appealing: the same conceptual content ('the goal of action A') results from a multiplicity of states subsuming it: sounds, observed and executed actions. These states, in turn, are subsumed by differently triggered patterns of activations within a population of 'audio-visual mirror neurons'.

The *action simulation* embodied by audio-visual mirror neurons is indeed similar to the use of predicates: the verb 'to break' is used to convey a meaning that can be used in different contexts: 'Seeing someone breaking a peanut', 'Hearing someone breaking a peanut', 'Breaking a peanut'. The predicate, similarly to the responses in audiovisual mirror neurons, does not change depending on the context to which it applies, nor depending on the subject/agent performing the action. All that changes is the context the predicate refers to.

The general picture conveyed by these results is that the sensorimotor integration supported by the premotorparietal F5-PF mirror-matching system instantiates simulations of actions utilized not only to generate and control goal-related behaviours, but also to provide a meaningful account of the goals and purposes of others' actions, by means of their simulation.

What is the importance of these data for our understanding of human social cognition? Several studies using different experimental methodologies and techniques have also demonstrated the existence of a similar mirror system in humans, matching action observation and execution (see Fadiga et al. 1995; Grafton et al. 1996; Rizzolatti et al. 1996b; Decety et al. 1997; Cochin et al. 1998; Hari et al. 1998; Iacoboni et al. 1999; Buccino et al. 2001). In particular, it is interesting to note that brain imaging experiments in humans have shown that during action observation there is a strong activation of premotor and parietal areas, the likely human homologue of the monkey areas in which mirror neurons were originally described (Grafton et al. 1996; Rizzolatti et al. 1996b; Decety et al. 1997; Decety & Grèzes 1999; Iacoboni et al. 1999; Buccino et al. 2001).

In humans, as in monkeys, action observation constitutes a form of action simulation. As anticipated above, this kind of simulation, however, is different from the simulation processes occurring during visual and motor imagery. Action observation *automatically triggers action simulation*. In mental imagery, as we have seen, the simulation process is triggered by a deliberate act of the will: one purposely decides to imagine oneself observing something or doing something.

An empirical validation of this difference comes from brain imaging experiments. If we compare the motor centres activated by action observation with those activated during action imagery, we will notice that only the latter leads to the activation of pre-SMA and of the primary motor cortex.

That said, it appears nonetheless that both mental imagery and action observation are kinds of simulation. The main difference is what triggers the simulation process: an internal event in the case of mental imagery, and an external event in the case of action observation. This difference leads to slightly different patterns of brain activation. However, both conditions share a common mechanism: the simulation of actions by means of the activation of parietal-premotor cortical networks. This process of automatic simulation constitutes also a level of understanding, a level that does not entail the explicit use of any theory or symbolic representation.

(c) Imitation

The neural bases of human imitation have just begun to be unravelled with the aid of the new brain imaging techniques. The first study showing which parts of the brain are activated during observation and actual, *nondeferred* imitation of the same motor behaviour was published only three years ago (Iacoboni *et al.* 1999). In their study, Iacoboni *et al.* contrasted conditions in which subjects observed hand movements (finger lifting), with conditions in which the subject had to imitate the observed movement. The results showed a cortical network active during both observation and imitation, with greater activation during the second condition. This circuit comprises the ventral premotor cortex, the posterior parietal cortex and the posterior region of the STS.

An interesting and unexpected result of the study of Iacoboni *et al.* (1999) was that the STS region, traditionally considered a purely sensory area, was more activated during imitation than during action observation. If the function of the STS were solely to provide a visual description of the observed action, it is hard to explain why it should be more active during imitation, since the imitated action was identical to that observed.

A possible explanation is that the activation of the STS during action imitation reflected the expected visual consequence of the imitated action, in other words the neural correlate of the activation of the forward model of the action, *simulating the sensory consequences of the action* to be imitated.

The results of a second fMRI study by the same authors corroborated this hypothesis (Iacoboni *et al.* 2001). In this second study, subjects were required to observe and imitate hand actions in two different configurations. During the *specular* configuration, subjects had to observe or imitate with their right hand a left-hand action. During the *anatomical* configuration, subjects had to observe or imitate with their right hand a right-hand action. The results showed that: (i) in the observation condition, STS activation was stronger when the observed hand was the right one; (ii) in the imitation condition, STS activation was stronger when the imitated hand was the left. A straightforward interpretation of these results holds that in order to imitate the observed action, the internal model of the action predicts *via simulation* the sensory consequences of the impending imitative action, thus allowing the possibility of establishing a match with the action to be imitated, and eventually bringing about corrections, if needed to attain a better match.

It appears therefore that actual imitation of observed actions involves a network of brain areas whose activation can be accounted for in terms of simulation.

(d) Empathy

As proposed by Damasio (1994, 1999), one of the mechanisms enabling feelings of emotion to emerge is probably the activation of neural 'as if body loops'. These automatic, implicit and non-reflexive simulation mechanisms, bypassing the body proper through the *internal* activation of sensory body maps, create a representation of emotion-driven body-related changes.

As anticipated above, my proposal is that the activation of these '*as if* body loops' can probably also be triggered by the observation of the behaviour of other individuals (see Adolphs *et al.* 2000; Goldman & Gallese 2000; Gallese 2001).

Preliminary evidence suggests that the same neural structures that are active during the experience of sensations and emotions are also active when the same sensations and emotions are to be detected in others. I take this type of externally driven activation to be a further instance of simulation. A whole range of different 'mirrormatching mechanisms' instantiating simulation routines might therefore be present in our brain. What does this preliminary evidence look like?

Hutchison *et al.* (1999) studied pain-related neurons in the human cingulate cortex, by investigating whether neurons in the anterior cingulate cortex of locally anaesthetized but awake patients responded to painful stimuli. These authors reported that neurons responded not only to noxious mechanical stimulation applied to the patient's hand, but also when the patient watched pinpricks being applied to the examiner's fingers. Both applied and observed painful stimuli elicited the same response in the same neurons. *Simulated* painful experience activates the same neurons normally active during actual painful experience.

Calder *et al.* (2000) showed that a patient who suffered a stroke damaging various cortical and sub-cortical structures such as the insula and the putamen was selectively impaired in detecting disgust in many different modalities (e.g. facial expressions, non-verbal emotional sounds and emotional prosody). The same patient was also selectively impaired in subjectively experiencing disgust and therefore in reacting appropriately to it. These results seem to suggest that once the capacity to *experience* and *express* a given emotion is lost, the same emotion cannot be easily *represented* and *detected* in others.

As we have learned from developmental psychology, emotions constitute one of the earliest ways available to the individual to acquire knowledge about its situation, thus enabling him to reorganize this knowledge in the light of the relations with others. This points to a strong interaction between emotion and action. The coordinated activity of sensorimotor and affective neural systems results in the simplification and automatization of the behavioural responses that living organisms have to produce in order to survive.

The strict coupling between affect and sensorimotor integration is highlighted by a recent study by Adolphs *et al.* (2000), where over 100 brain-damaged patients were reviewed. Among other results, this study showed that the patients who suffered damage to the amygdala and to the sensorimotor cortices were also those who scored worst when asked to rate or name facial emotions displayed by human faces.

A further empirical support to the theory put forward here, of a tight link between simulation and empathy, comes from a recent fMRI study by Iacoboni and coworkers on healthy participants (Carr *et al.* 2001). This study shows that both observation and imitation of facial emotions activate the same restricted group of brain structures, including the premotor cortex, the insula and the amygdala. It is possible to speculate that such a double activation pattern during observation and imitation of emotions could be due to the activity of a neural mirrormatching mechanism, constituting another kind of embodied simulation.

My theory also predicts the existence of 'somatosensory mirror neurons' giving us the capacity to map different body locations when observing the bodies of others, and to refer them to equivalent locations of our body. Experiments are currently underway in the laboratory to test this theory.

To summarize, motor imagery, action observation, imitation and empathy all share the same basic mechanism, the mechanism of embodied simulation: simulation of actions, simulation of emotions, simulation of feelings and sensations. Embodied simulation enables models of real or imaginary worlds to be created. These models are the only way we have to establish a meaningful relationship with these worlds, because these worlds are never objectively given, but always recreated by means of simulated models. In § 8 I provide a multilayered account of simulation that will allow me to describe different forms of interpersonal relations within a unitary framework.

8. THE SHARED MANIFOLD

I have suggested that the establishment of self-other identity is a driving force for the cognitive development of more articulated and sophisticated forms of interpersonal relations. It is this identity relation that enables us to understand others' behaviour, to imitate it, to share the sensations and emotions that others experience.

What I propose is to characterize an identity relation orthogonal to all the dimensions of our social cognition in terms of a 'shared manifold'. It is by means of the shared manifold that we recognize other human beings as similar to us that intersubjective communication, social imitation and the ascription of intentions become possible. The shared manifold can be described at three different levels: (i) a phenomenological level; (ii) a functional level; and (iii) a sub-personal level.

The *phenomenological level* is responsible for the sense of similarity, of being individuals within a larger social com-

munity of people like us, which we experience whenever we confront other human beings. It could be defined as the *empathic* level, provided that empathy is characterized as broadly as I do here. Actions, emotions and sensations experienced by others become meaningful to us because we can *share* their underlying basic format with others.

The *functional level* is characterized in terms of embodied simulation routines, '*as if*' modes of interaction enabling models of self/other to be created. The same functional logic at work during self-control operates also during the understanding of others' behaviour. Both instances are *models of interaction*, which map their referents on identical relational functional nodes. All modes of interaction share a relational character. At the functional logic of operation produces the self/other identity by enabling the system to detect coherence, regularity and predictability, independently from their situated source.

The *sub-personal level* is instantiated as the level of activity of a series of mirror-matching neural circuits. The activity of these neural circuits is, in turn, tightly coupled with multilevel changes within body states. *Mirror neurons instantiate at the sub-personal level the multimodal intentional shared space*. These are the shared spaces that allow us to appreciate, experience and understand the actions we observe, the emotions and the sensations we take others to experience.

There is one further important point that needs to be clarified. The shared manifold of intersubjectivity, as I conceive it, does not entail our experiencing others *as* we experience ourselves. The shared manifold simply enables and bootstraps mutual intelligibility. Of course, self-other identity constitutes only one aspect of intersubjectivity. As highlighted by Husserl (1989; see also Zahavi 2001), it is the otherness (*alterity*) of the other that provides the objective character of reality. The quality of our lived experience (*erlebnis*) of the 'external world' and its content are constrained by the presence of other subjects that are intelligible, while preserving their otherness.

We can recognize the otherness of the other at the subpersonal level also, as this is instantiated by the different neural networks that come into play when I act as opposed to when *others* act.

9. CONCLUSIONS

In this paper I have examined three fundamental aspects of interpersonal relations: imitation, empathy and the ascription of intentions, or mind reading. I have suggested that all these different levels and modes of interaction share a common basic mechanism defining a shared interpersonal space: embodied simulation. I have also suggested that this mechanism is automatic, pre-reflexive and unconscious. Embodied simulation, according to the characterization I provide, is a distinctive functional feature of the brain-body system, its role being that of modelling the interactions between a situated organism and its environment. According to this characterization of simulation, our understanding of interpersonal relations relies on the basic capacity to model the behaviour of other individuals by employing the same resources used to model our own behaviour.

As shown by an impressive amount of converging neuroscientific data, there is a *basic level* of our interpersonal interactions that does not make explicit use of propositional attitudes. This basic level consists of embodied simulation processes that enable the constitution of a shared meaningful interpersonal space.

This shared space relies heavily on action and action imitation, but is not confined to the domain of action. It covers a more global dimension, comprising all aspects defining a life form, from its particular body to its particular affect. This manifold shared space defines the broad range of implicit certainties we entertain about other individuals. Self and other relate to each other, because they both represent opposite extensions of the same correlative and reversible *we-centric* space. The observer and the observed are part of a dynamic system governed by reversible rules.

The shared intersubjective space in which we live from birth continues to constitute a substantial part of our semantic space. When we observe other acting individuals, and face their full range of *expressive* power (the way they act, the emotions and feelings they display), a meaningful embodied interpersonal link is automatically established by means of simulation.

Another interesting source of data that demonstrates the importance of embodied simulation is provided by social psychology. Brandt & Stark (1997) showed that subjects, while listening to syllogisms containing the words 'left' and 'right', moved their eyes prevalently in the horizontal dimension, while tending to move their eyes vertically when listening to sentences containing the words 'above' and 'below'. Spivey et al. (2000) showed that when listening to vignettes describing the top of a skyscraper subjects tended to gaze systematically upward, whereas they tended to look downward when the vignette was describing the bottom of a canyon. All these studies and several more (for a comprehensive review, see Barsalou et al. 2003) show that humans tend to accompany their understanding of sentences or their imaginative activities with body reactions that simulate real experiences. The triggering stimulus, regardless of its external or internal nature, induces a congruent embodied simulation as a default automatic reaction. These studies show a striking relationship between different aspects of higher cognition, such as sentence processing and embodied simulation.

To what extent embodied simulation explains the sophisticated, and unique, human capacity to interpret the inner world of others is an empirical issue to be addressed by future research.

This work was supported by MIURST and ESF.

REFERENCES

- Adolphs, R., Damasio, H., Tranel, D., Cooper, G. & Damasio, A. R. 2000 A role for somatosensory cortices in the visual recognition of emotion as revealed by three-dimensional lesion mapping. *J. Neurosci.* 20, 2683–2690.
- Baron-Cohen, S. 1995 Minblindness. An essay on autism and theory of mind. Cambridge, MA: MIT Press.
- Barsalou, L. W., Niedenthal, P. M., Barbey, A. K. & Ruppert, J. A. 2003 Social embodiment. In *The psychology of learning* and motivation, vol. 43 (ed. B. H. Ross). San Diego, CA: Academic Press.

- Blair, R. J. R. 2003 Facial expressions, their communicatory functions and neuro-cognitive substrates. *Phil. Trans. R. Soc. Lond.* B 358, 561–572. (DOI 10.1098/rstb.2002.1220.)
- Brandt, S. A. & Stark, L. W. 1997 Spontaneous eye movements during visual imagery reflect the content of the visual scene. J. Cogn. Neurosci. 9, 27–38.
- Buccino, G., Binkofski, F., Fink, G. R., Fadiga, L., Fogassi, L., Gallese, V., Seitz, R. J., Zilles, K., Rizzolatti, G. & Freund, H.-J. 2001 Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur. J. Neurosci.* 13, 400–404.
- Byrne, R. W. 1995 The thinking ape. Evolutionary origins of intelligence. Oxford University Press.
- Byrne, R. 2003 Imitation as behaviour parsing. *Phil. Trans. R. Soc. Lond.* B **358**, 529–536. (DOI 10.1098/rstb.2002.1219.)
- Calder, A. J., Keane, J., Manes, F., Antoun, N. & Young, A. W. 2000 Impaired recognition and experience of disgust following brain injury. *Nature Neurosci.* 3, 1077–1078.
- Carr, L., Iacoboni, M., Dubeau, M.-C. Mazziotta, J. C. & Lenzi, G. L. 2001 Observing and imitating emotion: implications for the neurological correlates of empathy. Paper presented at the *First Int. Conf. of Social Cognitive Neuroscience, Los Angeles, 24–26 April 2001.*
- Carruthers, O. & Smith, P. K. (eds) 1996 Theories of theories of mind. Cambridge University Press.
- Cochin, S., Barthelemy, C., Lejeune, B., Roux, S. & Martineau, J. 1998 Perception of motion and qEEG activity in human adults. *Electroenceph. Clin. Neurophysiol.* 107, 287– 295.
- Damasio, A. R. 1994 *Descartes' error*. New York: G. P. Putnam's Sons.
- Damasio, A. R. 1999 The feeling of what happens: body and emotion in the making of consciousness. New York: Harcourt Brace.
- Decety, J. & Grèzes, J. 1999 Neural mechanisms subserving the perception of human actions. *Trends Cogn. Sci.* 3, 172–178.
- Decety, J., Jeannerod, M. & Prablanc, C. 1989 The timing of mentally represented actions. *Behav. Brain Res.* 34, 35–42.
- Decety, J., Sjoholm, H., Ryding, E., Stenberg, G. & Ingvar, D. 1990 The cerebellum participates in cognitive activity: tomographic measurements of regional cerebral blood flow. *Brain Res.* 535, 313–317.
- Decety, J., Jeannerod, M., Germain, M. & Pastene, J. 1991 Vegetative response during imagined movement is proportional to mental effort. *Behav. Brain Res.* 34, 35–42.
- Decety, J., Grezes, J., Costes, N., Perani, D., Jeannerod, M., Procyk, E., Grassi, F. & Fazio, F. 1997 Brain activity during observation of actions. Influence of action content and subject's strategy. *Brain* 120, 1763–1777.
- Fadiga, L., Fogassi, L., Pavesi, G. & Rizzolatti, G. 1995 Motor facilitation during action observation: a magnetic stimulation study. J. Neurophysiol. 73, 2608–2611.
- Farah, M. J. 1989 The neural basis of mental imagery. *Trends Neurosci.* 12, 395–399.
- Farah, M. J. 2000 The neural bases of mental imagery. In *The cognitive neurosciences*, 2nd edn (ed. M. S. Gazzaniga), pp. 965–974. Cambridge, MA: MIT Press.
- Filion, C. M., Washburn, D. A. & Gulledge, J. P. 1996 Can monkeys (*Macaca mulatta*) represent invisible displacement? *J. Comp. Psychol.* **110**, 386–395.
- Fodor, J. 1992 A theory of the child's theory of mind. *Cognition* 44, 283–296.
- Fodor, J. 1994 The elm and the expert: mentalese and its semantics. Cambridge, MA: MIT Press.
- Fox, P., Pardo, J., Petersen, S. & Raichle, M. 1987 Supplementary motor and premotor responses to actual and imagined hand movements with positron emission tomography. *Soc. Neurosci. Abstr.* **13**, 1433.

- Frith, U. & Frith, C. D. 2003 Development and neurophysiology of mentalizing. *Phil. Trans. R. Soc. Lond.* B 358, 459– 473. (DOI 10.1098/rstb.2002.1218.)
- Gallese, V. 2000a The acting subject: towards the neural basis of social cognition. In *Neural correlates of consciousness. Empirical and conceptual questions* (ed. T. Metzinger), pp. 325–333. Cambridge, MA: MIT Press.
- Gallese, V. 2000b The inner sense of action: agency and motor representations. J. Consc. Stud. 7, 23–40.
- Gallese, V. 2001 The 'shared manifold' hypothesis: from mirror neurons to empathy. J. Consc. Stud. 8, 33–50.
- Gallese, V. 2003*a* A neuroscientific grasp of concepts: from control to representation. *Phil. Trans. R. Soc. Lond.* B **358**. (In the press.)
- Gallese, V. 2003*b* The roots of empathy: the shared manifold hypothesis and the neural basis of intersubjectivity. *Psychopathology*. (In the press.)
- Gallese, V. & Goldman, A. 1998 Mirror neurons and the simulation theory of mind-reading. *Trends Cogn. Sci.* 12, 493–501.
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. 1996 Action recognition in the premotor cortex. *Brain* **119**, 593–609.
- Gallese, V., Ferrari, P. F., Kohler, E. & Fogassi, L. 2002a The eyes, the hand, and the mind: behavioral and neurophysiological aspects of social cognition. In *The cognitive animal* (ed. M. Bekoff, C. Allen & G. Burghardt), pp. 451–461. Cambridge, MA: MIT Press.
- Gallese, V., Fogassi, L., Fadiga, L. & Rizzolatti, G. 2002b Action representation and the inferior parietal lobule. In *Attention and performance*, vol. XIX (ed. W. Prinz & B. Hommel), pp. 247–266. Oxford University Press.
- Goldman, A. 1989 Interpretation psychologized. *Mind Lang.* 4, 161–185.
- Goldman, A. 1992 In defense of the simulation theory. *Mind Lang.* 7, 104–119.
- Goldman, A. 1993*a* The psychology of folk psychology. *Behav.* Brain Sci. 16, 15–28.
- Goldman, A. 1993b Philosophical applications of cognitive science. Boulder, CO: Westview Press.
- Goldman, A. 2000 The mentalizing folk. In *Metarepresentation* (ed. D. Sperber), pp. 171–196. London: Oxford University Press.
- Goldman, A. & Gallese, V. 2000 Reply to Schulkin. Trends Cogn. Sci. 4, 255–256.
- Gopnik, A. & Meltzoff, A. N. 1997 Words, thoughts, and theories. Cambridge, MA: MIT Press.
- Gordon, R. 1986 Folk psychology as simulation. *Mind Lang.* **1**, 158–171.
- Grafton, S. T., Arbib, M. A., Fadiga, L. & Rizzolatti, G. 1996 Localization of grasp representations in humans by PET: 2. Observation compared with imagination. *Exp. Brain Res.* 112, 103–111.
- Hari, R., Forss, N., Avikainen, S., Kirveskari, S., Salenius, S. & Rizzolatti, G. 1998 Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proc. Natl Acad. Sci. USA* 95, 15 061–15 065.
- Harris, P. 1989 Children and emotion. Oxford: Blackwell Scientific.
- Hayes, C. M. 1998 Theory of mind in nonhuman primates. Behav. Brain Sci. 21, 101–148.
- Humphrey, N. K. 1976 The social function of intellect. In *Growing points in ethology* (ed. P. Bateson & R. A. Hinde), pp. 303–321. Cambridge University Press.
- Humphrey, N. K. 1978 Nature's psychologists. *New Scient.*, 29 June.
- Humphrey, N. K. 1980 Nature's psychologists. In *Conscious-ness and the physical world* (ed. B. D. Josephson & V. S. Ramachandran), pp. 57–75. Oxford: Pergamon.

- Husserl, E. 1989 Ideas pertaining to a pure phenomenology and to a phenomenological philosophy, second book: studies in the phenomenology of constitution. Dordrecht, The Netherlands: Kluwer.
- Hutchison, W. D., Davis, K. D., Lozano, A. M., Taskev, R. R. & Dostrovsky, J. O. 1999 Pain related neurons in the human cingulate cortex. *Nature Neurosci.* 2, 403–405.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C. & Rizzolatti, G. 1999 Cortical mechanisms of human imitation. *Science* 286, 2526–2528.
- Iacoboni, M., Koski, L. M., Brass, M., Bekkering, H., Woods, R. P., Dubeau, M. C., Mazziotta, J. C. & Rizzolatti, G. 2001 Reafferent copies of imitated actions in the right superior temporal cortex. *Proc. Natl Acad. Sci. USA* **98**, 13 995– 13 999.
- Jeannerod, M. 1994 The representing brain: neural correlates of motor intention and imagery. *Behav. Brain Sci.* 17, 187–245.
- Kohler, E., Umilta, M. A., Keysers, C., Gallese, V., Fogassi, L. & Rizzolatti, G. 2001 Auditory mirror neurons in the ventral premotor cortex of the monkey. *Soc. Neurosci. Abstr.* 27, 129.9.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V. & Rizzolatti, G. 2002 Hearing sounds, understanding actions: action representation in mirror neurons. *Science* 297, 846–848.
- Kosslyn, S. M. 1994 Image and brain: the resolution of the imagery debate. Cambridge, MA: MIT Press.
- Kosslyn, S. M. & Thompson, W. L. 2000 Shared mechanisms in visual imagery and visual perception: insights from cognitive science. In *The cognitive neurosciences*, 2nd edn (ed. M. S. Gazzaniga), pp. 975–985. Cambridge, MA: MIT Press.
- Kosslyn, S. M., Ball, T. M. & Reiser, B. J. 1978 Visual images preserve metric spatial information: evidence from studies of image scanning. *J. Exp. Psychol. Hum. Percept. Perform.* 4, 47–60.
- Kosslyn, S. M., Alpert, N. M., Thompson, W. L., Maljkovic, V., Weise, S., Chabris, C., Hamilton, S. E., Rauch, S. L. & Buonanno, F. S. 1993 Visual mental imagery activates topographically organized visual cortex: PET investigations. *J. Cogn. Neurosci.* 5, 263–287.
- Le Bihan, D., Turner, R., Zeffiro, T. A., Cuenod, C. A., Jezzard, P. & Bonnerot, V. 1993 Activation of human primary visual cortex during visual recall: a magnetic resonance imaging study. *Proc. Natl Acad. Sci. USA* **90**, 11 802–11 805.
- Leslie, A. M. 1987 Pretence and representation. The origins of 'theory of mind'. *Psychol. Rev.* 94, 412–426.
- Lipps, T. 1903 Einfulung, innere nachahmung und organenempfindung. In Arch. F. Ges. Psy., vol. I, part 2. Leipzig: W. Engelmann.
- Meltzoff, A. N. 2002 Elements of a developmental theory of imitation. In *The imitative mind: development, evolution and brain bases* (ed. W. Prinz & A. Meltzoff), pp. 19–41. Cambridge University Press.
- Meltzoff, A. N. & Borton, R. W. 1979 Intermodal matching by human neonates. *Nature* 282, 403–405.
- Meltzoff, A. N. & Moore, M. K. 1977 Imitation of facial and manual gestures by human neonates. *Science* 198, 75–78.
- Meltzoff, A. N. & Moore, M. K. 1997 Explaining facial imitation: a theoretical model. *Early Dev. Parent.* 6, 179–192.
- Parsons, L., Fox, P., Downs, J., Glass, T., Hirsch, T., Martin, C., Jerabek, J. & Lancaster, J. 1995 Use of implicit motor imagery for visual shape discrimination as revealed by PET. *Nature* 375, 54–58.
- Porro, C. A., Francescato, M. P., Cettolo, V., Diamond, M. E., Baraldi, P., Zuiani, C., Bazzocchi, M. & di Prampero, P. E. 1996 Primary motor and sensory cortex activation dur-

ing motor performance and motor imagery. A functional magnetic resonance study. *J. Neurosci.* 16, 7688–7698.

- Povinelli, D. J., Bering, J. M. & Giambrone, S. 2000 Toward a science of other minds: escaping the argument by analogy. *Cogn. Sci.* 24, 509–541.
- Premack, D. & Woodruff, G. 1978 Does the chimpanzee have a theory of mind? *Behav. Brain Sci.* 1, 515–526.
- Prigman, G. W. 1995 Freud and the history of empathy. Int. J. Psycho-Anal. 76, 237–252.
- Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. 1996a Premotor cortex and the recognition of motor actions. *Cogn. Brain Res.* 3, 131–141.
- Rizzolatti, G., Fadiga, L., Matelli, M., Bettinardi, V., Paulesu, E., Perani, D. & Fazio, G. 1996b Localization of grasp representations in humans by PET: 1. Observation versus execution. *Exp. Brain Res.* 111, 246–252.
- Rizzolatti, G., Fogassi, L. & Gallese, V. 2000 Cortical mechanisms subserving object grasping and action recognition: a new view on the cortical motor functions. In *The cognitive neurosciences*, 2nd edn (ed. M. S. Gazzaniga), pp. 539–552. Cambridge, MA: MIT Press.
- Rizzolatti, G., Fogassi, L. & Gallese, V. 2001 Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Neurosci. Rev.* **2**, 661–670.
- Roland, P., Larsen, B., Lassen, N. & Skinhoj, E. 1980 Supplementary motor area and other cortical areas in organization of voluntary movements in man. *J. Neurophysiol.* 43, 118–136.
- Romano, G. 2002 La mente mimetica: riflessioni e prospettive sulla teoria della simulazione mentale. PhD thesis, Cognitive Sciences, University of Siena, Italy.
- Roth, M., Decety, J., Raybaudi, M., Massarelli, R., Delon-Martin, C., Segebarth, C., Morand, S., Gemignani, A., Decorps, M. & Jeannerod, M. 1996 Possible involvement of primary motor cortex in mentally simulated movement: a functional magnetic resonance imaging study. *NeuroReport* 7, 1280–1284.
- Schaal, S., Ijspeert, A. & Billard, A. 2003 Computational approaches to motor learning by imitation. *Phil. Trans. R. Soc. Lond.* B 358, 537–547. (DOI 10.1098/rstb.2002.1258.)
- Schnitzler, A., Salenius, S., Salmelin, R., Jousmaki, V. & Hari, R. 1997 Involvement of primary motor cortex in motor imagery: a neuromagnetic study. *NeuroImage* 6, 201–208.
- Spivey, M., Tyler, M., Richardson, D. & Young, E. 2000 Eye movements during comprehension of spoken scene descriptions. In *Proc. 22nd A. Conf. Cogn. Sci. Soc.*, pp. 487–492. Mahwah, NJ: Erlbaum.
- Stern, D. N. 1985 The interpersonal world of the infant. London: Karnac Books.
- Tomasello, M. & Call, J. 1997 Primate cognition. Oxford University Press.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. & Rizzolatti, G. 2001 'I know what you are doing': a neurophysiological study. *Neuron* 32, 91–101.
- Visalberghi, E. & Fragaszy, D. 1990 Do monkeys ape? In 'Language' and intelligence in monkeys and apes (ed. S. T. Parker & K. R. Gibson), pp. 247–273. Cambridge, MA: Cambridge University Press.
- Visalberghi, E. & Fragaszy, D. 2001 Do monkeys ape? Ten years after. In *Imitation in animals and artifacts* (ed. K. Dautenhahn & C. Nehaniv). Boston, MA: MIT Press.
- Whiten, A. & Byrne, R. W. 1997 Machiavellian intelligence 2: evaluations and extensions. Cambridge University Press.
- Whiten, A. & Custance, D. 1996 Studies of imitation in chimpanzees and children. In *Social learning in animals: the roots* of culture (ed. C. M. Hayes & B. G. Galef), pp. 291–318. Academic Press.

- Wohlschläger, A., Gattis, M. & Bekkering, H. 2003 Action generation and action perception in imitation: an instance of the ideomotor principle. *Phil. Trans. R. Soc. Lond.* B 358, 501–515. (DOI 10.1098/rstb.2002.1257.)
- Wolpert, D. M., Doya, K. & Kawato, M. 2003 A unifying computational framework for motor control and social interaction. *Phil. Trans. R. Soc. Lond.* B 358, 593–602. (DOI 10.1098/rstb.2002.1238.)
- Yue, G. & Cole, K. 1992 Strength increases from the motor program: comparison of training with maximal voluntary and imagined muscle contractions. *J. Neurophysiol.* 67, 1114–1123.
- Zahavi, D. 2001 Beyond empathy. Phenomenological approaches to intersubjectivity. J. Consc. Stud. 8, 151-167.

GLOSSARY

AIM: active intermodal mapping

fMRI: functional magnetic resonance imaging

SMA: supplementary motor area

STS: superior temporal sulcus

ToM: theory of mind

TT: theory-theory