

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

Colin Allen

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 the 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 and Goldman 1998; Rizzolatti and 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 proposition 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 chapter 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 nontraditional 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 chapter discusses the propositions in reverse order, from 3 to 1.

Proposition 3: Monkeys Understand the Intentional Actions of Other Monkeys

A subpopulation of the neurons of the ventral premotor cortex (area F5) of rhesus macaques appears 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—that is, the same neurons are active when the monkey is grasping and when perceiving grasping, when holding and perceiving holding, and so forth. 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 and 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 have to be directly observed; the sequence of showing a monkey an object, obscuring it from view, and 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 functional magnetic resonance imaging (fMRI) exists to support the claim of the homologous brain region in humans serving similar functions (Fadiga et al. 1995; Rizzolatti and Craighero 2004; 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 and 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 and Goldman write as follows: “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 and 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 and Ham 1992; Heyes 1994; Tomasello and 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 and 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 and 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 and 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 and Craighero fall back on the more generic notion of "action understanding." However, this notion shares a common deficit with Gallese and 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 and Goldman nor Rizzolatti and 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 and 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 is responsible for activating the neurons. To support this claim about meaning, Rizzoli and Craighero cite a study by Kohler et al. (2002) in which it was shown that an auditory cue (the 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 and 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 and Marler 1993a, 1993b). Hauser (1992) describes the withholding of food calls as deception, and Gallese and 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 and 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 result 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, and so on, 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 and 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 with 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 one answers this question depends, in part, on some conceptual issues about what one means by "function" (Allen and 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, which 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 and Goldman, that the congruent F5 activity during action observation and action performance in monkeys is a precursor to “mind-reading” abilities. However, 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—that is, 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 makes 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 overinterpretation.

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 that in 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 and 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.

Proposition 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 and 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 and 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 (2002) 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. (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 toward providing a case against proposition 2 and of resolving the paradox in this fashion (see also Lyons, Santos, and 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?

Proposition 1: To Understand the Intentional Actions of Others Requires Knowledge of the Intentional States (i.e., Beliefs and Desires) That (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 his or 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. However, 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 (e.g.) 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 and von Cramon (2004) implicate F5 neurons in anticipating the outcomes of abstract nonbiological 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, unself-conscious) 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 prelinguistic infants—for example, dynamical models (Thelen et al. 2001; Beer, in press) or Bayesian models (Luttbegg and 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 antirepresentationalist 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 antirepresentational. I concur with this, and I believe that a similar point could be made about the other types of nonclassical models. 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 nonclassical 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. However, that knowledge may already be represented in the premotor cortex in such a way that it is intrinsically tied 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, personal communication). 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 and 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 and 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 and 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 toward 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 toward 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 nonprimate 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 nonprimates show social and cognitive skills that exceed primate abilities (see Emery and Clayton 2004 for a direct comparison of intelligence in corvids and apes, and Hare and 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 and Allen 1998; Flack et al. 2004; Bekoff 2004; Allen and 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 rather taken as a stimulant toward 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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References

- Allen, C. (2002). A skeptic's progress. *Biology and Philosophy*, 17, 695–702.
- Allen, C., and Bekoff, M. (1994). Function, natural design, and animal behavior: philosophical and ethological considerations. In N. S. Thompson (Ed.), *Perspectives in ethology: Vol. 11. Behavioral design* (pp. 1–47). New York: Plenum Press.

Allen, C., and Bekoff, M. (2005). Animal play and the evolution of morality: An ethological approach. *Topoi*, 24, 125–135.

Beer, R. (in press). Dynamical systems and embedded cognition. In K. Frankish and W. Ramsey (Eds.), *The Cambridge handbook of artificial intelligence*. Cambridge: Cambridge University Press (preprint at <http://mypage.iu.edu/~rdbeer/Papers/AIHandbookChapter.pdf>)

Bekoff, M. (2004). Wild justice and fair play: Cooperation, forgiveness, and morality in animals. *Biology and Philosophy*, 19, 489–520.

Bekoff, M., and Allen, C. (1998). Intentional communication and social play: How and why animals negotiate and agree to play. In M. Bekoff and J. A. Byers (Eds.), *Animal play: Evolutionary, comparative, and ecological perspectives* (pp. 97–114). Cambridge: Cambridge University Press.

Bekoff, M., Allen, C., and Burghardt, G. M. (Eds.). (2002). *The cognitive animal: Empirical and theoretical perspectives on animal cognition*. Cambridge: MIT Press.

Byrne, R. W. (2004). Detecting, understanding, and explaining animal imitation. In S. Hurley and N. Chater (Eds.), *Perspectives on imitation: From mirror neurons to memes* (pp. 255–282). Cambridge: MIT Press.

Cheney, D. L., and Seyfarth, R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.

Courville, A. C., Daw, N. D., and Touretzky, D. S. (2006). Bayesian theories of conditioning in a changing world. *Trends in Cognitive Sciences*, 10, 294–300.

Debes, R. (submitted). Which empathy? Limitations in the “mirrored” understanding of emotion.

de Waal, F. B. M. (2001). *The ape and the sushi master: Cultural reflections of a primatologist*. New York: Basic Books.

di Pellegrino, G., Fogassi, L., Gallese, V., and Rizzolatti, G. (1992). Understanding motor events: A neurophysiological study. *Experimental Brain Research*, 91, 176–180.

Emery, N. J., and Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903–1907.

Fadiga, L., Fogassi, L., Pavesi, G., and Rizzolatti, G. (1995). Motor facilitation during action observation: A magnetic stimulation study. *Journal of Neurophysiology*, 73, 2608–2611.

Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., and Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, 4, e302. DOI: 10.1371/journal.pbio.0040302.

Flack, J. C., Jeannotte, L. A., and de Waal, F. (2004). Play signaling and the perception of social rules by juvenile chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *118*, 149–159.

Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F., and Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*, 662–667.

Forum (2004). Discussion of Gallese (2004) at <http://www.interdisciplines.org/mirror/papers/1/1/printable/discussions>.

Gallese, V. (2004). Intentional attunement: The mirror neuron system and its role in interpersonal relations. Accessed at <http://www.interdisciplines.org/mirror/papers/1/> on Jan 15, 2007.

Gallese, V., Fadiga, L., Fogassi, L., and Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallese, V., and Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Science*, *2*, 493–501.

Gallup, G. G., Jr. (1970). Chimpanzees: Self-recognition. *Science*, *167*, 86–87.

Gallup, G. G., Jr., Anderson, J. R., and Shillito, D. J. (2002). The Mirror Test. In M. Bekoff, C. Allen, and G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 325–333). Cambridge: MIT Press.

Ghahramani, Z. (1997). Learning dynamic Bayesian networks. In C. L. Giles and M. Gori (Eds.), *Adaptive processing of temporal information: Lecture notes in artificial intelligence* (pp. 168–197). New York: Springer-Verlag.

Gordon, R. M. (2004). Folk psychology as mental simulation. In E. N. Zalta (Ed.), *The Stanford encyclopedia of philosophy* (Fall 2004 ed.), <http://plato.stanford.edu/archives/fall2004/entries/folkpsych-simulation/>.

Grèzes, J., Frith, C. D., and Passingham, R. E. (2004). Inferring false beliefs from the actions of oneself and others: An fMRI study. *NeuroImage*, *21*, 744–750.

Hare, B., and Tomasello, M. (2005). Human-like social skills in dogs? *Trends in Cognitive Sciences*, *9*, 439–444.

Hare, B., and Wrangham, R. (2002). Integrating two evolutionary models for the study of social cognition. In M. Bekoff, C. Allen, and G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 363–369). Cambridge: MIT Press.

Hauser, M. D. (1992). Costs of deception: Cheaters are punished in rhesus monkeys (*Mucaca mulatta*). *Proceedings of the National Academy of Sciences USA*, *89*, 12137–12139.

- Hauser, M. D., and Marler, P. (1993a). Food associate calls in rhesus macaques (*Mucaca mulatta*): I. Sociological factors. *Behavioral Ecology*, 4, 194–205.
- Hauser, M. D., and Marler, P. (1993b). Food associate calls in rhesus macaques (*Mucaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology*, 4, 206–212.
- Herman, L. (2002). Exploring the cognitive world of the bottlenosed dolphin. In M. Bekoff, C. Allen, and G. M. Burghardt (Eds.), *The cognitive animal: Empirical and theoretical perspectives on animal cognition* (pp. 275–283). Cambridge, MA: MIT Press.
- Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Review*, 6, 207–231.
- Hunt, G. R., Rutledge, R. B., and Gray, R. D. (2006). The right tool for the job: What strategies do wild New Caledonian crows use? *Animal Cognition*, 9, 307–316.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, G., Buccino, G., Mazziotta, J. C., and Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biology*, 3, 529–535.
- Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., and Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, 286, 2526–2528.
- Jones, S. S. (2005). The role of mirror neurons in imitation. In S. Hurley and N. Chater (Eds.), *Perspectives on imitation: From neuroscience to social science: Vol. 1. Mechanisms of imitation and imitation in animals* (pp. 205–210). Cambridge: MIT Press.
- Keysers, C., and Perrett, D. I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends in Cognitive Science*, 8, 501–507.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V., and Rizzolatti, G. (2002). Hearing sounds, understanding actions: Action representation in mirror neurons. *Science*, 297, 846–848.
- Kumashiro, M., Ishibashi, H., Uchiyama, Y., Itakura, S., Murata, A., and Iriki, A. (2003). Natural imitation induced by joint attention in Japanese monkeys. *International Journal of Psychophysiology*, 50, 81–99.
- Luttbeg, B., and Langen, T. A. (2004). Comparing alternative models to empirical data: Cognitive models of Western scrub-jay foraging behavior. *American Naturalist*, 163, 263–276.
- Lyons, D. E., Santos, L. R., and Keil, F. C. (2006). Reflections of other minds: How primate social cognition can inform the function of mirror neurons. *Current Opinion in Neurobiology*, 16, 230–234.

- Metzinger, T., and Gallese, V. (2003). The emergence of a shared action ontology: Building blocks for a theory. *Consciousness and Cognition*, 12, 549–571.
- Miklosi, A. (1999). The ethological analysis of imitation. *Biological Review*, 74, 347–374.
- Munn, C. A. (1986). The deceptive use of alarm calls by sentinel species in mixed-species flocks of neotropical birds. In R. W. Mitchell and N. S. Thompson (Eds.), *Deception: Perspectives on human and nonhuman deceit* (pp. 169–175). Albany: State University of New York Press.
- Murata, A., Fadiga, L., Fogassi, L., Gallese, V., Raos, V., and Rizzolatti, G. (1997). Object representation in the ventral premotor cortex (Area F5) of the monkey. *Journal of Neurophysiology*, 78, 2226–2230.
- Povinelli, D. J. (2000). *Folk physics for apes: The chimpanzee's theory of how the world works*. Oxford: Oxford University Press.
- Rizzolatti, G., and Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience*, 27, 169–192.
- Santos, L. R., Nissen, A. G., and Ferrugia, J. (2006). Rhesus monkeys (*Macaca mulatta*) know what others can and cannot hear. *Animal Behaviour*, 71, 1175–1181.
- Schubotz, R. I., and von Cramon, D. Y. (2004). Sequences of abstract nonbiological stimuli share ventral premotor cortex with action observation and imagery. *Journal of Neuroscience*, 24, 5467–5474.
- Sommerville, J. A., and Woodward, A. L. (2005). Pulling out the intentional structure of action: The relation between action processing and action production in infancy. *Cognition*, 95, 1–30.
- Thelen, E., Schöner, G., Scheier, C., and Smith, L. B. (2001). The dynamics of embodiment: A field theory of infant perseverative reaching. *Behavioral and Brain Sciences*, 24, 1–86.
- Thorpe W. H. (1956). *Learning and instinct in animals*. London: Methuen.
- Tomasello M., and Call, J. (1997). *Primate cognition*. Oxford: Oxford University Press.
- Tomasello, M., Carpenter, M., Call, J., Behne, T., and Moll, H. (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences*, 28, 675–691.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keyers, C., and Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, 31, 155–65.
- Valone, T. J. (2006). Are animals capable of Bayesian learning? An empirical review. *Oikos*, 112, 252–259.

Visalberghi, E., and Fragaszy, D. (1990). Do monkeys ape? In S. Parker and K. Gibson (Eds.), *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (pp. 247–273). Cambridge: Cambridge University Press.

Whiten, A., and Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In P. J. B. Slater, J. S. Rosenblatt, C. Beer, and M. Milinski (Eds.), *Advances in the study of behaviour* (pp. 239–283). New York: Academic Press.

Wimmer, H., and Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition*, 13, 103–128.

