

Running head: Macaque Mirror Neurons

**Mirror, Mirror in the Brain,
What's the Monkey Stand to Gain?**

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Abstract

Primatologists generally agree that monkeys lack higher-order intentional capacities related to theory of mind. Yet the discovery of the so-called “mirror neurons” in monkeys suggests to many neuroscientists that they have the rudiments of intentional understanding. Given a standard philosophical view about intentional understanding, which requires higher-order intentionality, a paradox arises. Different ways of resolving the paradox are assessed, using evidence from neural, cognitive, and behavioral studies of humans and monkeys. A decisive resolution to the paradox requires substantial additional empirical work and perhaps a rejection of the standard philosophical view.

Keywords: Intentionality, mirror neurons, action understanding, animal mind

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Abstract

Primatologists generally agree that monkeys lack higher-order intentional capacities related to theory of mind. Yet the discovery of the so-called “mirror neurons” in monkeys suggests to many neuroscientists that they have the rudiments of intentional understanding. Given a standard philosophical view about intentional understanding, which requires higher-order intentionality, a paradox arises. Different ways of resolving the paradox are assessed, using evidence from neural, cognitive, and behavioral studies of humans and monkeys. A decisive resolution to the paradox requires substantial additional empirical work and perhaps a rejection of the standard philosophical view.

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Introduction

Here are three mutually incompatible propositions:

1. To understand the intentional actions of others requires knowledge of the intentional states (i.e., beliefs and desires) which (rationally) motivated those actions.
2. Monkeys do not have knowledge of the intentional states (beliefs and desires) motivating the actions of others.
3. Monkeys understand the intentional actions of other monkeys.

Proposition 1 is based on the received Aristotelian analysis of intentional action and a commonsense view about understanding. Proposition 2 represents a consensus view among primatologists about absence of higher-order ‘theory of mind’ capacities in monkeys. Proposition 3 reflects a common interpretation of the functions of so-called “mirror neurons” found in the ventral premotor (F5) cortex of macaque monkeys (e.g., Gallese & Goldman, 1998; Rizzolatti & Craighero, 2004; Fogassi et al., 2005).

Taken at face value, then, this inconsistent triad presents a paradox for understanding the contribution of F5 neurons in macaques to their cognitive capacities. This paradox does not arise for humans because the human analogue to 2 is the obvious candidate for rejection. Nevertheless, the considerations relevant to resolving the paradox for monkeys are also important for a properly skeptical interpretation of the neurological evidence about the mirror neuron system in humans (see Debes, submitted).

In this paper I discuss each of the possibilities for resolving the paradox by rejecting one of the three propositions. Although my philosophical sympathies presently lie with rejecting Proposition 1, some of the arguments depend on empirical knowledge that is presently lacking. Nevertheless, I describe an approach to understanding the functions of F5 mirror neurons in macaques which entails a non-traditional understanding of the relationship between intentionality, in its ordinary English sense of 'purposefulness', and intentionality, in the philosophers' technical sense of 'aboutness' or representational content. Because my aim is to put the most pressure on the most philosophical leg of the inconsistent triad, this paper discusses the propositions in reverse order, from 3 to 1.

3. Monkeys understand the intentional actions of other monkeys

A subpopulation of the neurons of the ventral premotor cortex (area F5) of rhesus macaques appear to play a dual role in action and perception of action by these monkeys (di Pellegrino et al., 1992; Gallese et al., 1996). These neurons are active during the premotor and motor phases of specific actions as well as during observation of similar actions performed by other individuals, earning them the moniker "mirror neurons". Prior to the discovery of these neurons in rhesus macaques in the 1990s, Proposition 3 would have been the most likely candidate for rejection. Even given what is now known about these neurons, it may retain that status. Nevertheless, rejection comes at the cost of making the neural findings quite puzzling.

F5 mirror neurons in macaques are specialized by body part (e.g., hand vs. mouth), and they show a moderate to strong degree of specificity for particular actions (e.g., grasping vs. holding vs. tearing). This specificity is congruent between motor tasks and vision -- i.e., the same neurons are active when the

monkey is grasping and when perceiving grasping, when holding and perceiving holding, etc. This congruence is 'strict' in about one-third of the F5 mirror neurons, and 'broad' in the remainder, meaning that their activation during perception does not require exactly the same action as in their motoric role (Rizzolatti & Craighero, 2004). It is also important to note that the level and pattern of activation of these neurons is generally not identical between the motoric and perceptual cases. Of particular interest to Proposition 3 is that F5 mirror neurons appear to be sensitive to the goal-directedness of action. For instance, neurons that are activated during perception of goal-directed grasping motions are not activated by similar grasping motions which do not result in an object being touched (Gallese et al., 1996). Remarkably, the completion of the goal does not need to be directly observed; showing a monkey an object, obscuring it from view, then initiating a reaching motion to grasp the object behind the obstruction is sufficient to activate F5 neurons in the observing monkey (Umiltà et al., 2001).

While single-cell recordings of F5 neurons have thus far been limited to monkeys, a variety of evidence derived from EEG and fMRI exists to support the claim of the homologous brain region in humans serving similar functions (Fadiga et al., 1995; Rizzolatti & Craighero; Iacoboni et al., 2005). Indeed, the evidence for "mirroring" properties in other parts of the brain has led to the idea of a human mirror neuron system (Rizzolatti & Craighero, 2004; Iacoboni et al., 2005). On the basis of their fMRI study, Iacoboni et al. claim that ascribing intentions by inferring the goals of actions is something that the human mirror system does automatically.

In light of these discoveries, philosophers and neuroscientists have found it tempting to speculate that F5 mirror neurons may support higher-order intentionality in monkeys. Thus, for example, Gallese & Goldman write, "One possible function is to enable an organism to detect certain mental states of observed conspecifics. This function might be part of, or a precursor to, a more general mind-reading ability" (1998, p.493). Similarly, Rizzolatti & Craighero (2004) identify 'action understanding' as the perceptual function of F5 mirror neurons in macaques. (See also Fogassi et al., 2005.)

The dual role of F5 mirror neurons in perception and action is reflected in their classification as 'visuomotor' neurons. As such, they would seem to provide the perfect neural mechanism for the

proverbial “Monkey see, monkey do.” Aphorisms aside, however, most comparative psychologists think that ‘monkey see’ is a poor predictor for ‘monkey do’ — the general consensus is that monkeys are not good imitators, with the possible exception of neonates (Ferrari et al., 2006). Definitions of imitation are controversial (see Thorpe, 1956; Whiten & Ham, 1992; Heyes, 1994; Tomasello & Call, 1997; Miklosi, 1999; Byrne 2004), but successful cognitive imitation of an action is often taken to require both a close match of the motor patterns between model and imitator, and recognition of the purpose or intention underlying the action (Tomasello & Call, 1997). What is not controversial is that, regardless of definition, the imitation skills of monkeys that have been tested are much poorer than those of humans and the great apes (Byrne 2004). In humans, fMRI imaging reveals that regions included in the mirror neuron system are significantly active during human imitation (Iacoboni et al., 1999). However, in light of the absence of strong evidence for imitation in monkeys, the reasoning of most neuroscientists is represented by Rizzolatti & Craighero (2004, p. 172), who write: “Therefore, the primary function of mirror neurons [in monkeys] cannot be action imitation.” Byrne (2004) also remarks, “Monkeys are, *pace* conventional wisdom, not great imitators (Visalberghi & Fragaszy, 1990); mirror neurons are unlikely to have evolved originally as part of an imitative learning system, but rather as part of social comprehension, allowing subtle dispositions and objectives of social companions to be discerned.”

Action imitation nicely connects perception to action, and exploits the congruence between visual and motor tasks to explain successful imitation as a result of perceptual priming of imitators’ own actions. On abandoning imitation as the primary function of F5 mirror neurons in macaques, Rizzolatti & Craighero fall back on the more generic notion of ‘action understanding’. But this notion shares a common deficit with Gallese & Goldman’s (admittedly tentative) suggestion that mirror neurons function to detect mental states. Neither of these functional descriptions yields specific predictions for monkey behavior. Without operationalizing these ideas about function beyond measurements of the neurons’ responses to action-related stimuli, it would be circular to claim that the neural responses settle the question of whether F5 mirror neurons serve action understanding.

Neither Gallese & Goldman nor Rizzolatti & Craighero operationalize the notions of mental state detection or action understanding, but they do appeal to additional evidence to bolster their claims about

function. Rizzolatti & Craighero refer to two studies to support their claim that mirror neurons in monkeys serve the function of understanding actions. They cite the study by Umiltà et al. (2001), mentioned above, to argue that because similar movements do not evoke the same response in F5 mirror neurons unless the goal is the same (i.e., picking up an object), it is the meaning of the action not the visual features specifically which are responsible for activating the neurons. To support this claim about meaning, Rizzoli & Craighero cite a study by Kohler et al. (2002) in which it was shown that an auditory cue (sound of ripping) was sufficient to activate about 15% of the F5 mirror neurons normally activated by directly observing ripping. While these results are interesting, they would seem to be equally well predicted by a first-order association between auditory and visual stimuli (seeing ripping and hearing ripping). No understanding of the intentionality of the ripping agent seems to be required. Without identification of further behavioral consequences of 'action understanding', the encoding of such events by macaque F5 neurons does not provide a strong basis for asserting that monkeys understand the intentional actions of others.

Gallese & Goldman cite a study of free-ranging rhesus macaques who were observed withholding food vocalizations when vocalizing would have required them to share the food with others but where there was also a reduced chance of getting caught by other group members (Hauser, 1992; see also Hauser & Marler, 1993a,b). Hauser (1992) describes the withholding of food calls as deception and Gallese & Goldman assert that deception “calls for the existence of second-order intentionality” (1998, p. 499) but they don't explain their reasoning. While it is true that some philosophical analyses of deception invoke second-order intentionality, biologists also recognize a category of functionally deceptive behavior that does not commit them to higher-order states in deceivers (e.g., Munn, 1986). Monkeys who fail to alert their troop mates to the presence of food may have succeeded in functionally deceiving them about the presence of food, but the withholding of food vocalizations might be explained, without invoking higher-order intentionality, as the result of a first-order assessment of the likelihood of being caught with the food.

Nevertheless, there is some evidence from human fMRI studies that neurons related to the mirror system are activated during assessment of deceptive behavior (Grèzes et al., 2004). To connect F5 neurons to

intentionally deceptive abilities in monkeys, there would need to be plausible grounds for thinking that the visuomotor congruence of these neurons facilitates deceptive behavior or the detection of such behavior in others. If the congruent properties of F5 neurons in monkeys do support deception, then we should predict that the ability of a monkey to engage in deception would be different for actions which involve neurons with congruent visuomotor properties than for actions for which there is reduced or no congruent visuomotor neural activity. For example, we would expect there to be a difference between a monkey's deceptive capacities with respect to its grasping intentions and its capacity to engage in deceptive actions for which there are no specific mirror neurons, or the activated F5 neurons are much less specific. A contrast between deceptive hand movements and deceptive vocal communication might be especially interesting in light of Rizzolatti & Craighero's (2004) discussion of mouth-related F5 neurons that respond when communicative mouth movements are observed, but which are more strongly connected to ingestive functions than to vocalization on the motor side. If the 'mirroring' function of F5 neurons is significant for deception, then the looser linkage for actions involving mouth movements should have functional consequences when compared to actions involving hand movements.

The important point here is that the evaluation of Proposition 3 is a matter for further empirical investigation, requiring appropriately-designed behavioral tasks. If monkeys engage in intentional deception, we should seek evidence that their deceptive abilities are somehow structured by the properties of F5 neurons along the lines suggested in the previous paragraph. If there is currently a lack of evidence for imitation by monkeys, perhaps scientists can design more specific experiments in light of predictions that would follow from our knowledge of F5 neurons. One might propose, for example, that monkeys would perform better on imitating actions for which there is a specific, measurable mirroring response during perception of the action to be imitated. A hint in this direction is provided by Kumashiro et al. (2003), who reared Japanese macaques in a home environment that provided intensive interactions with humans, including extensive use of pointing gestures and extensive work to establish shared attention between the human caregivers and the monkeys. They report that these monkeys are more capable of imitating human actions spontaneously than monkeys housed and raised in more typical laboratory conditions. Their experiment is fascinating, but given the apparent need for special rearing it adds to the mystery about the role of F5 neurons for monkeys raised without the same kind of deliberate human

enculturation. Laboratory experiments testing the linkage of F5 neurons to imitative abilities are yet to be developed. It is worth remarking, too, that we have no evidence about the extent to which the development of F5 neurons in laboratory animals is a good model for the neural development of free-ranging monkeys in the wild. Studying the latter would provide better information about F5 neuron function, if the relatively impoverished social and ecological conditions of captive animals results in decreased functionality. However, free-ranging studies would require new technologies for collecting neural data in naturalistic conditions.

Because the attention to mirror neurons has been largely driven by excitement about their potential for grounding higher-order intentionality — intentional states representing the mental states of others — there has been little philosophical discussion of their role for the ordinary purposefulness (what I'll call the 'basic intentionality') of actions. F5 neurons are active just prior to and during grasping, holding, etc., and the purposefulness of these actions is generally just assumed. Any claim that F5 neurons serve higher-order intentional functions in observers during perception depends on these neurons serving a basic intentional function in the observed individuals. If what's detected by F5 neurons during perception is not appropriately 'mental', then the detection doesn't count as 'mind reading'. I do not wish to challenge the claim that the (pre)motor functions of F5 neurons are relevant to the basic intentionality of action, although a denial of this claim provides a route to denying Proposition 3. (I.e., one could join the strict behaviorists in denying that monkeys are intentional agents; it is a corollary of Proposition 3 that monkeys act intentionally.) Nevertheless, one might suspect that any correlation between the activity of F5 neurons in an observer and the intentional properties of the observed individual is a happy coincidence that is only of indirect cognitive significance to the observer. Furthermore, given that monkeys typically can see their own hands when reaching for things, there is an associative explanation for the visuomotor congruence of F5 neurons (Keysers & Perrett, 2004).

Compare what we might say about the neural responses of a predator to the high bounding (stotting) of an antelope that is running away. Antelopes stott when they have seen a predator, so the neurons in the predator that detect stotting are also correlated to the mental state of the prey having seen the predator. Does this mean that it is a function of these neurons to detect the prey-has-seen-predator mental states of

prey? How you answer this question depends, in part, on some conceptual issues about what one means by 'function' (Allen & Bekoff, 1994) but (almost) whatever position one takes on those issues, it seems that focusing on the perceptual side alone provides an inadequate basis for an answer. We need to know whether there are any behavioral consequences of having a prey-seeing-predator detector that aren't predicted by having a stotting detector. All other things being equal, a predator that has learned to give up the chase when it detects stotting is as biologically fit as one that has learned to give up the chase when it is informed by the prey's stotting that it has been seen by the prey. A deflationary account of the neural responses to stotting, that does not invoke any understanding of intentionality, seems quite adequate. Similarly for F5 neurons, when the focus is on the perceptual side only, it is far from clear what consequences there are for monkeys' behavior if F5 neurons are mental state detectors.

Nevertheless, there are significant differences between the stotting example and the responsive range of F5 neurons. Stotting seems to be an evolved behavior that has characteristics which are specifically designed to be salient to predators, making it easy for operant conditioning in the predator to work to the advantage of prey and predator alike. Furthermore, there is no reason, neurological or behavioral, to think there would be a positive answer to the question of whether the lioness observing a stotting antelope has mapped the antelope's behavior onto her own behavioral repertoire. (This is, of course, an empirical question whose answer it would be preferable to know, instead of guessing; but I'm not holding my breath on this one.) Any attempt to take a similar deflationary approach to F5 neuron function in macaques would be forced to explain away the fact that the actual visuomotor congruence would play no direct functional role. Without a way of connecting the perceptual function of F5 neurons to their motor functions in macaques, we would have two domains of activity for F5 neurons in macaques -- a perceptual domain and a motor domain -- each of which would be functional, but whose functions would be perhaps no more related than the reproductive and eliminative functions of the male urethra. It just happens to be the case that the same channel gets used for two purposes but any similarity between the two is due to the architectural constraints built into the channels.

On such a view, a possible evolutionary scenario is that the common ancestor of macaques and humans had independently functioning perceptual and motor systems using the same F5 machinery, but that

somewhere along the way to the great apes and humans, the congruence between the visual and motor functions of F5 neurons was co-opted for imitation and other higher-order capacities. In this case, there is a sense in which it would be accurate to say, with Gallese & Goldman, that the congruent F5 activity during action observation and action performance in monkeys is a precursor to 'mind-reading' abilities. But this tells us no more about the current cognitive abilities of monkeys than the fact that fins are evolutionary precursors to legs tells us anything about the walking abilities of fish. A more radical possibility that is also compatible with the co-option account is that the activity of F5 neurons during perception is strictly functionless in macaques -- i.e., it is epiphenomenal with respect to the macaques' cognitive capacities. While this single-function thesis has not been ruled out, I will assume that the specificity of F5 mirror neuron responses during perception make it unlikely. Nevertheless, because the term "mirror neuron" appears to prejudge the issue of function, we should prefer to refer to these neurons by their location (F5) whenever there is a danger of over-interpretation.

In light of all this uncertainty, the rejection of Proposition 3 may seem like a reasonable option. However, at least two considerations motivate considering the rejection of the other propositions. First, the empirical chips may yet fall in favor of the claim that monkeys have some kind of understanding of intentional agency, albeit more limited than humans. Indeed, Fogassi et al. (2005) presented evidence that F5 neuron activity in monkeys is sensitive to differences of intention in otherwise identical grasping actions (grasping-to-eat vs. grasping-to-place a food item). If the chips do fall this way, then something else will have to go, and it's worth considering the options now. Second, even if Proposition 3 does seem like the most likely candidate for rejection, other options present a greater challenge to the status quo, making them philosophically more interesting. More specifically, the *simulationist* view of social cognition favored by Gallese & Goldman (1998; see also Gordon, 2004) suggests that understanding of intentional actions need not be implemented as the kind of theoretical knowledge envisaged in the standard 'theory theory' account of human folk-psychological competence. In other words, mental simulation may enable a kind of understanding of intentional action that does not depend on explicit knowledge of the beliefs and desires alleged to be motivating the actions of others.

2. Monkeys do not have knowledge of the intentional states (beliefs and desires) motivating the actions of others.

What do macaque monkeys understand about the intentionality of others? “Very little,” would seem to be the consensus answer among primatologists, given the repeated failure of monkeys (many species) to perform well on various behavioral tests, such as ‘false belief’ tasks (Wimmer & Perner, 1983), laboratory tests of imitation, and other instruments of the ‘theory of mind’ industry, such as mirror self-recognition (Gallup, 1970; Gallup et al. 2002). Cognitive ethologists studying free-ranging populations were also skeptical that evidence in monkeys would be forthcoming. For instance, careful ethological observation of vervet monkeys communicating about predators led Cheney & Seyfarth (1990) to conclude that vervets do not distinguish whether conspecifics are knowledgeable or ignorant of a predator’s presence. However, more recent work by Laurie Santos (Santos et al., 2006) with free-ranging rhesus macaques, points in the opposite direction and will be described below.

The tasks that were originally used to test primates’ understanding of the mental states of others come from a tradition within comparative psychology which seeks general methods that can be applied to a variety of species. A more ethologically oriented approach might be to devise experiments that challenge animals in ways that are more ecologically relevant given the evolutionary history of their species. This kind of approach has, in fact, been taken by Hare and colleagues (see Hare and Wrangham, 2002 for an overview) in challenging the negative theory of mind results reported by Povinelli (2000). Hare’s innovation was to investigate chimpanzees’ knowledge of what others do and do not see under socially competitive conditions. Hare and Wrangham write that “when two pieces of food were placed in view of both competitors, the dominant subject retrieved the majority of food. If one piece of food was hidden behind an occluder from the dominant while the subordinate could see both, as subordinates, subjects preferred to retrieve the hidden piece of food that the dominant could not see. In addition, if one piece was hidden behind an occluder from the subordinate but the dominant could see both, as dominants, subjects preferred to retrieve the visible piece of food first to assure they obtained both pieces” (2002, p. 366). They argue that Povinelli’s negative results are due to the use of a ‘cooperative-communicative paradigm’ that is less natural for chimpanzees — that is, Povinelli asks his chimps to engage in

cooperative communication about food, whereas competition for food is the more normal problem that they face.

The point here is not to enter the debate about Povinelli's deflationary claims regarding chimpanzee theory of mind (for that, see Allen, 2002). Rather, the point is that one might hold out similar hope that novel species-appropriate tests for macaques might provide evidence for knowledge that beliefs or desires motivate (at least some of) the actions of others, and that macaques can use this knowledge to guide their own behavior. Such an approach is being pursued by Santos in her studies of free-ranging rhesus macaques on the island of Cayo Santiago in Puerto Rico (Santos et al., 2006). Like Hare, Santos places her subjects in a situation in which they are competing for food (in this case with humans) and finds that the monkeys appear to be sensitive to what the humans can or cannot see and hear. These innovative experiments go part way towards providing a case against Proposition 2, and of resolving the paradox in this fashion (see also Lyons, Santos & Keil, 2006).

Nevertheless, there remains widespread skepticism about the claim that monkeys have knowledge of the beliefs and desires of others, and even if pursuing other ideas generated by the study of F5 neurons revealed that limited forms of imitation and deception are within the range of macaques, these results would not provide strong evidence for knowledge of beliefs and desires as this is traditionally understood (although such results might, as Kristin Andrews pointed out to me, provide further support for Proposition 3). If macaques understand something about the intentional actions of other macaques, and it is not because they have knowledge of beliefs and desires of the other animal, what are we to make of the remaining proposition?

1. To understand the intentional actions of others requires knowledge of the intentional states (i.e., beliefs and desires) which (rationally) motivated those actions.

Proposition 1 presupposes a traditional philosophical analysis of intentional action according to which intentional action is behavior that is appropriately (rationally) motivated by beliefs and desires. This

traditional analysis links the two notions of intentionality that are in play throughout the discussion of F5 neuron functions. First, actions are said to be intentional in the ordinary English sense of 'purposefulness'. Second, beliefs and desires are said to be 'intentional' in the philosophically technical sense of being states with representational content. On the traditional analysis, intentional (purposeful) action is motivated by intentional (contentful) states according to an ends-means reasoning process that has been represented by philosophers since Aristotle in the format of a 'practical syllogism'.

One may reject Proposition 1 either by accepting the presupposed analysis of intentional actions, and offering a different condition for understanding them, or by rejecting the traditional analysis. The first approach yields an attenuated notion of understanding action. The second approach yields a novel understanding of intentional actions.

It might seem implausible to accept the traditional analysis while denying that knowledge of the underlying intentional states is required for understanding of intentional actions. If intentional action is appropriately motivated behavior, then how could one understand the action without having knowledge of the motivating states? The notion of understanding is, however, vague enough to allow this as a possibility. Water is a product of hydrogen and oxygen, and while one might deny that someone who knows nothing of hydrogen and oxygen can have a *full* understanding of water, nevertheless, one can understand quite a lot about water without knowing its chemical composition. Likewise, then, perhaps monkeys can partially understand each other's intentional actions without knowing anything about the intentional states assumed to produce them. I concede that the traditionalist might want to dig in her heels at this point and reject this notion of partial understanding. Such a traditionalist — a Davidsonian for instance — has probably already decided that to reject Proposition 3 is the way out of the paradox. But I am exploring the consequences of not making that move, and so will proceed with the idea of partial understanding to see how it might be applied to monkeys. (See also, Hunt et al., 2006 for discussion of the importance of a concept of partial understanding for interpreting animal cognition.)

One way in which such understanding might be manifested is in predicting or anticipating the visible or tangible outcomes of actions, rather than representing their mental causes (this suggestion is made by

several of the participants commenting on Gallese, 2004 -- see, e.g., the commentaries by Proust and Csibra (Forum, 2004)). On such a view, the macaque uses its F5 neurons during perception to anticipate that (for example) an object will end up in the grasp of another, and it does this by using the same machinery that would initiate and sustain a movement that would cause the object to end up in its own grasp. Such anticipation can be generated without any knowledge of the reasons the other has for grasping the object. Indeed, the results of Schubotz & von Cramon (2004) implicate F5 neurons in anticipating the outcomes of abstract non-biological movements.

So long as the ability to anticipate the outcome of other monkeys' actions counts as understanding their intentional actions, then this approach to rejecting Proposition 1 is compatible with accepting Proposition 3, although the significance of the latter is attenuated. Certainly, the functional description of F5 neurons in terms of 'mind reading' would be misleading if this meant nothing more than the ability to anticipate the physical outcome of an organism's movements. Furthermore, deflating action understanding in this way makes it harder to see how this function of F5 neurons would constitute a precursor to the full-blown folk-psychological mind-reading capacities that simulation theory is supposed to explain.

In his response to this kind of deflationary proposal, Gallese (in Forum, 2004) proposes that prediction of action outcomes — to avoid connoting a verbal performance we should prefer 'anticipation' to 'prediction' — is an important component of identifying intentions, hence showing that F5 neurons serve an anticipatory function is perfectly compatible with saying that they also function as intention detectors. I'm sympathetic to Gallese's position, but it is important to emphasize that without some way of behaviorally operationalizing the difference between anticipation of action outcomes and detection of intentions, it is unclear whether macaques are capable of the latter as well as the former.

Gallese (2004) also proposes that there is a phenomenological accompaniment to the latter, a feeling of familiarity that comes from what he calls 'intentional attunement'. Perhaps such a feeling would serve to maintain attention, enhancing learning by social facilitation. The spread of potato washing in Japanese macaques, described by Imanishi in 1952 (de Waal, 2001) shows that monkeys acquire behaviors from those around them. (This is not generally considered direct imitation because it seems that there is a

significant trial and error component involved in each individual's acquisition of the new behavior.) If Gallese is right that intentional attunement plays a role over and above anticipation of physical outcomes, social facilitation is one domain of monkey competence in which the difference might be operationalized.

The conservative approach to rejecting Proposition 1 does not challenge the traditional analysis of intentional action in terms of intentional states (propositional attitudes such as belief and desire) interacting according to a rational calculus of abstract content. On the traditional analysis, to say that a monkey acts intentionally in, say, reaching for a food container, is to say that he believes there is a food container within reach and he desires to hold the container (perhaps because he desires to eat what he believes is in the container) and he believes that reaching for the container will enable him to satisfy his desire(s). The monkey is conceived as having all these beliefs and desires even if he does not realize that he has them (i.e., he has no second-order awareness of his own intentional states). In such a case, his understanding of his own intentional actions may be as partial as his understanding of the actions of others. Perhaps the monkey reaching for the container is cognitively capable of nothing more than anticipating that the container ends up in his grasp or that the food ends up in his mouth, even though (because it is intentional, according to the traditional analysis) his behavior is the outcome of an unconscious (or, at least, unselfconscious) reasoning process that computed over beliefs and desires with propositional content.

One might think this view unstable, teetering as it does between a deflationary understanding of the monkeys' cognitive capacities and an inflationary view of the basis for those capacities as implemented by something like the traditional propositional attitudes. Indeed, insofar as alternative approaches to modeling or explaining the behavior of animals and pre-linguistic infants — for example, dynamical models (Thelen et al., 2001; Beer, in press) or Bayesian models (Luttbeg & Langen, 2004; Valone, 2006; Courville et al., 2006) — do not make use of folk-psychological notions, one might take the monkeys' inability to rationalize their own actions as a *reductio* of the view that one should appeal to rational relations among propositional attitudes in explaining those actions. Nevertheless, the elimination of the propositional attitudes may not be as direct a consequence as proponents of alternative (connectionist, dynamical, causal, or probabilistic) models have sometimes suggested. Eliminativist arguments based on

such models typically depend on a general anti-representationalist claim to the effect that representational notions play no explicit role in formulating the preferred models. However, Beer (in press, ms. p.19) argues that while the “situated, embodied, dynamical” approach to cognitive modeling encourages “representational skepticism” it is, an unsettled empirical question whether the internal states of dynamical systems are representational. Dynamical models are not, in his view, inherently anti-representational. I concur with this, and I believe that a similar point could be made about the other types of non-classical model. For reasons given below I am more inclined than Beer to think that some of the cognitive and behavioral sciences will continue to need and use representational ideas to explain (animal) behavior. But even if representational notions can be rehabilitated within non-classical models of cognition, it does not follow that those models will preserve the aspect of folk psychology which holds that discrete beliefs and desires interact within the framework of the Aristotelian practical syllogism. The familiar folk-psychological notions might disappear even if intentionality survives as a useful concept.

There are reasons, therefore, to consider a more radical approach to Proposition 1 that rejects the traditional analysis of intentional action. (Radical, that is, to many philosophers; but increasingly less so to cognitive scientists.) Of course, for a monkey successfully to reach out and grasp a food container, it must know something about the container’s location and other properties. But that knowledge may already be represented in the premotor cortex in such a way that ties it intrinsically to action. For example, Murata et al. (1997) showed that some F5 neurons encode the shapes of three-dimensional objects even when the monkey is not immediately required to perform any action. Likewise, an abstract desire may not be what underlies the action. Instead, it may be possible to distinguish intentions from desires by the involvement of concrete motor plans in the former, but not the latter (Franck Grammont, pers. comm.). Intentional action, on such an account, results from intentions and representations of external situations that are embodied concretely in motor patterns, rather than from beliefs and desires whose propositional contents are abstract and impersonal. A full understanding of the intentional actions of another agent, rather than consisting in being able to reason via the practical syllogism using abstract characterizations of knowledge and goals that are decoupled from specific actions, would involve the activation within the observer of a concrete motor plan that is below the threshold for actual motor output but that responds to environmental cues and has temporal dynamics similar to the states of the agent.

How best to model the dynamics of such a process, for example whether to use statistical methods such as dynamic Bayesian networks (Ghahramani, 1997) or the differential equations of dynamical systems theory (Beer, in press), remains an open scientific question.

On this account, the observer macaque whose F5 neurons more or less mirror the F5 neurons of the observed actor knows more or less all there is to know about the intentions of the actor. That is, there are no further beliefs and desires to which the observer is not privy. Rather, by activating corresponding representations, grounded in motor schemas, the observer is in more or less the same intentional mental state as the actor. The repetitions of ‘more or less’ here are deliberate, for there can be varying degrees of correspondence between the representations of action between observer and observed. By the same token, the congruence between visual and motor responses of F5 neurons can be more or less precise (recall the distinction between strict and broad congruence in the discussion of Proposition 3). A whole host of social, motivational, genetic, and developmental factors are likely to contribute to the degree of matching that can be accomplished between any two individuals, and for functional reasons it may be that precise matching would be too inflexible to support social transmission of skills. It is unsurprising that experiments that look for a generalized capacity for imitation in monkeys without taking such factors into consideration have produced negative results. And from this perspective, the success of Kumashiro et al. (2003) in producing monkeys who are adept at imitation is what one would predict from an experiment that explicitly manipulated social and developmental factors. The recent evidence for neonatal imitation in rhesus macaques (Ferrari et al., 2006) might also provide a further avenue for developmental studies, but the claim that mirror neurons play a role in the neonatal behavior is highly speculative. Jones (2005), coming from her perspective as a developmental psychologist, has argued that the evidence that mirror neurons play a role in neonatal imitation is very weak, including for humans, and she goes on to point out that such a role would be especially puzzling with respect to nonhuman primates, for “if mirror neurons *are* the mechanism underlying newborn behavioral matching, then newborn behavioral matching goes nowhere developmentally and is consequently less interesting than we thought” (Jones, 2005, p. 209; emphasis in original).

If we give up the traditional analysis of intentional action, what is left of the idea that behavior is to be

explained by mental states that are intentional in the philosophers' technical sense? I believe that the philosophers' notion of intentionality continues to have a place in our current best explanations of monkey cognition. Cognitive ethologists, cognitive neuroscientists, and developmental psychologists all continue to describe cognitive/neurological states in terms of their representational content, and it is important that the activation of motor schemas in animals, even though they may facilitate action, doesn't automatically entail that the animal will act. Hence there seems to be a need to attribute cognitive representations that are prior to action, even if the content of these states intricately involves the animals' own possibilities for action.

The new neuroscientific approaches to the premotor states of intentional agents are relevant to the philosophical debates insofar that they suggest alternative ways of describing the content and function of such states in terms of the organisms' own ways of interacting with the world. Part of our problem in describing the intentional states of nonhuman animals is that we lack easy conceptual access to their own ways of dealing with the world. Any propositional content described in a human language seems to import layers of meaning that are implausible when applied to other animals. By understanding the ways in which the motor system contributes to the brain's own ontology (Murata et al., 1997; Metzinger & Gallese, 2003) the neurosciences hold out the prospect of purposive action as the result of states involving intentional content, without presupposing that such content is as abstract as our sentences and words suggest.

Conclusions

We have now considered each of the three mutually incompatible propositions with which I began this essay. Perhaps all three should be rejected, as suggested by the eliminative materialists, but I don't believe that such a radical step is required by the data at hand. However, those data are not adequate to make any of the three propositions the obvious target for elimination. More research is needed, and the importance of an integrated approach to behavioral and neuroscientific experimentation cannot be stressed too strongly. It is significant that Gallese & Goldman (1998) turn to cognitive ethology to support their claims about monkeys' capacities for understanding intentions. Even though I argued that

their specific example was not conclusive, it is nevertheless the case that a proper understanding of neural-cognitive functions requires these functions to be investigated in the kinds of rich social and ecological contexts that ethologists use, and that are only rarely found in the lives of captive laboratory animals (although there are exceptions).

There is also conceptual work to be done. Proposition 1 describes a conceptual framework within which the behavioral and neurological evidence for the other two propositions can be assessed, but this does not place it out of the reach of empirical evidence. For instance, a study by Sommerville & Woodward (2005) indicates that in human infants the capacity for intentional understanding may precede the attribution of mental states to others, suggesting that the conceptual connection between intentional actions on the one hand and beliefs/desires on the other might not be as tight as is suggested by the traditional philosophical account. These empirical results may push us away from the traditional and towards new conceptions of intentionality. Those new conceptions do not come ready-made, and will themselves be shaped by the empirical discoveries subjected to philosophically reflective analysis.

What about the question implied by my title: Does the mirroring property of macaques' F5 neurons serve an important function for them? I'm reasonably confident that the answer is 'yes' — although this may not mean what we might have thought under the traditional account of intentional action. Most of the discussion of macaques' F5 mirror neurons has been focused on their implications for 'mind-reading' in humans. In this discussion, macaques are sometimes merely proxies for humans, enabling us to extrapolate findings from experiments that would not be approved for human subjects. When attention is turned towards the cognitive capacities of macaques themselves, the negative behavioral findings that support Proposition 2 are usually taken at face value, and Proposition 3 is called into question. The pressing questions become "What else do humans have that distinguishes them from macaques?" and "What are F5 mirror neurons for in macaques?" Taking a different tack, and challenging Proposition 1 has the potential to provide a more unified account of neuronal function between humans and macaques.

Finally, I want to emphasize the importance of continued dialogue between neuroscience, ethology, and philosophy. Ethology, with its historical concern for many non-primate species of animal, can help to

provide a broader perspective on intentionality than is usually provided by primatology, with its sometimes too-neat tripartite hierarchy of monkeys, great apes, and humans, all presumed to be sitting above the rest of the animal kingdom. Many non-primates show social and cognitive skills that exceed primate abilities (see Emery & Clayton, 2004 for a direct comparison of intelligence in corvids and apes, and Hare & Tomasello, 2005 for a comparison of dogs and chimpanzees; see Bekoff et al., 2002 for discussions of cognition in a wide variety of species). Imitation does not seem all that difficult for many birds, at least for some common activities, and dolphins seem to be good general imitators, even across species boundaries (Herman, 2002). Social play provides an especially rich area for studying intentional understanding in a wide variety of species because the social dynamics of play require constant signaling of intentions, monitoring of social rules and expectations, and turn-taking and interactive matching of behaviors for a common purpose (Bekoff & Allen, 1998; Flack et al., 2004; Bekoff, 2004; Allen & Bekoff, 2005). The study of nonprimate species would provide a much broader comparative perspective for evaluating claims about neural function. The discovery of mirror neurons shows how neuroscience can shake ethologists, comparative psychologists, and philosophers out of their dogmatic slumbers, suggesting new paths for behavioral investigation of old topics. In this vein, too, Gallese's (2004) bold suggestions about the phenomenology of intentional attunement should not be dismissed as automatically untestable or empirically vacuous, but as a stimulant towards further cognitive ethological investigation of all aspects of mental continuity among the nonhuman and human animals. Finally, philosophy can act as both brake and accelerator, by taking its traditional concerns as explananda as criteria for judging the success of scientific theories (Debes, submitted) and as a source of ideas for new approaches to old topics, such as how any organism can know the mind of another.

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