Serge Prengel: Hi Greg.

Gregory Hickok: Hi there, Serge.

Serge: So you wrote a book about mirror neurons and demystifying their role. Maybe we can start with the beginning. What are mirror neurons?

Gregory: Sure. Mirror neurons are cells in the motor cortex or motor system of Macaque monkeys. They were discovered in the context of doing some basic research on motor control, trying to figure out how Macaque monkeys and, by generalization, humans may code movement plans in terms of object-based coordinates. That is, when you reach for an object you have to take in information about the object’s shape and location and size into account to guide your reach. You pre-shape your hand when reaching for a cup versus a pen, for example. And so Giacomo Rizzolatti from Parma and his group were studying this process in macaques and they had discovered a class of cells in a motor area known as F5 for frontal area number five that seemed to respond or that did respond both during reaching behaviors and during the observation of object shape. The idea that they were exploring was that these were cells that were taking object shape information and using that to select from a vocabulary of appropriate grasps, the appropriate grasp gesture for reaching that object. So they were studying this population of cells and as they were swapping the objects in and out of the display case during the experiment they noticed that some of the cells that they were recording from started responding to the experimenter’s own actions. These were cells that responded when the monkey generated movements and as well as when they were observing the experimenter making similar movements. This is basically the response properties of mirror neurons; They respond both during action-execution and also action-observation. That was the basic discovery and the context in which it was made. The big question became “What are doing? What’s going on with these cells such as they respond to actions, as well as execution of actions?”
Serge: Okay. So from discovering that these very specific cells are activated during action and also during observation of action came the leap that they are responsible for more than that.

Gregory: That’s correct. So, in trying to figure out what they were doing, the most obvious interpretation or function that these cells could be supporting is direct imitation. So if you have a cell, for example, that responds both during observation and execution you might imagine that that cell allows the animal to directly imitate the actions that it is observing. That was considered briefly early on after mirror neurons were discovered, but that possibility was ultimately rejected on the basis of the observation that the Macaques don’t seem to imitate like that. They don’t do direct imitation like humans do. And so that was discarded as a possible interpretation of these cells and they looking for other possible interpretations. There was a theory that had been around since the 1950’s in the speech domain, my area of research, called the motor theory of speech perception, which held that when we perceive speech sounds, the goal of perceiving speech sound computationally, is not to recover its acoustic form but to recover the gesture of the speaker. That is, the motor plan that generated the sound that you’re listening to. It was very much a motor theory of perception, and mirror neurons kind of looked like that. They were responding during the observation of actions. The Parma researchers considered the hypothesis that maybe these cells were responsible for action understanding, that’s how the monkeys understand others actions, and the method they proposed was one of simulation. The logic kind of goes like this: When the monkey generates an action, say a reaching action towards something, it knows what it’s doing, it knows its intentions behind the movement. When it observes another animal generating an action, if it can simulate those movements in its own motor system, then by the same token it will be able to understand other people’s actions. And so you simulate to allow understanding. That’s the basic idea.

Serge: So, in a way, the part in there is not just that its possible to simulate in order to understand, but the question and some of what you discuss in your book is about the nature of understanding. Is how we understand sayings based on basically imitating the movement? And so it raises the question of how we know what we know, and how we understand what we understand, and how we attach meaning to things.

Gregory: That’s exactly right. The big problem with this idea is that the movements themselves contain meaningful information, or that by observing or simulating the actions it will automatically tell us what the meaning of those actions is. If you think about it for a little while, it’s obvious that it’s not the case and there’s several reasons why if we look closely. For example, if I reach for a pitcher and tip it over so that it pours water out into a cup that action can mean many different things depending on the context. So if there’s no water in the pitcher, it’s just a tilting motion, it doesn’t really do anything, it’s not pouring. If there’s water in there then we can think of it as pouring. If we think about it from the perspective of the cup then it’s filling. The movements are identical, so you can generate very similar or identical motor patters and achieve the same goal. The movements really don’t define the meaning, they’re actually quite ambiguous. It really depends on the context and a lot of the mirror neuron experiments demonstrated this, that the same movement that the monkey observed gave rise to mirror neuron activity not depending on the movement but depending on the context, and that’s in the mirror neuron literature. It’s not the movements themselves that are defining it.

Serge: So the interesting part then is that it is more complex, that the movement itself is one source of information and the processing involves many sources of information.
Gregory: Right. In order to understand something you need all this additional context and the movement is only a small part of it. It may be that, perceptually, it’s an important part to process that movement, but it doesn’t mean that simulating that movement in your own body is going to tell you much of anything. We know empirically that in individuals that don’t have the ability to move, they seem to be able to understand the world quite well. We all can understand action that we have never performed previously, say a reverse slam-dunk in a basketball game for example. Not many of us can do that, but we can understand it quite well. Other animals that have movements that we can’t possibly generate we can still understand, so flying or slithering or things like that. And there’s good evolutionary reasons why we would want to understand the actions of other animals, because sometimes they’re predators and we want to know what they’re up to. Sometimes they’re prey, and we want to predict what they might do so that we can catch them better. There’s lots of reasons why we should have neural systems that allow us to understand the actions of others without having to simulate these actions.

Serge: So, in other words what you’re saying is that mirror neurons are certainly a source of information, but they’re not the source and certainly not the source of meaning.

Gregory: Well, not quite. The way I view mirror neurons is they’re essentially important for motor control just like these cells in F5 are important for using sensory information about object shape to guide action selection. I see mirror neurons as doing exactly the same thing. Instead of object shape they’re using action, they’re using dynamic information about movement in order to guide responses. Generally, you can understand that the actions of other animals or people are important for selecting our own actions. If I thrust my hand out towards you when we first meet you’ll likely respond with a similar gesture to shake hands. If I do something else like throw a punch, you’re going to want to select a different action, a blocking or ducking action for example. Presumably, this is very important in the monkey world as well, and I think it’s that action selection function that mirror neurons are actually doing. I think the understanding is coming from different circuits, it’s coming from sensory circuits that are involved in recognizing actions, connecting them to meaning, integrating them with context, and all sorts of things. The involvement of the motor system is just to select actions that are appropriate to the understanding we get from other systems.

Serge: So is there maybe a hierarchy there of some things, some situations where there’s more instinctual reactions, and some cases where there’s more involved, more processed reactions?

Gregory: Certainly it’s the case that we have reflex-like responses. Like I said, if I threw a punch at you, reflexively you would want to duck, or block, or do something like that. I think one way to think about it is in terms of general brain organization into what’s often been referred to as dorsal and ventral streams, sensory streams. The dorsal stream is thought to be involved in sensory-motor integration. This is a parietal-frontal circuit that is taking sensory information and is using that to guide actions and that can be thought of as more of a reflexive, online, immediate system. That’s the system that mirror neurons are apart of. And then there’s a ventral stream circuit that’s more involved in recognizing what is going in the sensory environment. You can think of it as taking sensory information and trying to link it up to medial-temporal lobe structures involved in memory, episodic memory, all sorts of things like that. So you can think of it as hierarchical in the sense that you have in some sense a lower level motor circuit that can respond reflexively taking information from a more cognitive or higher level conceptual system that’s involved in recognizing, attaching meaning, attaching emotional relevance to information that’s in the environment. I think it is kind of
helpful to think about organization of these circuits in terms of that kind of hierarchy and placing mirror neurons and other sensory motor circuits within one stream. It’s not particularly involved in recognition, but it’s involved in taking action.

Serge: And involved in taking action, but there is a difference anyway in the action that’s being taken in terms of the context. So that’s where you would make the difference, say, between the action you take at first and the action you take once more you’ve had time to process at a higher level?

Gregory: Yeah, certainly it’s the case that some things are very reflexive. I mean, generally you can think of the nervous system as being layers of control, so at the lowest level you have things like spinal reflexes which will get triggered automatically, but on top of that you have other circuits that are built to modulate that low-level reflexive response, because we don’t want to always respond reflexively. Sometimes, depending on the situation, we may not want to release that hot pan knowing that it might make more of a mess, knowing that if we drop it than if we quickly set it down or do something else. So yes, it’s always the case that we have some sort of higher level of control over these things. We can decide after observing an action and understanding it whether we want to respond to it or not. And, of course, there are degrees of how reflexive our responses are. But I think the important thing is that mirror neurons are essentially in a motor control circuit, that they are not the basis for understanding, they’re kind of the endpoint for understanding. They respond after the understanding takes place, which is very much characteristic of the way that these cells respond in monkeys. So, for example, in one experiment the researchers placed an object behind a screen so that the monkey couldn’t see it anymore and then reached for it and mirror neurons fired. It is interesting that mirror neurons will not fire if the experimenter is reaching for nothing or just pantomiming a reach. That object has to be there in order for that to happen. It doesn’t physically have to be there in the sense that you could put it behind a screen that is physically in view, you can put it behind a screen, the monkey knows it’s there, and it will respond to it even though it can’t see it. So-

Serge: I just want to interrupt you here, because as you’re talking you’re clarifying something for me. When you first said, at the beginning of your answer that something comes first, in a way takes me in a little bit of a loop. I think of the word understanding as referring to more conceptual, abstract understanding, as if in a way rational thinking preceded action. And as you’re talking more about this it’s actually something different that’s coming up. It is not understanding as some kind of abstract reasoning, but as having a context so that reaching is not a gesture in and of itself, but that is reaching for something. And it’s that mix of a gesture, and a goal, and a total context that is what you call understanding. Is that what you’re talking about?

Gregory: Yeah, I mean if we go back to the experiments that show when mirror neurons fire and when they don’t, they will fire if there is an object to be grasped. They won’t fire is there’s not an object to be grasped, and that’s going to depend on the context, the non-motoric context. And so there’s got to be some level of understanding of what the goal of that actual action is going to be before the mirror neurons will even fire. The typical interpretation out there in terms of mirror neurons is that they fire to tell you what the goal is. If they have to know what the goal is in order to fire then some level of understanding needs to be taking place before this circuit gets recruited. And so yes, I do think that there is some sort of contextual understanding of what the goal of a reach is and what actions that might map onto in the monkey before these cells will actually fire.
Serge: So then in a way even at the level of something relatively basic like mirror neurons we’re still in a system where it’s not just sensory is pure stimulus and pure stimulus gives the reaction. Even in that case we have a more complex process where we are attaching context and processing information before the reaction happens.

Gregory: Sure, yeah, and just think of your everyday life. If we were completely reflexive, every cup, every object that you looked at you would reflexively reach for. Or, anyone who reached out for something or did something, you would mirror it or perform a similar action.

Serge: When you say this, actually it’s an interesting point. One of these reasons that the concept of mirror neurons caught on so well with psychotherapists is that in our everyday life seeing clients we catch ourselves “mirroring” the movements, the hand gestures, the body language, the moving of hands, the moving of legs of our clients, and vice versa. So in that way, it’s very tempting to jump into it and say “Oh, this must be mirror neurons.”

Gregory: Yes, that is a documented phenomenon, it’s known as the Chameleon Effect, and it’s something that I discuss in the book in the chapter on imitation. Humans do it. Macaques don’t do it, which is kind of interesting because Macaques have mirror neurons and they have the system that presumably would allow this, and yet they don’t do it. And so it’s something beyond mirror neurons that’s actually allowing this ability. What’s it for? It seems to serve a social function. These sorts of things have been demonstrated experimentally in work that has people perform an irrelevant task in the company of a confederate to the experiment who’s generating some behaviors. When the confederate scratches their head the experimental subject will tend to scratch their head. The interpretation of this Chameleon Effect is that it is serving a social function to essentially provide social acceptance, or provide in-group status, or something like that. It’s interesting that humans tend not to imitate or mirror people that they don’t like or don’t identify with, so it is a kind of unconscious imitation, mirroring if you want to call it that, but it is not a dumb process, it’s not a reflexive process. Presumably what’s happening, as is the case with other kinds of mirroring or motor control, is that there is some sort of higher-level circuit that is controlling or enabling this process to take place. It’s that process that we want to understand to know what’s happening with this kind of Chameleon Effect mirroring. We need to think about what this higher-level circuit is doing such that it can activate the lower-level mirror-like circuit.

Serge: Right. And so, the image of mirror is the same that, say, can be used in contemplative approaches to life; that wish that our minds were like a mirror that simply reflects the world as it is, and with some training and skill we can eliminate what gets in the way of that and have the purity of outside experience. What you’re reinforcing and what you’re saying is that actually everything in our brain is designed to interpret experience as opposed to reflect it.

Gregory: Well, if we look to perceptual science, perceptual neuroscience- you’re talking about things that are way beyond my ability to comprehend myself, fairly abstract things- but if we ground those things in perceptual science, we know as a matter of fact that we don’t simply perceive or resonate with the world. Our brain actively constructs a representation of what the world looks like. If that’s true, even at the perceptual level, even in perceiving cups and things like that, if you scale up to human experience or more complicated situations, that with more force is a construction of our mind in terms of how it interprets the world.
Serge: And so, in a way, how does this bring us, in terms of concept of how we know what we know, how we conceptualize what we experience, and that whole concept and discussion you have in the book about embodied experience, embodied cognition? On the one hand, you know, there is it seems like we must have evolved in way that we developed abilities to deal with the world that were more complex, but based on simpler processes. On the other hand, such possible mechanisms as mirror neurons appear flawed as explanations of it.

Gregory: Yeah, the embodied cognition movement is an interesting thing. I think there are parts of it that are quite accurate and that are reasonable, so one of the things I like about it is that the movement tries to take complicated cognitive processes, and cognitive is kind of a loaded term as I talk about in the book, but complicated processes like categorization, or problem solving, or decision making, things like that, try to think about how these might be done in terms of lower level circuits and sensory-motor circuits. I think that’s an interesting research direction to take. Where I think the program has gone wrong is this notion of simulating. Basically the idea is the way we think about, say, cats or dogs or something, is we simulate the sensory experience, and that’s often taken as an explanation of how it’s done. “Oh, we just simulate it, the concept of cat in our sensory-motor systems, or whatever,” and that’s actually how we understand it, but this doesn’t tell us much at all. Simulation is just a term for, basically, information processing, and what we really want to do is figure out what happens in the initial process. So to say that we simulate our experiences with cats in order to understand them, that’s fine, but then we want to know “What is this experience with cats?” How is it coded in our sensory-motor systems or whatever, to give rise to our understanding in the first place? To say that we simulate it doesn’t really help, it kind of renames the problem, essentially.

Serge: Just like calling it a process, essentially.

Gregory: Yeah, that’s right. And so the embodied program is interesting, I but I think as a replacement for traditional cognitive psychology it has failed. It doesn’t really change much of anything except to look for lower level processes in the brain, which themselves are quite abstract in terms of trying to explain some of these higher-level behaviors.

Serge: So the flaw, as you see it, is that it tries to provide an explanation for what happens, but in a way that doesn’t match the information we have about how it happens.

Gregory: That’s right. There’s lot’s of empirical evidence that I discuss in the book showing that essentially you don’t need a motor system in order to understand actions. I go through that in the speech case, which is a domain that mirror neurons were first generalized to in humans. Speech was really the human connection between monkey mirror neurons and what’s happening in humans because we have a lot more data on that. There was this motor theory about speech perception that was out there; incidentally, that theory was rejected by speech and language scientists before mirror neurons were discovered, so it’s kind of a poor analogy to use to help interpret mirror neurons since the theory was essentially dead. But, there’s evidence, for example, of individuals with cerebral palsy who can’t control their speech muscles. They had never spoken yet could nonetheless understand speech quite well. There’s examples from people who can’t move and can understand actions quite well, for example in apraxia or congenital disorders like cerebral palsy, or ALS, or other things like that there are examples of people who can’t generate emotional facial expressions. This is Mobius Syndrome. They can nonetheless understand emotional facial
expressions as well as anybody else. So there’s example after example like this that show that you don’t need the ability to move in order to understand, so this explanation is just empirically false.

Serge: Right, right. So, it’s not necessarily that we are replicating the movement in order to understand it, but that maybe the information about movement is accessed by that part of our brain, our mind, that processes information that processes representations and influences our pre-motor information?

Gregory: Yeah, I mean there’s another area that isn’t discussed much in the mirror neuron literature that’s been discovered in Macaque monkeys as well as in humans, posterior (spoken at 28:30) superior temporal sulcus, which seems to respond quite well to the perception of all sorts of movements, eye gaze, and all sorts of interesting interactions between eye gaze and observed movements, and this sort of thing. This region is probably the hub for understanding actions. In humans it’s involved in biological motion perception, so it’s a big candidate for an area that’s processing this sort of information and relating it to contextual information, to long-term memories, to all these sorts of things. For actions that are recognized in this way and that are appropriate for generating a response, because not everything we observe is selected for response, then this information can be the sensory-motor parietal-motor parietal-frontal circuits can then be mapped onto motor circuits for action selection that may or may not be mirror related. So, if I thrust my hand out to shake your hand then you’re going to generate a mirror movement, but if, like I said, throw a punch, you don’t want to generate a mirror movement in that case. And so, I see these mirror neurons as part of a much broader sensory-motor circuit only some of which are coding mirror-like movements. There are plenty of others that code anti-mirror movements, and those were actually discovered alongside mirror neurons in Macaque monkeys in the original experiments, but these were not discussed theoretically.

Serge: Great. So Greg, is there something else you might want to say to conclude this conversation?

Gregory: Well, there’s one other topic that I dealt with in the book that might be of interest, and that’s autism, because the Broken Mirror Theory of Autism is quite popular, and like many theories of autism it assumes that something is broken, that these individuals have a lack of empathy, or an inability to empathize or read other people’s minds, things like that. But, there’s another possibility in that they’re hypersensitive and that can lead to avoidance behavior, which can then affect their ability when you assess them to show empathy. This is not because they can’t do it, but because they’re avoiding it.

Serge: They’re flooded and therefore avoided.

Gregory: Exactly. So there’s lots of reasons to think that a mirror neuron hypothesis and even just a deficit hypothesis for autism is valid and there’s lots of data suggesting that we should be considering alternative possibilities. So that’s another thing that was discussed that may be of some interest to people.

Serge: Great, great. Well, thanks Greg.

Gregory: Sure, thank you.