Big Myth or Major Miss? Gregory Hickok's "The Myth of Mirror Neurons: The Real Neuroscience of Communication and Cognition"

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Ginger Campbell is the host of the Brain Science Podcast. She begins podcast 112 about Hickok's "The Myth of Mirror Neurons" (Hickok, 2014) by stating, "This is a really misleading title…" I could end my review there.

But to be fair to Hickok, by the end of the interview Campbell does endorse the book. And to be fair to mirror neurons, the topic is too important to let a misleading title slip by.

Mirror neurons were first reported in 1992 (di Pellegrino et al., 1992) and named a few years later. Using single-cell recording in the macaque premotor cortex, a team lead by Giacomo Rizzolatti discovered neurons that were active during action execution, and the same neurons were equally active during the visual observation of similar actions performed by the experimenter. Why were cells in a motor area of the brain responding to visual stimulation? One answer is the action recognition hypothesis. Mirror neurons allow a matching between the behavior of the observed animal and the motor system of the observing animal. By virtue of this matching, the observing animal has a better understanding of the action, that is, the understanding is not simply based on visual analysis, but it includes the motor plans and goals that the observing animal would have if performing the same action. In short, this motor matching, or motor resonance, provides a mechanism for understanding those actions which the observer can perform. This mechanism does not require complex inferences based on learned rules. Perhaps, then, mirror neurons (or better, a mirror neuron system, MNS) play a major role in social interactions from language understanding to joint action to empathy.

Furthermore, a MNS provides a neurophysiological underpinning for several claims of embodied cognition such as a) perception and action are intimately linked, and b) what appears to be high-level or abstract cognitive phenomena (e.g., language, goal understanding, mind reading) are based in sensorimotor systems and bodily states. No wonder Ramachandran (2000) suggested that "mirror neurons will do for psychology what DNA did for biology: they will provide a unifying framework and help explain a host of mental abilities that have hitherto remained mysterious and inaccessible to experiments."

Hickok's book provides a clear introduction to the cognitive neuroscience of communication, and is entertainingly written. Some of my favorite lines: "We can think of action potentials as the basic element in the language of neurons and single unit recordings as a way of wiretapping that conversation" (page 9); "While phrenology was right about the cortex being nonuniform in function, it was wrong about the neuroarchipelago architecture" (page 59); and in discussing the Motor Theory of Speech Perception that Hickok claims has been completely discredited, "Nonetheless, the theory lives, in zombie form I would argue…" (Page 101).

So what is it about the title—and other parts of the book—that are misleading? In regard to the title, Hickok admits (in the podcast and the book) that both macaques and humans have mirror neurons, so their existence is not a myth. In regard to other parts of the book, there are oversights and misinterpretations that are difficult to explain. For example, Hickok discusses on page 39 one of the most direct pieces of evidence for mirror neurons in humans, namely Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried's (2010) use of single-cell recordings to

document, in humans, neurons with mirror properties. But incredibly, the citation to this seminal finding is not provided despite the fact that the book contains some 345 other footnotes.

For Hickok, the myth is that mirror neurons play an important role in human cognition, as implied by the action recognition hypothesis and exemplified by Ramachandran's quote. Hickok marshals empirical and logical evidence in support of an alternative claim: Mirror neurons (or a MNS) do not contribute to action recognition, instead the MNS functions as an action selection mechanism with few implications for other forms of cognition. Although much of that evidence can be disputed [as is the case for his widely cited, "Eight Problems for the Mirror Neuron Theory of Action Understanding in Monkeys and Humans" (Hickok, 2009)], doing so would require a book-length treatise. In fact, Kemmerer's (2014) review runs to 26 journal pages, and it too addresses just part of Hickok's book. Instead, I will focus on three of the arguments that Hickok believes are the most persuasive. The first argument is that it is obvious that a MNS (and motor competence in general) cannot be the basis for action recognition because we can easily recognize actions that we cannot produce. The second argument is that the mirror neurons play little or no role in language, speech perception, in particular. The third argument is that macaque monkeys have mirror neurons, but they do not have language (nor many other human abilities), and so a MNS is probably not very important for human cognition.

Argument 1: We recognize actions that we cannot perform.

This argument would have some force if mirror neuron theorists proposed that the MNS is the only mechanism for action understanding. But do they? Let's revisit a quote from Rizzolatti & Craighero (2004) on page 20 of Hickok's book. Commenting on the contribution of a MNS to action recognition, Rizzolatti and Craighero write that "…there are other mechanisms that may mediate action recognition…" Furthermore, Rizzolatti and Craighero are not the only ones to suggest multiple routes to action understanding. For example, Gallese (in Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011) writes,

> "In conclusion, it is fair to say that action understanding, even at a basic level, *does not necessarily* require the activation of MNs. It has been shown that communicative actions, when implying motor acts outside of the human motor competence (e.g., observing a barking dog) are easily understood without any involvement of the observer's cortical motor system (Buccino et al., 2004). However, this does not imply that action understanding obtained without mirroring is the same as that based upon it" (emphasis added).

And Iacoboni (also in Gallese et al., 2011)) writes,

> When I watch the same backhand volley, my internal motor knowledge of how to hit a backhand volley gives me a much richer understanding… Taken together, the empirical data support the hypothesis of an important *contribution* of MNs to action understanding" (emphasis added).

Consider also Rizzolatti & Sinigaglia (2010) discussing an example originally proposed by Hickok (2009),

> Finally, saxophone playing has been used as an example to show that the mirror view of action understanding is "untenable": no motor competence is required to understand that someone is playing a saxophone... This is true, but such competence leads to a different understanding of saxophone playing. The non-motor-based understanding implies a mere semantic knowledge of what a saxophone is for, whereas the motor experience allows an individual to understand what saxophone playing really means — that is, it provides a musical knowledge 'from the inside'.

Thus many of the major players investigating the role of a MNS in action understanding are explicit in noting that the MNS gives an extra dimension to action understanding, not that the MNS is the exclusive neural mechanism for action understanding.

Not only does Hickok quote Rizzolatti and Craighero, he is also a co-author of Gallese et al. (2011) from which I took two of the previous quotes. Given that, I find it hard to understand how many of Hickok's arguments seem to be against a claim that a MNS is the *only* mechanism of action understanding. Here are some examples. On page 48, Hickok discusses data from one study indicating that a third of the patients with apraxia (difficulty in producing coherent actions) had no trouble recognizing actions. Hickok writes, "What this shows conclusively is that the ability to understand actions does not require the ability to execute them, contrary to the predictions of the mirror neuron theory of action understanding." But given the

quotes above, mirror neuron theory does not "require" motor competence for all action understanding. On page 153, in a discussion of Gibson's idea of affordances, Hickok writes, "But we should not confuse the fact that action is an important part of perception with the idea that motor representations alone are the basis of perceptual understanding." But, no one is asserting that motor representations "alone" are the basis of perceptual understanding. On page 154 he writes, "Having experience in performing an action *can* lead to a better understanding of those actions, but this does not imply that the meaning is stored in the motor system or that motor simulation is necessary to achieve understanding" (emphasis in original). Again, given the quotes above, mirror neuron theory does not propose that motor simulation is "necessary" to achieve understanding. Consequently, one can hardly resist the temptation to conclude that Hickok's first argument (we can recognize actions we cannot perform) is arguing against a straw man interpretation of mirror neuron theory.

Does it make sense to propose that a MNS can contribute to action understanding without being necessary for action understanding? An example from vision provides a useful analogy. Vision scientists have identified stereopsis (that fact that the two eyes respond to slightly different areas of the visual field) as a contributor to depth perception. Nonetheless, when we close one eye, the world does not suddenly appear flat. That is, there are other cues to depth, such as texture gradients and occlusion. Similarly, there are multiple cues to understanding the goal of an action. The interesting issue, of course, is to figure out how each of these cues makes a contribution.

Argument 2: Mirror neurons do not make important contributions to speech perception.

In his second argument, Hickok proposes that a keystone in the mirror neuron account of action understanding centers on language. Broca's area, which has long been associated with speech production, is a component of the human MNS. Given that the MNS is supposed to contribute to both action production (including speech production) and action recognition (including speech perception), the ineluctable conclusion is that the MNS and Broca's area should contribute to speech recognition. Does it? Hickok notes that there are few proponents of the Motor Theory of Speech Perception as proposed by Liberman, Cooper, Shankweiler, and Studdert-Kennedy (1967). Even some of the previously strong supporters agree that the theory, as proposed in 1967, is no longer tenable (Galantucci et al., 2006). But the Motor Theory of Speech Perception is not equivalent to the proposition that motor system contributes to speech perception. That is, although specifics of the Motor Theory led to its demise, the general notion of motor contributions to speech is alive and well.

Much of the recent work examining the contribution of motor system to speech perception has used Transcranial Magnetic Stimulation (TMS). When applying TMS, an external electromagnet is held next to the head and is used to direct a magnetic pulse toward an area of cortex (in this case, motor cortex). The magnetic pulse forces the firing of neurons aligned perpendicular to the magnetic field. Depending on the timing and frequency of the pulses, TMS may facilitate or inhibit further processing. A number of studies (e.g., D'Ausilio et al., 2009; Meister,

Wilson, Deblieck, Wu, & Iacoboni, 2007; Mottonen & Watkins, 2009; for reviews, see Möttönen & Watkins 2012; Murakami, Ugawa, &Ziemann, 2013) have used TMS to demonstrate a causal effect of motor cortex on speech perception.

Hickok argues, however, that most of these TMS studies suffer from two problems. First, effects are generally found only when the speech is degraded by noise (but see Bartoli, D'Ausilio, Berry, Badion, Bever, & Fadiga, 2013). Second, most of the tasks have not tapped into meaning of the speech stimulus. Instead, the participant must identify a phoneme embedded in a nonsense syllable (but see Möttönen, Dutton, & Watkins, 2013). However, the ability to break apart a syllable and identify the phonemes is associated with skill in reading, and that suggests that conscious phoneme detection is not an intrinsic part of speech perception. So, Hickok argues, the TMS data are not relevant for understanding natural speech perception (of meaning) in context.

In addition to the studies cited above, a recent study that addresses Hickok's concerns (although in fairness, it was not available when Hickok was writing his book) is Schomers, Kirilina, Weigand, Bajbouj, and Pulvermuller (2014). In this experiment, a brief train of TMS pulses was directed toward the area of motor cortex controlling the lips or the tongue. Shortly after the pulses, participants listened (without noise) to a word that began with a lip-related consonant (e.g., "pool") or a matched word that began with a tongue-related consonant (e.g., "tool"). Then, the participant chose between two pictures to indicate which word was heard. Thus, the task was clearly at the level of word meaning, not just the identification of phonemes. The results were striking: For words beginning with a lip-related

consonant, TMS to the lip-area reduced the time needed to identify the word compared to TMS to the tongue-area. Just the opposite was found for words beginning with a tongue-related consonant, that is, TMS to the lip-area increased the time needed to identify the word compared to TMS to the tongue-area.

One study is unlikely to resolve this contentious issue. And, this one study does not directly address many of the other types of data Hickok marshals against the contribution of motor cortex to speech perception (although see the introduction and discussion of Schomers et al., 2014 for counterarguments). Nonetheless, it is clear to me that what Hickok takes as some of the strongest reasons for discounting the importance of the MNS are much weaker than portrayed in the book.

There is also a growing literature on the contribution of motor system to language understanding (not just speech perception). Using fMRI, Aziz-Zadeh, Wilson, Rizzolatti, and Iacoboni, (2006) found that similar areas of premotor cortex are active during a) the perception of actions, and b) the comprehension of sentences describing similar actions. Also using fMRI, Hauk, Johnsrude, and Pulvermüller (2004) reported somatotopic activation of motor cortex during the perception of verbs describing hand, lip, or leg action. Aravena et al., (2010) found that language understanding affects components of the EEG signal attributed to motor processes, and simultaneously, motor preparation affects components of the EEG signal attributed to semantic activity. Behavioral work on language understanding similarly points to motor contributions to the understanding of language describing actions (e.g., Glenberg & Kaschak, 2002), and some of this

behavioral work attempts to implicate the MNS itself (e.g., Zarr, Ferguson, & Glenberg, 2013).

Argument 3: Monkeys have mirror neurons, so why don't they talk?

The third of Hickok's arguments that I will address is that monkeys have mirror neurons but not speech and not much culture, consequently humans must have evolved mechanisms in addition to a basic MNS that accomplish these cognitive skills. Although I am no expert on evolution, I find many components of Hickok's argument puzzling. Here are some examples with my comments.

On page 49, in discussing the possibility of multiple systems contributing to action understanding, Hickok writes, "If another [non-MNS] mechanism exists, what selection pressure could have led to the evolution of mirror neurons? If the cells are effectively redundant, then there is nothing for natural selection to work with." The answer seems simple enough: Mirror neurons make action recognition better, that is, faster, more accurate, and more contextually appropriate. It is not that the MNS is redundant and adds nothing. Furthermore, if random variability produced a system that increased fitness (survival and reproductive success), then that is a good start for natural selection to spread the system widely.

On page 200, "Macaques don't imitate on a scale that humans do, not for lack of the foundational neural machinery—they clearly have it in mirror neurons!—but because they don't have the cognitive systems in place to get as much out of imitation as humans do." In some ways this statement must be true, but a) it is not clear that whatever humans have would work without mirror neurons in place, and

b) it may not be new cognitive systems that are needed, but better (or different) mirror neurons. For example, human mirror neurons do appear to be different from monkey mirror neurons in that the human cells are sensitive to intransitive movements (such as flexing a finger or lifting an arm), whereas macaque mirror neurons are not. Thus, these human cells support imitation of movement specifics, not just movement goals. It is this sort of specificity that Tomasello (e.g., Herrmann, Call, Hernandez-Lloreda, Hare, & Tomasello, 2007) suggests is important for the "ratchet effect" that producers cumulative advances in culture.

On page 206, "Macaque brains, however, are not set up to take full advantage of imitation for language learning or social networking. Human brains, on the other hand, are built to take better advantage of what imitation can offer. We have the same fundamental associative mechanism, we probably have the same type of mirror neurons, but we differ in the cognitive (information processing) mechanisms that have evolved to put those fundamental associative mechanisms to good use." Again, it is possible that a) better (or more, or different) mirror neurons help humans, and b) that the advance might come in ways that are not classical information processing mechanisms. For example, the human hand is the most complex in nature, and it requires some of the most complex, hierarchically structured neural machinery to control it. Much of that neural machinery is in Broca's area. Consequently, evolution of the hand might have provided the ingredients for evolution of neural machinery (along with mirror neurons) to control the speech articulators.

On page 227, "If mirror resonance is the basis of human language, why don't macaques talk…If mirror resonance is the basis of empathy, social cognition, and all things human, why don't macaques act more like us? *Something* must have evolved that is causing the human mirror system to behave differently than the macaque mirror system" (emphasis in the original). Indeed, perhaps different mirror neurons, perhaps the hand, perhaps the human vocal tract. But none of this speaks against the usefulness of a MNS as an important component of human cognition and action recognition.

I know Greg Hickok and I like him. Also, I think that he is a great cognitive neuroscientist. Thus, it is a bit bewildering that Hickok can have such a jaundiced view of mirror neuron theory, whereas I look at much of the same data and see a Nobel-quality achievement. I offer three related and speculative explanations.

First, psychology deals with complex issues, but our theories are simple and our experiments crude. In the abstract, I am a great believer in the late Sir Karl Popper's notion of falsification, namely that scientific theories cannot be proven true, but one failed prediction is enough to show that the theory is wrong. But given our crude experiments and our simple theories, it is probably impossible to definitively falsify theoretical statements such as "the motor system plays an important role in action recognition."

The second speculation is a consequence of the first. Namely, scientific thinking in psychology is Bayesian, not Popperian. We begin with some prior odds that a theoretical statement is true. Then, as each new piece of evidence (e.g., a

published report) becomes available, we adjust the odds. My hunch is that there is also an insidious component to our Bayesian thinking. Namely, not only do we use data to update the prior odds, but the prior odds are used to evaluate the data. If I am already a strong believer in the importance of a MNS, then I will more positively evaluate new positive data and negatively evaluate new negative data. Thus, perhaps Hickok and I look at the same data through different-colored lenses.

Third, we need to consider where those priors come from. For me, I first met Rizzolatti in 2003 at a symposium on language and action sponsored by one of the Max Planck Institutes in Munich. I was amazed by the data and impressed by the man. Both increased during my six months in Parma working in Rizzolatti's Department of Neuroscience. Of course, it also helped that my own behavioral research had resulted in data consonant with mirror neuron theory. Given these experiences, my priors in favor of the importance of a MNS are very strong.

What about Hickok's priors? Putting on my psychoanalytic hat, I can uncover some hints in the book. As noted above, Hickok holds very strong odds against the Motor Theory of Speech Perception. When he applies those odds to the evaluation of new data (e.g., data using TMS to investigate motor contributions to speech perception), it is hard for him to accommodate any contribution of motor system to language understanding.

But more critically, he has a strong belief that real knowledge is abstract and thus cannot be part of the sensorimotor system. For example, on page 54 Hickok discusses research related to Catmur, Walsh, and Heyes (2007) and he reasons "that TMS-induced 'mirror responses' reflect nothing more than associative pairing." But

why isn't associative pairing part of understanding? If I associate "bread" and "butter," isn't that association part of my understanding of both bread and butter? Apparently, Hickok wants more. On page 156, he writes, "Important information is stored in the motor system, but that information is motoric, not meaningful (semantic) information…" Why not? Is knowing how to use a hammer completely unrelated to what a hammer is? Certainly there is more to knowledge about hammers than motor information, but why exclude the motor information? On page 163, he writes, "on the other hand, what really defines these concepts isn't tied down to particular experiences; the core meaning is abstracted across sensory and motor experiences." I am not convinced: when considering the meaning of any concept—even abstract concepts such as democracy and love—we seem to begin by considering specific, concrete instances, and proceed to the abstract by noting similarities between the concrete instances or even simply by using non-specific language to verbally describe a specific experience. On page 195, "Macaques reach for and grasp things all the time and they observe their own actions visually. Pretty soon, an association builds between the execution of an action and the (self) observation of that action…Now, when the animal sees the experimenter execute an action similar to those that the monkey has previously executed, the cells fire because of the preexisting association built on self-observation. It's got nothing to do with understanding." Why not? If I associate the outcome of my action (I hear a tone) with the execution of the action (pressing a door bell), isn't that associated outcome an important component of my understanding of the action? And on page 197, "When the monkey then observes the same objects in the same context, this

could activate the associated goal-directed action. Again, this is classical conditioning." And why isn't classical conditioning a component of understanding? If I am classically conditioned not to touch a flame, isn't that part of my understanding of what a flame is? The point of this inexcusably-long paragraph is that Hickok seems to believe that true knowledge must be abstract. Given that strong prior, there may be no data strong enough to tip the odds in favor of the action recognition account of mirror neuron function.

So what's the upshot? Some might consider that Hickok has done the field a service by exposing the mirror neuron theory of action recognition as a big myth. But from my perspective, Hickok has done the field a disservice because his strong priors have clouded his evaluation of the enormous contributions of mirror neuron theory to our understanding of cognition and behavior. That is, the book is a major miss.

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