

A Curious Commentary on a Book on Mirror Neurons and Other Tales of Scientific Misses: Response to Rizzolatti & Sinigaglia and to Glenberg

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Let me state up front that I am honored by the opportunity to engage in a discussion of the neural basis of communication and cognition with Giacomo Rizzolatti and Art Glenberg, two scientists that I deeply respect. They both have contributed a great deal to the field and stimulated me personally to push harder to understand the systems I study. But respect and illustrious contribution does not entail automatic agreement. I would be a bad scientist indeed if I let personal admiration drive my scientific arguments. So let me be clear, none of what I have said or say below is intended to minimize anyone's contribution. The proposals put forward by Rizzolatti, Glenberg, et al., and before them Liberman, Skinner and many others were (are) interesting and innovative; they deserve serious evaluation. I respected the mirror neuron claims enough to read about them carefully from primary sources and to think hard about the theoretical implications and empirical predictions. And when I came to a different conclusion than most of the field, I similarly felt obliged to share my concerns.

Although there is some overlap in the issues raised by Rizzolatti & Sinigaglia and Glenberg, I organize my response around their two reviews. Their comments are addressed in roughly chronological order.

Rizzolatti & Sinigaglia

Straw theories

Rizzolatti & Sinigaglia (RS) criticize my arguments as superficial straw man attacks in that I failed to understand that the mirror mechanism works differently and is potentially distributed differently for various functions such as understanding actions goals, recognizing emotions, or perceiving speech sounds. In fact, I evaluated individual claims within their own systems. I asked whether damage to the motor speech system affected speech perception, whether damage to the limb control system affected manual gesture understanding, whether facial paralysis affected the recognition of facial emotional expressions, and so on. In each case, the answer was no. Theirs is a straw critique.

They suggest it is similarly naïve to ask whether the mirror system is needed to understand actions that we cannot perform because they never suggested it was. They assert that I hid the truth of their theory from the reader to make the group appear foolish. But in fact I discussed their view on the matter near the front of the book--“Rizzolatti and Craighero admit that the brain can understand actions without the mirror system” (p. 44)—and went on to make a deeper point. If another mechanism exists, what evolutionary pressure is there to develop a new one? Assuming that the mirror mechanism “is of great evolutionary importance” (Rizzolatti & Craighero, 2004) (p. 172) it's a problem for their theory if it is largely redundant. Accordingly, I then went on immediately to discuss their proposal regarding what *extra* benefit the mirror system

confers, “action understanding from the inside”, thus getting around the evolutionary conundrum. In this context I discussed the same result that RS mention in clarifying their position to me--observing “biting” activates the human mirror system but observing “barking” does not--and followed this up with a study that they don’t discuss, showing that humans understand dog barks remarkably well (without mirror system involvement), thus questioning their speculation that “understanding from the inside” adds much at all. Again, the accusation that I am hiding their position from the reader or giving it superficial treatment is plainly countered by what is written in the book. (See my response to Glenberg below for a more thorough discussion of the multiple routes to action understanding issue.)

Relation to the motor theory of speech perception

RS correct my observation (based on written and personal communications) that the mirror neuron theory of action observation was inspired by Liberman’s motor theory of speech perception. RS state instead that Liberman’s ideas were helpful but their mirror neuron theory was based on principles of motor coding. It is implied that I am wrong, therefore, to use facts about the fate of Liberman’s theory (it failed to stand up to empirical facts) to argue against the Parma theory. This would be true if the theories differed in their claims, but Rizzolatti and colleagues have repeatedly drawn parallels between them:

mirror neurons represent *the* link between sender and receiver that *Liberman postulated in his motor theory of speech perception* as the *necessary prerequisite* for *any type* of communication [p. 189 (Rizzolatti & Arbib, 1998); emphases added]

So, no matter the ultimate source of the ideas, if the claim is that mirror neurons are at the basis of action understanding then we can assess that claim directly, just as Liberman’s theory was put to the test. The fact that the Parma theory had a different source of inspiration doesn’t change the empirical facts.

The role of imitation and the malleability of mirror neurons

RS suggest that my counter-mirror neuron training experiment (Catmur, Walsh, & Heyes, 2007) is irrelevant to the mirror neuron claims for two reasons. One is empirical. They refer to a more recent experiment showing that the counter-mirror effects have a different time course than the standard mirror effects. However, an even more recent study showed that this is incorrect: mirror and counter-mirror effects span the same time scales (Cavallo, Heyes, Becchio, Bird, & Catmur, 2014).

In any case, RS dismiss these studies because they investigate imitation behavior without the involvement of action goals such as grasping an object. Perhaps, then, Rizzolatti and colleagues should abandon their claim that “in humans, in addition to action understanding, the mirror-neuron system plays a fundamental role in action imitation” (Rizzolatti & Craighero, 2004)(p. 169). If they did make that theoretical move I would

actually disagree as I think mirror neurons do play a partial role in imitation, imitation learning in particular, which is a pervasive behavior across a range of species including macaques, as I discuss in Chapter 8 of my book. The main point here is that one cannot simultaneously hold that the human mirror system plays a fundamental role in action imitation and dismiss data on action imitation because it doesn't fit the theory.

On networks of mirrors

RS correct my apparent misunderstanding that mirror neurons in and of themselves (“in a dish” as they say) are capable of understanding actions.

The crucial point is that action understanding is not determined, as Hickok believes, by the activation of mirror neurons as such, but by the activation of the *mirror mechanism* of which they are endowed, i.e. by their capacity to transform sensory information concerning the observed action into a motor representation of the goal to which that action is directed.

This line of argument seems to be intended to thwart lesion-based assessments of the Parma theory: if damage to the mirror system doesn't produce the kinds of understanding deficits one might expect, it is because they are part of a larger network. The mirror neurons themselves are not doing the understanding, they just trigger it. Continuing immediately from the quote above, RS write,

This transformation *ignites* the activity of a complex cortical and subcortical network. [their emphasis]

I discussed this kind of argument on pages 20-21 on my book, which was put forward previously by the Parma group (Rizzolatti & Craighero, 2004), and I discussed similar ideas regarding the potential for mirror neurons to modulate understanding (e.g., via predictive coding) in Chapter 10.

Three points are relevant here. One is that the Parma team has repeatedly stressed the centrality of the mirror neuron mechanism in “action understanding” (their unqualified term and despite RS's statement that “To speak of the mirror mechanism as the basis of action understanding is mere nonsense” (p. xxx, this volume)). See my response to Glenberg below for an array of quotes on this matter.

The second relevant point is that if this system is so important to action understanding, disrupting it should produce fairly dramatic effects. This holds even if mirror neurons only apply to actions within one's motor repertoire and are only “igniting” the broader network. Even though spark plugs aren't themselves the motor that drive the car, take one out and performance drops off quite noticeably; take them all out and the motor won't run. So whether we call it “the basis of” or the thing that “ignites” action understanding, the prediction is that damage should yield deficits. When we assess this prediction either by examining the effects of anatomical damage to the proposed mirror system (Hickok, Costanzo, Capasso, & Miceli, 2011; Rogalsky, Love, Driscoll, Anderson, & Hickok,

2011) or by comparing *functional* motor deficits with functional action understanding deficits (Hickok et al., 2008) (and see many other examples discussed in the book ranging from apraxia to ALS to cerebral palsy), one fails to find the effects one expects given how fundamental the system is proposed to be for action understanding.

RS may still want to argue that the system is so pervasive—on par with EPSPs!—that there is no way to put the theory to a strong test. As Rizzolatti and Craighero wrote, “vast lesions as those required to destroy the mirror neurons system may produce more general cognitive deficits that would render difficult the interpretation of the results” (p. 173). This raises the third point. If this view dictates that the theory is effectively untestable, then it is not a scientific theory at all.

Luckily, RS point out several examples of studies that they believe provides evidence indicative of the mirror system’s contribution to action understanding; that is, what understanding “from the inside” adds to understanding “from the outside.”

Studies measuring the effect of “understanding from the inside”

In my book I discussed several demonstrations similar to the ones RS cite. After careful consideration, I concluded that the studies failed to support the conclusions. But given RS’s point that I neglected other work, it is worth undertaking the same exercise with these reports that RS find convincing. I will discuss them in turn.

Casile and Giese (Casile & Giese, 2006) report that non-visual motor training (learning a novel movement while blindfolded) improved visual recognition of that movement from a point-light display stimulus. There are two serious problems with this study. The first is that while overt visual input was controlled during motor learning, somatosensory (proprioceptive) learning was not. Given the tight relation between proprioceptive and visual input involved in self-generated movements, it impossible to attribute the effect to the motor system. Second, as is typical of many TMS studies of the motor effect on perception (Hickok, 2014b), the authors failed to control response bias, using only the percent “same” responses in their analysis. This renders the finding uninterpretable. Specifically, it is impossible to know whether the change in recognition accuracy resulted from an increase in detectability or to a change in response bias (Green & Swets, 1966). This is not just a theoretical objection. Previous work has shown that modulation of the motor system can lead to shifts in response bias in perceptual tasks without affecting discriminability (Sato et al., 2011) and that modulation of response bias activates motor systems (Venezia, Saberi, Chubb, & Hickok, 2012).

Aglioti, et al. (Aglioti, Cesari, Romani, & Urgesi, 2008) studied expert basketball players’ ability to predict the outcome of an observed “free throw”, reporting that this group was not only superior to that of expert watchers (coaches) and novices but also that better prediction accuracy was evident even before the ball left the shooter’s hands. This study demonstrates what appears to be a very robust effect supporting the idea that motor expertise improves action understanding. But again there are fundamental confounds. Since motor expertise is tightly linked to sensory expertise (both visual and

somatosensory) it is impossible to tie the results to the motor system alone. More specifically along this line of reasoning, it is important to note that players are regularly in a situation of having to rebound free throw shots if the shot misses, which provides a competitive advantage in learning to predict the outcome of others' shots. This is not the case for expert or novice watchers who do not have to use the visual information to select time-sensitive appropriate action responses. Given these confounds, the sensory experience of players and watchers is simply not equated and the result is perfectly compatible with an action selection account of mirror neurons function.

Boria et al. (Boria et al., 2009) report on action understanding in autism suggesting that some aspects are preserved while others are impaired. It is assumed by the authors that the impaired components are due to motor-related deficits. But much other work contradicts this claim, however (Berger & Ingersoll, 2014; Bird, Leighton, Press, & Heyes, 2007; Cusack, Williams, & Neri, 2015; Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011; Hamilton, Brindley, & Frith, 2007), suggesting in contrast that action understanding is well-preserved in autism.

Urgesi, et al. (Urgesi, Candidi, Ionta, & Aglioti, 2007) report a TMS study on form versus action discrimination. Stimuli were static images of body parts in the middle of performing some action. The general task was match to sample (no object goal depicted). In the form version, a body part image was displayed from one actor, then two images, one from same actor and one from a different actor, were simultaneously displayed performing the same action. The task was to select the body part image that belonged to the same actor. The action version involved similar sample images but the response choices involve different actions (e.g., precision grip versus whole hand grip). The task was to select the matching action. Two critical stimulation sites were studied, the ventral premotor cortex (vPMC) and the extrastriate body area (EBA, in visual-related cortex). It was reported that EBA stimulation resulted in longer reaction times on the form task than vPMC stimulation. The reverse effect was found for the action task: longer reaction times with vPMC compared to EBA stimulation. There are several complications to note here. The most important is that the pattern of results could also have obtained even on standard assumptions about the roles of sensory (EBA) and motor (vPMC) cortex. For example, if EBA stimulation interferes with form discrimination and vPMC stimulation interferes with *action selection* (index versus middle finger button press), and if the EBA effect is larger than the vPMC effect, the same pattern of results would emerge, specifically slower RTs with vPMC than EBA stimulation (action selection interference) and slower RTs with EBA than vPMC stimulation (form discrimination interference>action selection effects). Another point worth noting in the context of some of RS's comments on the Heyes and colleagues' work is that the stimuli in the Urgesi et al. experiment were not object-directed actions and in fact half of the items were meaningless movements, similar to what Catmur et al. (Catmur et al., 2007) studied. By RS's own reasoning, the Urgesi et al. study similarly "lack[s] theoretical relevance" and "[does] not really have to do with the role of mirror neurons in action understanding". Finally, it is worth pointing out that Urgesi et al. report no effect of stimulation on accuracy. Thus, even if we take the study at face value, the magnitude of the effect of "understanding from the inside" equates to a 33.44 msec speed advantage with no effect

on depth of understanding.

Costantini et al. (Costantini, Ambrosini, Cardellicchio, & Sinigaglia, 2014) report an interesting study showing that eye movement response times during object directed actions were slowed following vPMC stimulation. This suggests a link between hand-action motor codes and eye movements, which makes sense given the need to coordinate these two actions during self-generated actions. What the study does not show, however, is that these effects contribute to understanding since action understanding was not measured. Perhaps RS would argue that seeing is a prerequisite for understanding, which is a reasonable argument. But then this suggests that mirror neurons are playing more of an action selection role than understanding role as I proposed in my book: perceptual information is mapped onto motor circuits for selecting appropriate actions, some mirror, many non-mirror, and perhaps including eye movements.

Finally, Michael et al. (Michael et al., 2014) report that TMS to lip motor cortex disrupts the understanding of lip more than hand actions and vice versa. This study *did* assess comprehension and due to the nature of the task is less susceptible to response bias effects and so I view this as some of the best evidence in favor of the claim that the motor system plays a role in action understanding. I can certainly quibble with the result—it was variable across tasks and motor cortex may modulate understanding not because it is critical but simply because it is connected to conceptual networks—but let's take the result at face value and examine the magnitude of the effect. The primary result is a two-way interaction in understanding accuracy between stimulation type (lip vs. hand) and action type (lip- vs. hand-related). This interaction is not graphed directly in their article (means are broken down by complexity as well), but a close examination of their Figure 3 allows for one to approximate the values in the individual conditions, collapse the complexity conditions and graph the two-way interaction. I have plotted the result in Figure 1. Numerically, the effect amounts to somewhere between a 1-2% modulation of performance. If this is what “understanding from the inside” contributes, it is modest indeed and begs for a theory of the remaining 98-99% of action understanding. One might argue that this small effect size is the result of a ceiling effect. Perhaps. But an analogous study was performed in the speech domain ((Schomers, Kirilina, Weigand, Bajbouj, & Pulvermuller, 2014) mentioned by Glenberg) that set baseline performance to 69% accuracy specifically to avoid ceiling effects. This study reported *no effect* of motor cortex stimulation on accuracy. See below for further discussion.

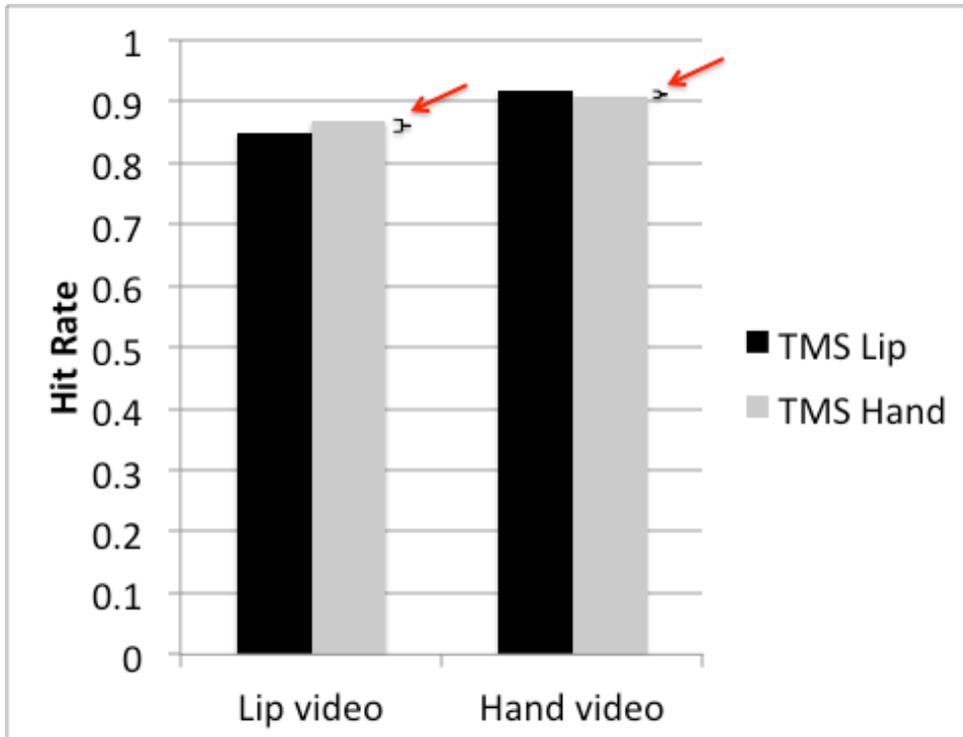


Figure 1: Graph of the magnitude of the interaction effect estimated from Michael et al. (2014).

The role of the STS

RS attempt to summarize my non-mirror neuron centric position on how actions are in fact understood:

Hickok, after a passionate defence of complex circuits as a neural basis for psychological functions (and the consequent obvious irrelevance of mirror neurons for this role), abruptly changes his mind and in the same chapter suggests that high-order visual neurons, like those located in the STS, can do the job of encoding others' actions and goals.

RS misrepresent what I said. Here is a quote from the book that correctly reflects my view:

“Understanding” is a complicated thing with lots of moving parts. You can’t pull out one part and call *that* the “basis of action understanding.” It doesn’t work for just the motor bits and it doesn’t work for just the sensory bits. Nor is the one high-level posterior temporal STS and/or MTG bit enough to define what it means to understand, say, GRASPING in all its guises.

On this point, I think I agree with RS. Neither the mirror system nor the STS is the “basis of action understanding” on its own. Rather, these areas are viewed as “hubs” in a broad network that as a whole enable understanding. Where we differ, I believe, is which sub-

network we take to serve as the critical hub. The Parma group has argued for a motor-based, mirror neuron hub. I would argue for a sensory-based, STS hub. And I think we can test these two theories straightforwardly. If the STS theory is right, then bilateral damage to the STS should dramatically affect action understanding. If the mirror neuron theory is right, then unilateral (or perhaps bilateral) damage to the frontoparietal mirror system should dramatically affect action understanding. I presented several examples in my book showing that unilateral or even bilateral damage to the motor/mirror system fails to disrupt action understanding substantially. To this we can now add that the ability to comprehend sign language gestures by deaf signers is not impaired by frontal lobe damage affecting the proposed mirror system (Corina & Knapp, 2006; Rogalsky et al., 2013). On the contrary, my own research on speech perception, a form of action understanding according to Rizzolatti and colleagues, has shown that bilateral damage to the superior temporal lobe is severely disruptive (Hickok & Poeppel, 2000, 2004, 2007).

On the interpretation of neuropsychological data

RS challenge my logic regarding the interpretation of neuropsychological data, specifically, my argument that lesions to a critical system should cause severe and consistent deficits to the behaviors that the critical system supports. They raise an interesting point regarding research on the effects of optic tract lesions that reinforces the fact that we need to be careful in interpreting lesion studies, just as we need to be careful in interpreting data from any source. This is precisely why I did not build my arguments on any single method. Lesions to motor cortex thought to house mirror neurons (e.g., Broca's area or frontoparietal regions generally) do not have the effect predicted by the Parma theory. But this could be because the mirror system can operate relatively normally with partial sparing, analogously to the optic tract finding. So, to address this possibility I also examined *functional deficits*, cases in which the motor system is severely dysfunctional either acutely (e.g., Wada procedures), as a result of degenerative disease (e.g., ALS), or failed to develop at all for various reasons (e.g., cerebral palsy, developmental anarthria, Mobius syndrome). In these cases too, action understanding is not substantially affected providing strong evidence against the view that the motor system is the "basis of" action understanding.

Concerning the optic tract result itself, it is interesting to note that Galambos et al.'s finding caused quite a stir in perceptual neuroscience precisely because it flew in the face of common assumptions. That is, researchers at the time applied the same logic that I have applied in regards to the mirror neuron claims. Indeed, a few years after Galambos et al.'s paper appeared and after similar findings were reported in other experiments, Doty wrote, "this result is clearly unexpected and raises difficult questions concerning the functions and organization of the neocortical visual system" (Doty, 1973)(p. 484). It raises difficult questions because if we believe that the optic tract and geniculostriate pathway is the basis of visual pattern discrimination, damage to it *better* produce the expected deficit, otherwise we need to rethink things. Happily for the optic tract, that evidence was readily available: while RS quote from Galambos et al.'s paper titled, "Optic tract lesions *sparing* pattern vision in cats", there is a companion paper, published back to back with the first, titled "Optic tract lesions *destroying* pattern vision in cats"

(Norton, Galambos, & Frommer, 1967). This report showed that if you destroy enough of the optic tract, pattern vision indeed fails, as expected.

The difficult question that Doty referred to, then, was not how vision is possible without an optic tract (it isn't), but how retinotopically organized visual cortex can manage with such a sparse and presumably topographically focal input. This question helped spark decades of research on sensory cortical plasticity from which a major conclusion was that cortical topographic maps are more plastic than we thought (Buonomano & Merzenich, 1998), thus potentially allowing for sparse retinotopically focal inputs to redistribute onto a wide topographical range. Interestingly, Rizzolatti himself joined the discussion early on in a review paper published in the same volume as Doty's comment (Sprague, Berlucchi, & Rizzolatti, 1973). He and his co-authors urged caution in interpreting ablation results (particularly with respect to cortical ablation) and hint, citing Galambos et al. among others, that much of this work ignores another important visual pathway, that involving the superior colliculus. Other researchers pointed out additional problems such as the possibility that fiber mixing in the optic tract may result in the spared inputs being topographically distributed already and further that the cat is a difficult model for studying sensory maps due to wider range of projection pathways (Keating & Horel, 1976).

Glenberg

More Straw Men

Similar to comments made by RS and also by Christian Keysers in a previously published review (Keysers, 2015), Glenberg claims that (in one of my arguments) I am attacking a straw man. He provides several quotes demonstrating that the Parma group has always held that the mirror system is not the only mechanism for action understanding, therefore my point that we can understand actions that we cannot ourselves perform is a frivolous observation.

This would be an accurate point except that the position being advocated by Rizzolatti and colleagues is often less than clear. Consider these quotes, which seem to point to a different view compared to that emphasized by Glenberg:

we understand an action because the motor representation of that action is activated in our brain. [p. 661 (Rizzolatti, Fogassi, & Gallese, 2001);]

When the motor schema of the agent is different from that of the observer—as in the case of the mechanical demonstrator, or for mirror neurons, in the case of grasping achieved by using a tool — the observed action cannot be matched on the observer's motor repertoire, and therefore the intended goal cannot be detected and/or attributed to the mechanical agent. [p. 36 (Gallese, 2001)]

Two main hypotheses have been advanced on what might be the functional role of mirror neurons. The first is that mirror-neuron activity mediates imitation (see

Jeannerod 1994); the second is that mirror neurons are at the basis of action understanding (see Rizzolatti et al. 2001) [p. 172 (Rizzolatti & Craighero, 2004)]

The claims have not been tempered in recent publications that I have been accused of ignoring:

...crucial for action understanding are those areas that contain neurons that encode the goal with a high degree of generality. With the problem posed in these terms, the evidence shows that generalization is an aspect that characterizes the parieto-frontal mirror network rather than STS neurons. [(Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014)]

...these data indicate that action information from STS is sent to the ventral premotor cortex (F5) [where mirror neurons are found] along two distinct functional pathways. One pathway links the upper bank of the STS with area PFG that, in turn, projects to area F5c. The other connects the lower bank of the STS with area AIP that in turns projects to areas F5a and F5p. Both pathways provide information necessary for understanding the observed motor act. (Rizzolatti et al., 2014)

To be fair, the Parma group *has* consistently acknowledged that the mirror system is not the only mechanism for action understanding, as noted above. But at the same time, the role of this other mechanism has been minimized to the point of being insufficient for the kind of understanding characteristic of human (and monkey) experience.

...among the neurons in various areas that become active during action observation, only those that can encode the goal of the motor behavior of another individual with the greatest degree of generality can be considered to be crucial for action understanding, and the available evidence shows that this capacity for generalization characterizes the parieto-frontal mirror neurons rather than STS cells. [p. 269, (Rizzolatti & Sinigaglia, 2010)]

However, we must ask whether this selectivity [in STS neurons] -- or, in more general terms, the capacity to connect different visual aspects of the observed action -- is sufficient to justify using the term 'understanding'. The motor activation characteristic of F5 and PF-PFG adds an element that hardly could be derived from the purely visual properties of STS -- and without which the association of visual features of the action would at best remain casual, without any unitary meaning for the observer. [p. 99; (Rizzolatti & Sinigaglia, 2008)]

Thus, Glenberg's quotes seem to point clearly to one view, that mirror neurons are but one mechanism for action understanding, while the quotes I've provided here point to another rather clear and opposing position, that mirror neurons are "*the basis of*", "*necessary for*", "*fundamental in*", "*crucial for*" action understanding (unmodified), without which the "intended goal" of an action "*cannot be detected*" and remains "*causal, without any unitary meaning for the observer.*" We can sum up this confusing state of affairs by juxtaposing the following to claims from the Parma group:

Claim 1: “mirror neurons are at the basis of action understanding (see Rizzolatti et al. 2001)” [p. 172 (Rizzolatti & Craighero, 2004)]

Claim 2: “To speak of the mirror mechanism as the basis of action understanding is mere nonsense” (Rizzolatti & Sinigaglia, present volume)

It is reasonable to conclude that some readers might be confused by such apparently contradictory statements. Even if the Parma team never intended to communicate the idea that mirror neurons are truly necessary for action understanding, this proposal is what they have said in so many words and in various places and this is the interpretation that many readers took away. The claim may be a straw man in the minds of Rizzolatti, Glenberg, and Keyserers but it is no straw man in the minds of many scientists and consumers of this research. As such, it the claim deserved to be addressed.

Speech perception

Glenberg points to a new TMS study of speech perception that gets around the many concerns I've had regarding similar previous studies. I object to this previous work because it typically fails to control response bias, assesses perception using tasks that are weighted toward motor system involvement (syllable discrimination or identification), and presents speech at near threshold levels (typically in noise). This new study avoids the first two concerns, but not the third in contrast to Glenberg's suggestion. While it's true that speech stimuli were not noise masked, they were presented at very low sound levels such that baseline accuracy was actually quite low at 69%.

There are problems with this study, which I discuss elsewhere (Hickok, in press) but for the sake of argument let's agree that this study indeed reveals the motor contribution to speech perception. As we did above, we again can ask, what is the magnitude of this effect? What does motor information add? First, the study reported no effect on accuracy. The effects were only found in reaction time measures. And second, the effect only reached significance one of the two classes of speech sounds they assessed (tongue-related, not lip-related sounds). So according to this study what the motor system contributes is this: slightly faster recognition of some speech sounds under significantly degraded listening conditions. It contributes nothing to the depth of understanding according to this research and adds nothing under more audible listening conditions. We have suggested previously that in cases of perceptual uncertainty listeners resort to alternative strategies for decision making which may be influenced by motor-induced bias ((Venezia et al., 2012), see also (Sato et al., 2011)). This would not affect discriminability if response bias is controlled, but it could affect RT if response bias leads to faster decision time.

Glenberg also brings up the standard observations purported to show that the motor system contributes to the semantics of language. I addressed these arguments at length in my book and won't rehash them here. I will point the reader to a much deeper discussion of these points in David Kemmerer's critique of my book (Kemmerer, Published online:

02 December 2014) and my response (Hickok, in press).

Mirror neuron evolution

Glenberg takes issue with several of my comments regarding mirror neuron evolution. One is a general comment I made regarding the lack of selection pressure in the case where a non-mirror mechanism can support action understanding (also discussed above). Glenberg points out that if mirror neurons add something beyond this that confers survival value, then there *will* be selection pressure for them to evolve. I agree. But then the question becomes, how much does the mirror system add? As I argued above (and throughout the book), the answer seems to be very little if anything, thus undermining the claim that mirror neurons are of great evolutionary importance to the human mind. If mirror neurons are just plain old sensory-motor neurons that support action selection as I hypothesized, no such concerns arise regarding how they could have evolved.

Glenberg's remaining evolutionary concerns center on the role of mirror neurons in human behaviors such as language. My point was simple: appealing only to the mirror neuron mechanism (motor resonance) as an explanation for these human abilities explains nothing because monkeys have this mechanism but don't talk, don't imitate like us, and so on. Therefore, something else *must* have evolved. On this we all agree. Where we differ is what we believe evolved. Glenberg, echoing Rizzolatti and colleagues, speculate that mirror neurons evolved in some way to support complex human abilities. I speculate that mirror neurons are sensory-motor association cells that have roughly the same fundamental capacities in humans and monkeys (and no doubt many species as discussed in my chapter on imitation). What evolved, in my view, are the more complex systems such as language than can put the sensory-motor circuits to good use.

Glenberg questions my conclusions saying first that "it is not clear that whatever humans have would work without mirror neurons in [the first] place". I spent a good deal of time in the book showing precisely that humans don't need mirror neurons in order to perceive speech (Ch. 5), understand language (Ch. 6), understand actions (Ch. 4), and so on. This shows that *it is clear* that whatever humans have *does work* without mirror neurons. In fact, that was the main point of the book. An off the cuff assertion doesn't argue away the data I presented. Secondly he suggests that, "it may not be new cognitive systems that are needed, but better (or different) mirror neurons." If we stick to RS's definition of what the mirror mechanism is "*a very general, widespread mechanism transforming sensory information into a motor format*" then we can test Glenberg's speculation by assessing the effects of sensorimotor (dorsal stream) disruption on cognitive system operation. Again, this is the task I undertook in my book and the answer I found in the empirical record was that the mirror system is necessary for motor control but not other cognitive functions. Glenberg points to imitation, hinting that the human mirror system's capacity to mimic specific movements rather than reflect action goals provides an important evolutionary mechanism. But he's falling into the same trap as the Parma group. The mirror mechanism derives its power from the simplicity of the resonance mechanism. It automatically resonates with movements—no inferential processing necessary—which in turn "ignites" understanding. The human system, they argue, has

evolved to resonate more broadly than the macaque system to include motor mimicry.¹ The problem with this reasoning is that there is an inferential man behind the mirror neuron curtain. If mirror neurons simply resonate, how do they know to resonate only with goal directed actions (if they are in a macaque) or to resonate both with goal directed actions and meaningless movements (if they are in a human)? Something else must have evolved to *orchestrate* the resonance. Until we have a theory of *that*, speculations about mirror neuron evolution are near vacuous.

Does the mirror system—or sensorimotor system, as I would call it—contribute to human language and other human functions? Yes, of course! It is the mechanism for controlling movement, both of the hand and the mouth (and more). It is therefore clearly involved in things like language and imitation, which both involve a motor output component. Can the development of more complicated neural systems for controlling these motor effectors (such as the hand) contribute to higher-level cognitive function? Perhaps. In my *own* research program I have been pursuing the idea that principles of motor control can be applied productively to models of speech production, including at traditionally linguistic levels (Hickok, 2012a, 2012b, 2014c; Hickok, Houde, & Rong, 2011). I actually believe, quite in the spirit of Glenberg’s remarks, that what we call phonological processes evolved from motor control circuitry. But this is still a story about motor control as it is applied to different motor effectors (hand, vocal tract) and at increasing levels of abstraction (low-level kinematics up to high-level sensory-based movement goals). The neuropsychological evidence tells us that this motor control circuit is not the basis of understanding speech or manual gestures. For this we need a different (but tightly linked) neural model (Hickok & Poeppel, 2000, 2004, 2007).

Finally, I agree with Glenberg’s point that we approach scientific ideas and data in a very Bayesian manner. But he completely misses in his guess about my priors. He speculates that, “it is hard for [Hickok] to accommodate any contribution of motor system to language understanding.” In all three of my major theoretical papers on the organization of the language system (Hickok & Poeppel, 2000, 2004, 2007) I assumed that the conceptual system is “widely distributed” citing authors such as Damasio who have promoted what might now be called an embodied view (bound by convergence zones) (Damasio, 1989). I have done historical work showing that Wernicke was ahead of his time in arguing for a distributed system of concept knowledge that included sensory and motor systems (Gage & Hickok, 2005). And in the middle of writing *The Myth of Mirror Neurons* I published a paper in which I claimed, “On the input side, while the motor speech system is not necessary for speech perception, it is activated during passive listening to speech and may provide a *modulatory* influence on perception of speech sounds” (p. 411); I then proposed a computational mechanism for how the motor system might do this (Hickok, Houde, et al., 2011). More broadly, I have argued extensively that

¹ It’s actually unclear whether this claim is correct because in contrast to Glenberg’s statements an fMRI study of the macaques mirror system co-authored by Rizzolatti revealed a region that responded to intransitive actions similar to what is observed in humans (Nelissen, Luppino, Vanduffel, Rizzolatti, & Orban, 2005). But it is dangerous to put too much theoretical weight on one study alone.

a traditional cognitive module, the phonological loop, can best be understood in terms of sensorimotor circuits for speech (Buchsbaum et al., 2011; Hickok, Buchsbaum, Humphries, & Muftuler, 2003) and, as noted, that abstract linguistic categories might be “grounded in” sensorimotor circuits (Hickok, 2014a, 2014c). In the *Myth of Mirror Neurons* I proposed a hierarchical/hybrid model of conceptual knowledge representation:

If we assume that perceptual and motor systems are part of the conceptual system, as the embodied theorists argue, then we have merged the two ingredients and built a hybrid model of conceptual organization in the brain that includes both low-level sensory and motor systems as well as abstract categories. We involve low-level representations when we are thinking about particular details and we involve more abstract, higher-level representations when we are thinking more abstractly.

By any metric, my publication record shows that I am quite sympathetic to the idea that sensory and motor systems play a substantial role in what we have traditionally viewed as “higher cognition.” Some cognitive psychologists might even label me as an embodied cognition theorist for all the reasons noted above.

But at the same time I have no interest in putting the theoretical cart in front of the data horse. If the motor system plays a role, for example along the lines that Kilner (Kilner, Friston, & Frith, 2007), Arbib (Arbib, 2004), and I have suggested, then it plays a role. I have no ideological objection to it. But the existing data, as reviewed in my book, point to either no role or a very small role indeed for the motor system in understanding actions.

Glenberg suggests that the book is a “major miss” because it has clouded the contributions of mirror neuron theory to our understanding of cognition and behavior. He’s partially right. My book *has* clouded the contributions of the theory, but this is only because the *theory* is cloudy. *The Myth of Mirror Neurons* reveals this state of affairs and offers some alternatives for emerging from the mist.

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