

BRAIN SCIENCE PODCAST

With Ginger Campbell, MD

Episode #35

Discussion of *Mirrors in the Brain: How Our Minds Share Actions and Emotions*, by Giacomo Rizzolatti and Corrado Sinigaglia

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INTRODUCTION

This is the *Brain Science Podcast* – the podcast for everyone who has a brain – and I’m your host, Dr. Ginger Campbell. On the *Brain Science Podcast* we explore how recent discoveries in neuroscience are unraveling the mysteries of how our brains make us who we are. For more information including Show Notes, links to previous episodes, and information about how to subscribe please go to the website brainsciencepodcast.com. We also have a Discussion Forum at brainscienceforum.com, and you can send me email at docartemis@gmail.com.

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Welcome to Episode 35 of the *Brain Science Podcast*. Today we are going to talk about one of the most exciting recent discoveries in neuroscience: mirror neurons. Mirror neurons were discovered in monkeys, and they are active when an animal performs a specific movement and when the monkey observes someone else doing the same motion. This discovery has a lot of implications in understanding how we do a lot of different things. This discussion is a little bit more technical than some of the recent *Brain Science Podcasts*, so if you are new to the *Brain Science Podcast* you might want to listen to Episode 21 and 23.

These are episodes about body maps that will give you a little bit of background information.

But before we get into our discussion I do want to remind you of just one thing, and that is about my other podcast *Books and Ideas* at booksandideas.com. *Books and Ideas* is the podcast that I put out once a month where I put things that just don't quite fit in the *Brain Science Podcast*. I cover a variety of topics and I interview interesting people who aren't neuroscientists. So, I hope you will check that out. It's also available on iTunes, and you can find subscription information at booksandideas.com. I'll put the rest of the announcements at the end of the episode so that we can go ahead and get on in to our discussion.

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DISCUSSION

Today I am basing our discussion on a book by Giacomo Rizzolatti, who was one of the discoverers of mirror neurons at the University of Parma in the early 1990's. His book is, *Mirrors in the Brain: How Our Minds Share Actions and Emotions*. This book was originally written in Italian. *Mirrors in the Brain* describes the discoveries that Rizzolatti made while working with monkeys. We're also going to talk a little bit about what we know about mirror neurons in humans.

It's important to consider that since this discovery is relatively new—being made only in the early 90's—as far as I know it has not been determined whether any non-primates have mirror neurons. I haven't had a chance to do a literature search on this, so if any of you have heard of mirror neurons being discovered in non-primates please either send me email or post it up on the Discussion Forum. At any rate, in this book Rizzolatti only addresses mirror neurons in monkeys and the question of their existence in people. My goal in this episode is to introduce

you to the implications of the discovery of mirror neurons so that we can talk about them at a deeper level in future podcasts.

In the preface of *Mirrors in the Brain*, Rizzolatti observes that few people really imagine the implications that the discovery of mirror neurons will have on how we perceive and understand the architecture and functions of the brain. And his focus in this book is to try to bring our attention to some of these implications. One of the important concepts in this book is the fact that motor regions of the brain are much more complex than was once thought, because they're not only active during complex goal-directed motor acts but they also respond selectively to certain shapes of objects, both when we interact with them and when we just observe them. And the coding in the motor area seems to be based on the range of potential actions offered by the objects. I'll explain what I mean by this in more detail in just a minute.

Evidence indicates that at the cortical level the motor system is not just involved in single movements, but with actions. It's very rare for us to move our arms, our hands, or our mouth without a goal. One thing I want you to come away from this episode with is an understanding of the fact that the rigid division between perceptive, motor, and cognitive processes in the brain appears to be largely artificial. Perception actually seems to be imbedded in the dynamics of action. He says the acting brain is an understanding brain. The kind of understanding I'm talking about here is pragmatic, preconceptual, and prelinguistic, but such understanding clearly forms the basis for our more celebrated cognitive abilities. This understanding is also reflected in the mirror neurons, as we shall see.

As I mentioned in the introduction, mirror neurons were discovered in the early 90's. Mirror neurons imply that our recognition of actions of others, and even understanding their intentions, depends on our own motor repertoire. Think about what that means. It implies that we are going to have difficulty

understanding people's actions when they're doing something outside of our repertoire—at least this kind of motor understanding.

It is becoming clear that mirror neurons are what allows our brain to match observed movements with movements that we ourselves can perform. He says that mirror neurons appear to be essential to the “sharing of experience that is at the root of our capacity to act both as individuals, but also as members of society.” Mirror neurons are also the key to being able to understand the emotional expressions of others. Therefore mirror neurons are the key to the bond we feel with others. This implies that mirror neurons are a key to what makes us social beings.

Now, before we can really get into mirror neurons specifically we need to look a little bit at the motor system. This book, *Mirrors in the Brain*, is not really a book aimed at a general audience. It contains detailed descriptions of quite a few different experiments. My goal is to highlight what these experiments have revealed. Despite the technical nature of this book, I think the author does a very good job of relating the experiments to real life. He starts out by describing the simple act of picking up a cup of coffee.

I suggest that as you're listening—if you're not driving a car—that you might want to just pick up a nearby object and kind of observe what happens. Notice that your fingers begin to assume the shape of that object before you touch it, and you have expectations about how it will feel, and also how much effort will be required to pick it up—that is, how heavy it's going to be. Consider what happens when you pick up an object that turns out to be a lot heavier or a lot lighter than expected. That simple experience has been used as a source of a great deal of visual humor over the years. The point is that even something as simple as picking up a cup of coffee involves a complex intertwining of sensations, motivations, expectations, and motor actions.

The discovery of mirror neurons has actually caused neuroscientists to completely reevaluate the neural mechanisms of simple actions. The traditional viewpoint has been that sensory, perceptive, and motor mechanisms are isolated into clearly distinct cortical areas, with the sensory areas in the back of the brain, the motor areas in the back of the frontal lobes, and the association areas mainly in the parietal lobes which are in between these two areas. The association areas were thought to be where all the information from the various senses was put together.

In this old view the motor areas were seen as rather simple, and almost peripheral. This view is still perpetuated by the brain maps you find in textbooks, because with these maps you tend to get the impression that the motor areas are devoid of any kind of perceptive or cognitive role. However, modern electrophysiological techniques are revealing that the motor cortex actually has what Rizzolatti calls “a plurality of functions that are not compatible with the concept of a sole purely executive map.” For example, the monkey’s motor cortex has been found to have a number of maps that are functionally distinct from one another. In other words, it’s not like the motor cortex just has one simple map.

Probably even more important have been the discoveries that have been made by recording from single neurons, because they have actually been shown to respond in different ways to sensory stimuli. The bottom line is that the anatomical and functional structure of the motor cortex is much more complex than was thought in the past. Now, if this is true for the monkey it is likely true in humans. And I will consider the evidence for this a little later.

Now, it’s not actually an entirely new idea, since it’s been known for some time that the retina and the cochlea have multiple representations in the cortex. The question is what is the significance of the multiple representations in the motor cortex? The challenge is how do these various areas perform in the organization and control of movement. The discovery that the situation is more complex than

previously thought implies that these questions need to be examined in a new way. Another important consideration is how these motor areas are connected, both to one another and to other parts of the brain. This idea of the importance of connections is something that I've emphasized on previous podcasts.

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In terms of connections you have the intrinsic connections, which are the connections to other parts of the motor cortex, and extrinsic connections to other parts of the brain and to the spinal cord, or the descending connections. In the monkey the primary motor cortex is called F1, and the anterior areas of the motor cortex are numbered F2 through F5, and the most posterior part of the motor cortex is called F6 and F7. And they found so far that there are significant differences between the more anterior regions and the more posterior regions; in other words, between F2 through F5 and F6 and F7.

What we now know is that the anterior regions are what give rise to the spinothalamic tracts—in other words, the descending tracts to the body. In contrast the posterior regions lack a direct connection to the spinal cord, which implies that their influence on movement is only indirect. What about the inputs to this area—or the afferents? The motor cortex receives afferents from three principal areas: the prefrontal cortex, the cingulate gyrus, and the parietal lobe. For the monkey this includes an area called S1, which is the primary somatosensory cortex, and the posterior parietal cortex, which is where a lot of the sensory information comes together.

So, what I'm saying is that it turns out the motor area is actually receiving both primary sensory information and sensory information that's already come together and had some processing. You may recall that the prefrontal cortex is involved in higher-order functions like planning. We don't understand the

cingulate gyrus very well, but it does appear to be important for providing emotional and motivational information.

The parietal lobes—now that's the part of the brain that's just behind the big central sulcus, or the big groove that you see on the top of the brain. So, it's basically the top of the head, behind the frontal lobe but in front of the occipital lobe. I think we've talked in the past about the importance of the somatosensory association regions in the parietal lobe, especially when we were talking about acquiring the ability to read. The posterior parietal lobe is actually somewhat different; sort of like the motor areas of the frontal lobe need to be distinguished from the prefrontal cortex. In this posterior parietal lobe they've actually observed neural activity in connection with motor acts, and this is in areas that were thought to be association areas.

Rizzolatti actually argues that the posterior parietal cortex really ought to be considered part of the motor system. He says that this view is supported by the specificity of the frontal parietal connections which seem to be involved in translating particular sensory stimuli into particular motor acts. The posterior parietal cortex seems to get most of its connections from the anterior parietal cortex. This contrasts with the more familiar anterior motor regions which get their information from the prefrontal cortex and the cingulate gyrus.

This implies that there are two types of motor areas with different functions. The posterior areas receive a wealth of sensory information from the anterior parietal areas and they use this to organize and control movements such as knowing how big an object is that we want to grasp. Meanwhile the anterior motor areas don't get very much sensory information. They receive information from the prefrontal cortex and the cingulate gyrus regarding the long-term goals and motivations for doing the activity.

So, in this view the anterior regions are performing mainly control functions; determining whether a potential motor action which has been chosen by the posterior region is actually carried out. So, for example, you see a cup of coffee and the posterior parietal region sees this as an object to pick up. Your prefrontal cortex might overrule this potential activity. For instance, it might be someone else's cup of coffee, or your friend just said, 'Don't touch that, it's too hot.'

What can we conclude about this new information about how the motor system works? Well, the main idea is that the recent discoveries have shown that our previous ideas about how the motor cortex worked need to be reevaluated. Also, we now know that both the frontal and posterior parietal cortex are composed of what he describes as a mosaic of regions that are strongly interconnected but that are also anatomically and functionally distinct. We now know that the associative posterior parietal cortex not only receives strong inputs from the sensory areas but that it also has motor properties. Meanwhile the areas that were once thought to be purely motor are turning out to be much more complex, implying that the motor areas have other functions beyond organizing our motor behavior, such as understanding the behaviors of others.

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This book, *Mirrors in the Brain*, contains excellent discussions about experimental design which may be of interest to many of you, but I'm going to have to leave that out just in the interest of time constraints. I would mention that how an experiment is designed will have a critical effect on what can be discovered. And he makes some important points about this along the way. Now, notice I haven't actually gotten to mirror neurons yet. Our first step is understanding that motor and sensory properties aren't isolated from each other like was once thought.

So, now we're ready to talk a little bit more about how actions happen. I'm going to refer to some of the areas again that are in the monkey brain, specifically F1 which is the primary motor cortex. And it's important to understand that it actually has the ability to control individual fingers, but it doesn't get any sensory input. F5, on the other hand, has a majority of neurons that code for motor acts like grasping, but not movements of individual fingers. So, a particular neuron might be active during one act—say, grasping something—and not during another act that seems fairly closely related.

One of the things about F5 is it has overlapping motor representations of both the hand and the mouth. Many of the F5 neurons, if not most, code for a certain shape of the hand. It's estimated that 50% discharge for movements related to grasping and 50% discharge at the sight of certain objects. A similar level of activation is seen in humans using functional MRI. When they look at the part of the brain that's considered to be the homolog of F5 they see that this area responds to seeing graspable objects. Now, don't get hung up on the names of the areas; I'm just giving them for the sake of helping us to keep one area separate from another.

F5 connects to what's called the anterior intraparietal area, which is an area in the parietal lobe whose neurons also discharge during hand movement. Now, in the anterior intraparietal area there are three categories of neurons: ones that are motor dominant, ones that respond to visual and motor, and ones that are so-called visual dominant. So, the circuit is between this anterior intraparietal area and the F5 area. This circuit is thought to be involved in the so-called visual-motor transformations needed in order to grasp an object. In other words, you have to be able to take the visual information about where the object is, and its shape, and so forth, and then translate that into the right shape of the hand.

It's been shown that if you knock out the AIP—which is another name for the anterior intraparietal region—if you knock this out it impairs the ability of trained

monkeys to grasp familiar objects with the opposite hand. You get a similar result if, instead of knocking out AIP, you knock out F5. This appears to confirm the hypothesis that the visual-motor transformations connected to grasping depend principally on this AIP-F5 circuitry. Again, similar deficits have been seen in people that have lesions to the homolog of AIP.

How do AIP and F5 interact? It's thought that the information might be coded in the form of what has been called affordances, so that AIP codes the possibility of grasping the object and then F5 codes the motor acts congruent with the affordance—in other words, the shape of your hand or type of grip that you're going to need to pick up that particular object. This idea of affordance also implies meaning. Consistent with this hypothesis is the fact that while F5 has weak connections to the frontal lobes, the AIP has strong frontal lobe connections. Now, that brings up some much more complicated questions about the pathways for visual processing, but I'm going to skip over those for today.

Instead I'm going to return to the neurons of F5. A surprising finding from single neuron recordings was that the neurons appear to be highly selective for specific motor acts, say like gasping, or holding, or tearing, and for specific elements of the actions. Some seem to indicate the general goal of the actions while others are involved in a particular aspect such as the type of grip; while there is even another group that seems to code for the timing, such as when to open and close the hand. Consider the fact that we tend to do familiar activities the same way every time. This might be the reason.

It appears that the motor system has a repertoire of acts that is the basis of the cognitive functions that are traditionally attributed to the sensory system. I'm going to come back to why this is important. The key idea is to recognize that activities don't really divide neatly into pure categories such as motor and sensory. In observing that there are F5 neurons that fire in the same manner in response to an object, whether it is manipulated or just observed, Rizzolatti

concludes that “the only possible interpretation of the behavior of these neurons is that both visual and motor responses have the same functional meaning.” That is, that these F5 visual motor neurons are going to send out the same message to the other parts of the brain whether or not you’re doing the action or just looking at the object.

If the actual action occurs you’re going to see activities in other parts of the cortex such as F6. He also says that this finding in both F5 visual-motor neurons and in the AIP indicates that the object in question, such as a cup of coffee, is coded the same way in both conditions—that is, whether you’re picking the object up or just looking at the object. And the coding that we’re talking about might be acquired by babies during the first month of life. Because, remember, we have talked about several times in the past that you need to have motor experience to develop normal vision. So, probably in the early months of babyhood as you reach out and grab stuff you start to get this coding tied together.

Let’s think briefly about how we see the world around us. Without really thinking, per se, we see a world full of objects that we can interact with in different ways, such as door knobs, drawers, food. If you see a dog you probably think of it in terms of whether or not you want to pet it. What these objects have in common is that we have some experience with them. I think I mentioned on a previous episode how we tend to ignore unfamiliar objects that are in a room if we don’t know how to use them.

One implication of the work involving the monkeys’ F5 and AIP in grasping or observing graspable objects is that we have the beginnings of the possibility of understanding how this happens. This is important because it’s intimately related to our ability to move and orient ourselves in our surrounding space, as well as our ability to understand the actions and intentions of others. Perhaps the most surprising thing is that some of the information appears to be coded in parts of the brain that we don’t associate with cognition. That this is occurring in

the monkey shows that a surprising level of understanding is possible without any language.

OK, so for the motor part of grasping—and we just use grasping as an example—we have learned that there is an area in the motor cortex called F5 that has an important circuit connected to an area in the parietal cortex called AIP; that basically the AIP seems to code for the possibility of picking up an object and the F5 seems to code for how to pick up the object.

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Before we can really get into mirror neurons themselves there's one other issue that we have to talk about. And that is about space—our perception of the space around us—because obviously we can't grasp an object unless we know where it is. So, part of that coding has to include that information. I talked about F5. Now I'm going to talk about F4, which is also in the motor cortex. F4 contains representations of the neck, mouth, and arm movements, and this has been demonstrated using microstimulation studies.

About 70% of F4 neurons become active both during the execution of a motor act and in response to sensory stimuli such as superficial touch. There are bimodal neurons that respond to somatosensory input and vision. They seem to be more sensitive to moving objects, but some also respond to stationary objects. And then there are the trimodal neurons that respond to somatosensory, visual, and auditory inputs. The receptive fields for the individual neurons are the face, neck, arms, and hands, and these fields can be fairly large—up to several square centimeters.

A key idea is the fact that the bimodal neurons respond only to visual stimuli that appear within the vicinity of the tactile field; that is, close enough to touch. So, the same neuron that responds to touching the monkey's arm responds when our

hand is close to the monkey's arm. It appears that these neurons are mapping the peripersonal space of the monkey. Another surprise is the visual receptive fields of F4 are tied to their respective somatosensory fields, which means that they are independent of the direction of gaze. And this is true for about 70% of the neurons. And he describes in the book the experiments that they did to prove this concept. Now, the reason this is important is it means that the information is not coded in retinal coordinates and it doesn't depend on the position of the stimulus on the retina.

Another important point is that these coordinates don't refer to a single reference system situated in a specific part of the body such as the head or shoulders. Instead the visual space is coded by many different body reference systems. It could be the head, the neck, the arms, the hands, etc. It's as if these fields represent a three-dimensional extension of their respective somatosensory fields, and they appear to be essential to anticipating contact with objects nearby. Again, remember that coffee cup. You anticipate touching it, and it's because of your peripersonal maps that you know whether or not something is close enough to touch.

If you've listened to the previous episodes about body maps it shouldn't surprise you to hear that these experiments throw doubt on the traditional concept of a unitary body map. Rather it seems clear that the various parts of the cortex have different maps for different purposes. In this case the maps appear to control different motor goals. When it comes to visual receptive fields it turns out that if the neurons respond to visual stimulus independently of the distance at which the object is located, then their visual fields are coded in retinal coordinates. This would be true for the neurons that are only concerned with eye movements.

In contrast the neurons and circuits that are involved in the peripersonal space have their fields tied to various parts of the body. There appear to be different circuits involved for dealing with near, or peripersonal space and far, or

extrapersonal space—that is, things that are outside of our reach. In the book he gives an example of a patient who had a lesion causing neglect only of objects in his near space. He was still able to enjoy his favorite hobby, which was darts, because that was something that was actually in the far space. While the experiments described in this book were done with monkeys, function MRI studies in humans seem to show similar bimodal areas. In the human this seems to be the floor of the intraparietal cortex, the ventral motor cortex, and around an area known as the secondary somatosensory area.

So, you might wonder what are the purpose of these peripersonal space maps. First of all they are our starting points for mapping the world around us. Think about how difficult it is to conceive of objects that are much larger or smaller than human scale. So, the peripersonal space maps help us start to map the world around us. They're also essential for performing motor acts, including protecting ourselves from potential threats. It is thought that even before birth, babies have motor representations of space that they acquire by moving around in the womb. And then when they're born they can only see about 20 centimeters, so during the early time that's probably when we are really developing our peripersonal space maps.

It's interesting that these maps of space are dynamic. When an object is coming toward an animal, the size of the receptive field increases if the object is going fast. Presumably this is to allow evasive action. Experiments with tools have really demonstrated this convincingly. I think we talked about this one before, but it was shown that when the monkey was trained to use a rake the receptive fields anchored to its hand expanded in size to actually include the space of the rake. And we talked about how this applies with us when we're using tools and even things like tennis racquets.

Another example in the book was of a patient who had neglect that involved only near space. This is not the same guy that enjoyed darts, but she had the similar

sort of deficit. When she was given a rod so that she could interact with objects a little further away she began to neglect the objects that were in far space also; anything that was within the range of the rod. Because basically what the rod did was extend her peripersonal space, and since she had total neglect of peripersonal space the space she was neglecting became larger. This whole spacial neglect thing is really weird. A person with spatial neglect cannot perceive objects in the area that they're neglecting.

What unifies our consideration of the perception of objects and the perception of space is that in terms of the motor cortex these areas are goal-centered representations of movement. So, for example, for the coffee cup we map the shape of the coffee cup and its location. And it can also be argued that we use objects to form our conception of space. I think there's been a long-running philosophical argument about that one. Considering how our perception of space and objects is interconnected and entwined in the motor system, Rizzolatti emphasizes the shortcomings of any approach that tries to describe the brain's functioning in rigid dichotomies. It also probably means that there cannot really be any such thing as a simple stream of information containing what or where.

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We're finally ready to talk about the actual mirror neurons. That's the subject that's gotten the most press. To remind you, mirror neurons are the ones that are active both when an action is performed and when the animal sees the action. Now, this is different from the neurons that I described earlier where they're active when they see an object and when the animal is picking up the object. That wouldn't be a mirror neuron. So far we have seen that in F5 the majority of neurons code for specific motor acts like grasping, and that some of them also respond to visual stimuli. Importantly there is a clear congruence between the motor act type of grip and their visual selectivity—the shape, for example.

The neurons that respond to both have been called canonical neurons because for a long time it was thought that they were the key players in the visual-motor transformation. But that was before the so-called mirror neurons were discovered in the early 1990's. The discovery that there are neurons that are active both during a specific motor act and when an animal observes someone else doing the same motor act took the research community completely by surprise. I've heard several different accounts of the discovery of mirror neurons, but they all seem to agree that the original discovery happened by chance in Rizzolatti's lab at Parma.

The first mirror neurons were discovered in F5 and they were identical in terms of how they discharge during motor acts. It was their visual properties that were markedly different. They didn't discharge at the sight of food or of other objects. They specifically responded to observing specific motor acts involving an object or a body part, such as the interaction between food and the mouth, or a hand grasping an object. Their response didn't seem to depend on how far away the observed action was, and most of the time it was fairly specific; that is, a given neuron would respond to only one motor act, although there were a few neurons that responded to two. Neurons that respond to three or more acts seem to be very rare.

There are two types of these mirror neurons. There are those that are strictly congruent, which is where the motor act and the observed act are virtually the same; and then there are the ones called broadly congruent where the motor act and the observed act are similar but not identical. We don't really know the significance of the two types. In the monkey it appears that about 70% of the mirror neurons in F5 are broadly congruent.

Different sorts of actions have been studied. Early on the focus was on hand motion and then later they started looking at motions involving the mouth, such as ingesting food, or grasping, or chewing, or sucking. And finally they moved on

to what they called the communicative neurons which respond to what are called intransitive acts, that is, ones that don't involve objects. And this would be something like protruding the lips.

They've also found mirror neurons in the parietal lobe. The parietal cortex contains neurons that respond to seeing an action. Some of the neurons are purely visual. They respond to seeing it but they don't have a motor component, so they aren't really mirror neurons, because in order to be a mirror neuron you have to have that essential combination of the visual and the motor properties.

Interestingly, these neurons that responded to a specific action didn't respond to just the object or to the miming of an action without the actual interaction with the object. Again, remember we're talking about in the monkey. However, they did actually find true mirror neurons in the parietal cortex of the monkey, and the most recent estimate is that as many as 70% of the parietal neurons that respond to observing a specific motor act also possess motor properties. And like those that are purely visual they don't respond, in the monkey, to the object alone or to miming.

It's important to notice that just like we found that the motor cortex contains neurons with sensory properties, we have also found that the parietal cortex, which has traditionally been seen as sensory, contains motor neurons. This discovery might actually be more important than the discovery of mirror neurons because of its wide-reaching implications for how we understand brain function.

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Getting back to mirror neurons: what are they for? We know that they're not related to preparing to act because they aren't activated when the monkey is offered food that it can reach. One proposal is that they are essential to imitation, but Rizzolatti doesn't think that imitation is their primary function because

mirror neurons are found in species of monkeys that are unable to imitate in the sense that humans and maybe some apes do. Therefore he argues that their primary function is in understanding the meaning of a motor event— understanding the actions performed by others.

Remember that the mirror neurons are firing only in response to object-related actions by another, not to the movement alone and not to the object by itself. Again the book goes over several experiments that support this hypothesis, and these experiments also show that the goal of a specific act determines which neurons will fire, such as the difference between putting food in the mouth or on a tray. One implication is that the motor knowledge of our own acts is the necessary and sufficient condition for an immediate understanding of the acts of others. This implies that motor knowledge of our own acts is a fundamental building block in cognition. It's this motor knowledge that allows us to understand instantly what another person is doing and their intention. Obviously this also has implications about our ability to understand unfamiliar actions by others.

Well, what about humans? Can we prove that humans have mirror neurons? Obviously it's impractical to do single neuron recordings in humans because even though having electrodes in the brain is not painful, it's just clearly not practical in a human except under very rare conditions. The reality is that at this time all the evidence for mirror neurons in humans is indirect. And actually the first evidence completely predates the discovery of mirror neurons. Back in 1954 Henri Gastaut showed that the normal resting alpha rhythm of the posterior cortex was desynchronized, both by performing a motor act and by observing it being performed. And this work has been reproduced by several modern researchers including V.S. Ramachandran.

A more sophisticated approach is the use of transcranial stimulation studies. These have provided convincing evidence because they were able to record the

motor-evoked potentials when people observed movements and also when they did them. One thing they discovered was that unlike monkeys, people will respond to non-object-oriented movements. Also, humans appear to encode more temporal information.

The main method for establishing the existence of mirror neurons is via brain imaging such as PET scans and functional MRI. These methods do have limitations with regard to localizing exactly where things are occurring. You can't really tell which neurons in a region are responding. Two things could light up the same area and actually be activating different neurons. Interestingly, the first PET scan experiment failed because they tried having the person observing a virtual hand on the computer screen and there was no response. It turns out that we respond to a real human hand but not to a virtual hand.

One area that is active in the functional MRI studies appears to correspond to what's called Brodmann's area 44, which is an area involved in language. But there's also evidence mounting that this area contains a representation of the hand and mouth. The question that might arise is whether or not what's happening is a verbal representation of what we have observed. They did experiments where subjects were asked to watch different kinds of actions, including mime, and they found different areas of the motor cortex were activated depending upon which parts of the body were involved. Miming seemed to activate only the frontal lobe.

So, experiments seem to indicate that the mirror system in humans includes large parts of the premotor cortex and the inferior parietal lobe, as well as Broca's area, which is another area involved in language. It's interesting that humans do respond to mime, which monkeys do not. So, what we find is that the electrophysiology and brain imaging studies indicate that humans have a mirror neuron system analogous to that of monkeys. However, we also find that there are several important differences.

First, the mirror neuron system appears to take up significantly more cortical space in humans, though exact comparisons are impossible because of the difference in the experimental methods. More important, the human system has additional properties that are not seen in monkeys. The human system codes for more types of activities, it appears to code for both intent and movements, and actual interaction with an object is not required—humans respond to mime.

The primary role is still thought to be understanding the actions of others. But obviously the human system can accomplish a wider range of other tasks. Iacoboni has done experiments that seem to indicate that intent is also encoded. But again this is something I'm going to have to skip over for now. Obviously the mirror system can't explain all the assumptions we make about the actions of others, but does explain how we understand the basic intent of motor actions. A very important implication is that this understanding is not based on mentalizing or verbalizing; it's the motor understanding, a preverbal understanding.

What happens when we observe movements that are not part of our repertoire? To look at this they did an experiment where a person was shown a video that was of a man, a monkey, or a dog doing various things. They first had them do eating something, which would be an action that would be in all of their motor repertoires. In this situation they saw that the left hemisphere was equally active whether it was man, monkey, or dog, but the right hemisphere was more active if it was a man.

In contrast when they looked at a communicative act—in this case for the man it was talking, for the monkey it was lip smacking, and for the dog it was barking—the human showed a strong response to the man, a weak response to the monkey's lip smacking, and no response to the barking. And this wasn't really due to difference in visual information because they don't look all that different. It's assumed that this is because barking isn't part of the human repertoire. Now,

that doesn't mean we don't understand what barking is; because we do. It just means that we're not using our mirror neuron system to understand it.

Interesting differences have also been observed for individuals of the same species, depending on their particular motor competencies. For example, experienced dancers are going to respond more strongly when they're watching someone else dance, and they also seem to respond more strongly when they're watching someone of the same sex dance. Experiments confirm the decisive role played by motor knowledge in understanding the meaning of the actions of others. Perhaps the simplest example of this is when you're watching a sport on television. Think about how different it is to be watching a sport you have played yourself compared to one that you've never played. It's just that you seem to understand sports you've played, you might say, at a different level.

[music]

We're running really long, but there are a couple of things that I do want to talk about before I close. In terms of imitation and language there are a lot of questions about the role of mirror neurons. I'm probably not going to have time to get into language as much as I would like. I'm going to save that for a follow-up podcast. But let's talk about imitation. First of all, Rizzolatti makes two clear definitions of imitation. He says for the purposes of our discussion it's either the capacity of an individual to replicate an act that already belongs in his motor repertoire, after seeing it executed by others, or a process by which an individual learns a new pattern of action by observation, after which he is able to reproduce it in some minimal detail.

We know experimentally that the mirror neuron system is more active during active imitation. One of the experiments he describes in the book is just the person is told to lift their finger, and they're supposed to do it either because they see a finger on the screen lift vs. some other cue. There is more activity when

they see another finger. The other one was they used transcranial stimulation to knock out the mirror neurons temporarily and then they asked the person to press a key, either when a light was flashed or when they saw a familiar movement performed by another person. When they had the area knocked out they had an impaired ability to imitate the person pressing the key, but they were still able to press the key, say, when they saw a light flash. This is an experiment that strongly suggests the mirror neuron plays a fundamental role in imitation.

Learning a new movement also involves the mirror neuron system, but the process is much more complicated and it seems to involve working memory, which may be one of the things that creates some of the gap between us and, say, chimpanzees in the ability to imitate. Either type of imitation seems to involve more than just the mirror neuron system. Think about this. When we watch somebody doing something, something's got to determine whether or not we repeat the acts that we observe. So, clearly there has to be a control system that has both inhibitory and excitatory components, since we don't imitate everything that we see. The importance of inhibition is demonstrated clinically. There are some patients with frontal lobe lesions who have what's called *ecopraxia*. They can't stop themselves from repeating everything.

Now, in terms of language, I hope in the future to talk about a hypothesis known as the mirror neuron hypothesis for language, which is an idea that the mirror neurons were involved and that language actually grew out of the use of gestures. There are also some controversies, because not everyone agrees with this theory. We will come back to that later because it's a really interesting idea.

Before we close today I do want to talk a little bit about emotions. Besides understanding the actions of others it is very important to perceive and understand their emotions. And it has been shown that even very young babies can tell the difference between happy and sad faces. So, one might naturally

wonder whether mirror neurons are involved in our ability to easily recognize emotions of others.

Now, not all the emotions have been studied on this, but the one that has received the most study so far involves disgust. There is an area deep in the brain known as the insula, which you may recall in the body maps episode we talked about its importance in being able to detect our body's internal state. Basically we know that activating the insula, both in monkeys and neurological patients, can cause nausea, retching, and other unpleasant sensations, and the anterior part of the insula is stimulated by expressions of disgust when seen on the faces of others.

Now, the insula doesn't seem to be involved in other emotions; just specifically disgust. And if you have a damage to this region you lose the ability to recognize disgust. And they even documented the case of a patient that had bilateral insula damage and completely lost the ability to experience disgust. So, he would eat some pretty amazingly disgusting things. Imaging studies indicate that experiencing disgust and perceiving it in others have the same neural basis, which is activation of the anterior left insula and the right cingulate gyrus. So, this supports the hypothesis that understanding emotions is based on a mirror mechanism.

Other emotions, such as suffering, also seem to have a mirror neuron mechanism. Our ability to instantly understand the emotions of others is a necessary condition for empathy. But empathy is more than just understanding the emotions. Recognition of the emotion of the other person is automatic and immediate. But just like we don't imitate every action that we see, we don't necessarily take on other people's emotions indiscriminately.

However, the key idea to remember is that the mirror neuron mechanism embodies a way of understanding which is prior to any form of conceptual or linguistic meditation. The key idea that he describes on page 192, he says as

follows: “The mirror neuron mechanism embodies a modality of understanding which, prior to any form of conceptual and linguistic meditation, gives substance to our experience of others.”

Putting it more simply, having the mirror neuron system makes it possible for us to understand what other people are doing and what they’re feeling, and we do this in essence instantly without conscious effort because of the mirror neuron system. This is not a system that requires any kind of a language ability or concepts, because we see that this understanding occurs in animals that do not have language. I look forward to talking about this in more detail in the future, especially exploring the applications of the mirror neuron system both to trying to understand language, but also another area of research is understanding the role of the mirror neurons in how we learn.

[music]

While this episode has been a little bit more technical than most episodes of the *Brain Science Podcast*, there are actually only a few basic ideas that you need to remember. First, of course, is the basic definition of mirror neurons, which is that these are neurons that are active both when an animal—specifically a human or a monkey—is performing a specific motor action, or when he sees another animal or person perform the same or similar action. Mirror neurons are thought to be very important to understanding the actions and emotions of others, although at this point the evidence for the existence of mirror neurons in humans is indirect.

Another very important principle that we learned in this episode is the fact that in parts of the brain that were once thought to be purely motor, neurons have been discovered that not only have motor properties but that have sensory properties. Similarly, in parts of the brain that were once thought to be purely sensory or associative, motor properties have been discovered.

We also learned that there are neurons that respond both to somatosensory information and visual or auditory information. And what that means is that there are neurons that respond not only to being touched on a certain part of the body, but to seeing or hearing objects that are approaching that same area of the body. And this is very important to how we sense our peripersonal space.

Now, the motor neurons that sense objects and the neurons that sense our peripersonal space all share a property of being multimodal—that is, responding to more than one type of activity, be it motor or different types of sensory inputs. An important idea to remember from this episode is the fact that the discovery of these multimodal neurons is drastically changing our understanding of how the brain works. That’s the reason I spent so much time on the details of this today, because understanding these principles is going to be important to understanding a lot of the new discoveries that are happening in neuroscience.

[music]

Well, that’s it for today’s episode. I’ll be back in a couple of weeks. The next episode is going to be an interview with Dr. Art Glenberg from the University of Wisconsin’s Laboratory of Embodied Cognition. We’re going to be talking about how our bodies affect our understanding of language.

As always I’d love to have your feedback. You can send me email at docartemis@gmail.com. You can post comments at brainsciencepodcast.com, and you can participate in the Discussion Forum at brainscienceforum.com.

Don’t forget to listen to *Books and Ideas* at booksandideas.com. *Books and Ideas* is also available on iTunes. I have an interview coming up probably next week with Dan Ariely, who wrote the best-seller, *Predictably Irrational*, and I think you’ll enjoy that interview. Dr. Ariely’s book, *Predictably Irrational*, is available on Audible.com. Audible is still sponsoring *Books and Ideas* and I still have an

ad for them on the *Brain Science Podcast* website, so you can still go and get your free audiobook download from Audible. You can get Dr. Ariely's book, *Predictably Irrational*.

I want to thank those of you who have made contributions and those of you who are subscribing to the *Brain Science Podcast* through PayPal. Even if you can't afford to make any donations to the *Brain Science Podcast*, you can help support the show by telling your friends about the podcast, by putting up your reviews on iTunes, and by blog posts or whatever else you can think of to help get the word of mouth out.

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Thanks again for listening. I'll talk to you again soon.

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